METACOMMUNITY SPATIO-TEMPORAL DYNAMICS: CONSERVATION AND MANAGEMENT IMPLICATIONS

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METACOMMUNITY SPATIO-TEMPORAL DYNAMICS: CONSERVATION AND MANAGEMENT IMPLICATIONS

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EDITORIAL
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Editorial: Spatio-Temporal Dynamics of Metacommunities - Implications for Conservation and Management

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Editorial on the Research Topic

Spatio-Temporal Dynamics of Metacommunities - Implications for Conservation and Management

According to metacommunity theory (Leibold et al., 2004), the structure of local communities results from the interplay between local factors (e.g., environmental filtering, species interactions) and regional factors (e.g., dispersal rates, landscape configuration). The relative importance of these factors is highly dependent on the organisms' biological traits, landscape connectivity, and the spatial and temporal scales considered (Heino et al., 2015; Tonkin et al., 2018; Viana and Chase, 2019; Almeida-Gomes et al., 2020; Cañedo-Argüelles et al., 2020; Lansac-Tôha et al., 2021). However, the differences in metacommunity assembly mechanisms found among studies are far from being fully understood. The evaluation of temporal dynamics of metacommunities has only emerged recently (Cañedo-Argüelles et al., 2020; Jabot et al., 2020; Li et al., 2020; Lindholm et al., 2021) and the application of the metacommunity theory in other fields, such as biomonitoring, conservation biology or ecosystem restoration, is yet to be fully explored (Bengtsson, 2010; Heino, 2013; Leibold and Chase, 2018; Chase et al., 2020; Cid et al., 2020; Heino et al., 2021).

In this Research Topic, our aim was to invite researchers working in different biogeographic regions and ecological systems (**Figure 1**) to publish a number of innovative papers on metacommunity spatio-temporal dynamics. We expect to obtain a better understanding of how the factors and processes that structure metacommunities vary in space and time, as well as the implications of such dynamics for biodiversity conservation and ecosystem management.

RELATIVE IMPORTANCE OF ENVIRONMENTAL AND SPATIAL FACTORS ON METACOMMUNITY STRUCTURE

This Research Topic provides several examples on how the interplay of environmental and spatial factors shapes biodiversity. Czeglédi et al. evaluated the importance of the degree of urbanization, the local stream environmental conditions and the regional species pool on the community assembly of stream fishes. They found that the degree of urbanization is not a strong determinant of local stream habitat and fish community characteristics. Historical species pool and stream features shaped fish communities, with urbanization playing a rather individual role in some streams. These authors conclude that rehabilitation of urban streams should not only focus on local

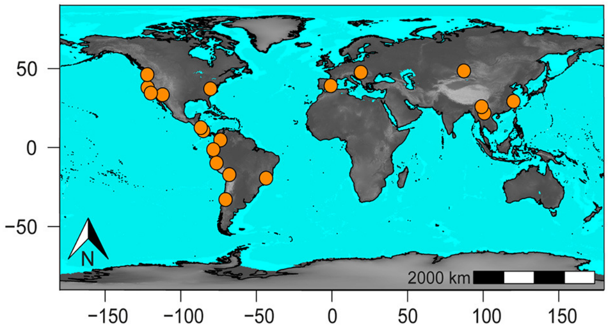

FIGURE 1 | Geographic distribution of the studies (i.e., study sites for field studies, author's affiliation for reviews) contained in the Research Topic. The background map is the elevation gradient derived from ASTER GDEM (https://asterweb.jpl.nasa.gov/gdem.asp).

habitat improvements, but also consider how dispersal influences metacommunity organization. Kurthen et al. examined the metacommunity structure of diatoms and macroinvertebrates in river-connected and lake-connected streams. Diatoms exhibited the same metacommunity structure in both systems, while macroinvertebrates did not. Also, environmental filtering had a stronger effect on community dissimilarity in the lake-connected system than in the river-connected system for both groups. Finally, He et al. examined the spatial and environmental distance decay of the same organismal groups within three Chinese drainage basins. They found that environmental filtering was the strongest within the basin with the highest levels of environmental heterogeneity among sites. These findings are important because increased environmental heterogeneity may foster higher diversity of organisms in rivers and because anthropogenic impacts homogenizing the underlying abiotic template are likely to decrease aquatic biodiversity.

THE IMPORTANCE OF TEMPORAL AND SPATIAL SCALES ON METACOMMUNITY STRUCTURE

Metacommunities are shaped by environmental, spatial, and temporal processes, but their relative importance can vary with the study scale. Gálvez et al. examined variation in multiple organism groups across tropical temporary ponds. They found that environmental, spatial, and temporal processes were all important for metacommunity dynamics. However, the relative roles of these processes differed among taxa, and the environmental and spatial factors varied among sampling periods when the periods were analyzed separately. These findings indicate that a snapshot survey is not likely to reveal the dynamics of pond metacommunities, thereby hindering planning suitable conservation and management programs.

Beta diversity has played a prominent role in investigating the processes that determine the distribution patterns of communities (Anderson et al., 2011). In this Research Topic, Benito et al. evaluated the drivers of spatial and temporal beta diversity of modern and paleolimnological data of tropical South American diatoms from high elevation lakes and found different trajectories of lake diatom diversity as a response to environmental changes. These authors showed that unifying diatom ecology, metacommunity theory, and paleolimnological approaches can facilitate our understanding of the responses of tropical Andean lakes to global change effects in the near future. Nunes et al. evaluated the temporal patterns of an ant metacommunity across an elevational gradient, focusing on both taxonomic and functional facets. These authors found that taxonomic and functional temporal beta diversity did not increase with elevation. Their results indicate that at low elevations the replacement of species can cause loss of some traits, yet preserving the most common functions (nested functional communities), while at high elevations functional capabilities may change over time (replacement of traits). In the scenario of climate change, it is important to consider the role of the substitution of species on the temporal variation in functional traits of metacommunities at higher elevations.

Combining simulated metacommunities with empirical data, Castillo-Escrivà et al. investigated how temporal variations in environmental conditions and species' dispersal can affect metacommunity organization of aquatic invertebrates. According to the simulations, the importance of the temporal scale increased at high dispersal rates. However, this was not confirmed by empirical data, which showed complex spatio-temporal variations that depended on the type of organisms and ecosystems under study.

Focusing on disturbance, seasonality, multi-year climate variation, and dormancy, Holyoak et al. synthesize our current knowledge of temporal metacommunity dynamics. Although empirical studies are relatively scarce, the authors show that the four forms of temporal dynamics considered can play a significant role in metacommunity ecology and conservation planning. Since global climate change is expected to increase both the frequency and severity of different types of disturbance, metacommunities might be more frequently structured by dispersal processes in the future.

APPLICATIONS IN CONSERVATION AND MANAGEMENT

Short-term field studies have limitations to identify the underlying processes of observed patterns because both the environment and communities change through time (Li et al., 2020). Record et al. provided evidence from a synthesis effort of the United States Long Term Ecological Research (LTER) program that such data can improve our ability to explain and predict biodiversity change with observational and experimental data at various spatial and temporal scales. Long-term studies that include multiple sites within a regional species pool enable a more thorough assessment of biodiversity change relative to long-term studies at a single site. Such an approach can also improve the development of metacommunity theory and its applications contributing to improved conservation efforts.

Globally, biological invasions are a major cause of biodiversity loss (Courchamp et al., 2017, Pyšek et al., 2020). Brown and Barney argue that invasion biology is currently limited by the consideration of species in isolation (i.e., disregarding the community context), and metacommunity ecology can greatly help to overcome this barrier. The combined analysis of environmental factors and dispersal (i.e., propagule pressure) can help to assess the degree of spread of an invader. The authors show multiple parallelisms between invasion biology and metacommunity ecology that pave the way for cross-disciplinary research. Finally, the paper provides direct applications of the metacommunity theory for managing biological invasions.

CONCLUDING REMARKS AND SUGGESTIONS FOR FUTURE RESEARCH

The metacommunity perspective has clear applications in conservation and management (Bengtsson, 2010; Heino, 2013). However, metacommunity ecology and conservation biology have barely begun to be connected in an applied fashion (Leibold and Chase, 2018, Chase et al., 2020). More emphasis on the importance to understand metacommunity assembly has been given in applied contexts recently, especially in river networks (Cid et al., in press) and lakes considered as sets of interconnected systems in a landscape (Heino et al., 2021). However, terrestrial and marine ecologists have not considered metacommunity theory from this direct perspective, even though similar ideas pertaining to the importance of metapopulation dynamics (e.g., Hanski, 2005) and connectivity conservation (e.g., Ament et al., 2014) in anthropogenically affected landscapes have received considerable attention. We highlight that metacommunity structure should be studied in all realms by jointly considering environmental, spatial, and temporal dynamics, as well as anthropogenic impacts if we expect to manage and conserve biological diversity in a sustainable manner.

In a changing world, our current understanding of the underlying drivers of biodiversity patterns and ecosystem functioning will only improve with further research jointly focusing on both spatial and temporal dynamics of metacommunities (Heino et al., 2021). Metacommunity theory (Leibold et al., 2004) should also be combined with the traditional approaches in environmental assessment (Heino, 2013) and conservation planning (Hanski, 2005) that have not paid enough attention to the dynamics of ecological communities in changing landscapes, regions, and continents so far. We suggest that there should be a paradigm shift in applied research on understanding biodiversity change and environmental degradation through the joint consideration of multiple scales and underlying metacommunity assembly mechanisms.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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REFERENCES

Almeida-Gomes, M., Valente-Neto, F., Pacheco, E. O., Ganci, C. C., Leibold, M. A., Melo, A. S., et al. (2020). How does the landscape affect metacommunity structure? A quantitative review for lentic environments. *Curr. Landscape Ecol. Rep.* 5, 68–75. doi: 10.1007/s40823-020-00049-6

Ament, R., Callahan, R., McClure, M., Reuling, M., and Tabor, G. (2014). *Wildlife Connectivity: Fundamentals for Conservation Action*. Bozeman: Center for Large Landscape Conservation.

Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., et al. (2011). Navigating the multiple meanings of beta diversity: a roadmap for the practicing ecologist. *Ecol. Lett.* 14, 19–28. doi: 10.1111/j.1461-0248.2010.01552.x

Bengtsson, J. (2010). "Applied (meta)community ecology: diversity and ecosystem services at the intersection of local and regional processes," in *Community Ecology: Processes, Models and Applications,* eds, H.A. Verhoef and P.J. Morin (Oxford: Oxford University Press), 115–130.

Cañedo-Argüelles, M., Gutiérrez-Cánovas, C., Acosta, R., Castro-López, D., Cid, N., Fortuño, P., et al. (2020). As time goes by: 20 years of changes in the aquatic macroinvertebrate metacommunity of Mediterranean river networks. *J. Biogeogr.* 47, 1861–1874. doi: 10.1111/jbi.13913

Chase, J. M., Jeliazkov, A., Ladouceur, E., and Viana, D. S. (2020). Biodiversity conservation through the lens of metacommunity ecology. *Ann. N. Y. Acad. Sci.* 1469, 86–104. doi: 10.1111/nyas.14378

Cid, N., Bonada, N., Heino, J., Cañedo-Argüelles, M., Crabot, J., Sarremejane, R., et al. (2020). A metacommunity approach to improve biological assessments in highly dynamic freshwater ecosystems. *Bioscience* 70, 427–438. doi: 10.1093/biosci/biaa033

Cid, N., Eros, T., Heino, J., Singer, G., Jähnig, S., Cañedo-Argüelles, M., et al. (in press). From meta-system theory to the sustainable management of rivers in the Anthropocene. *Front. Ecol. Environ.*

Courchamp, F., Fournier, A., Bellard, C., Bertelsmeier, C., Bonnaud, E., Jeschke, J. M., et al. (2017). Invasion biology: specific problems and possible solutions. *Trends Ecol. Evol.* 32, 13–22. doi: 10.1016/j.tree.2016.11.001

Hanski, I. (2005). *The Shrinking World: Ecological Consequences of Habitat Loss.* Oldendorf: International Ecology Institute.

Heino, J. (2013). The importance of metacommunity ecology for environmental assessment research in the freshwater realm. *Biol. Rev.* 88, 166–178. doi: 10.1111/j.1469-185X.2012.00244.x

Heino, J., Alahuhta, J., Bini, L. M., Cai, Y., Heiskanen, A.-S., Hellsten, S., et al. (2021). Lakes in the era of global change: moving beyond single-lake thinking in maintaining biodiversity and ecosystem services. *Biol. Rev.* 96, 89–106. doi: 10.1111/brv.12647

Heino, J., Melo, A. S., Siqueira, T., Soininen, J., Valanko, S., and Bini, L. M. (2015). Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. *Freshwater Biol.* 60, 845–869. doi: 10.1111/fwb.12533

Jabot, F., Laroche, F., Massol, F., Arthaud, F., Crabot, J., Dubart, M., et al. (2020). Assessing metacommunity processes through signatures in spatiotemporal turnover of community composition. *Ecol. Lett.* 23, 1330–1339. doi: 10.1111/ele.13523

Lansac-Tôha, F. M., Bini, L. M., Heino, J., Meira, B. R., Segovia, B. T., Pavanelli, C. S., et al. (2021). Scale-dependent patterns of metacommunity structuring in aquatic organisms across floodplain systems. *J. Biogeogr.* doi: 10.1111/jbi.14044. [Epub ahead of print].

Leibold, M. A., and Chase, J. M. (2018). *Metacommunity Ecology*. Princeton: Princeton University Press.

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., et al. (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.* 7, 601–613. doi: 10.1111/j.1461-0248.2004.00608.x

Li, Z., Xing, Y., Liu, Z., Chen, X., Jiang, X., Xie, Z., et al. (2020). Seasonal changes in metacommunity assembly mechanisms of benthic macroinvertebrates in a subtropical river basin. *Sci. Total. Environ.* 729:139046. doi: 10.1016/j.scitotenv.2020.139046

Lindholm, M., Alahuhta, J., Heino, J., and Toivonen, H. (2021). Temporal beta diversity of lake plants is determined by concomitant changes in environmental factors across decades. *J. Ecol.* 109, 819–832. doi: 10.1111/1365-2745.13508

Pyšek, P., Hulme, P. E., Simberloff, D., Bacher, S., Blackburn, T. M., Carlton, J. T., et al. (2020). Scientists' warning on invasive alien species. *Biol. Rev.* 95, 1511–1534. doi: 10.1111/brv.12627

Tonkin, J. D., Altermatt, F., Finn, D. S., Heino, J., Olden, J. D., Pauls, S. U., et al. (2018). The role of dispersal in river network metacommunities: patterns, processes, and pathways. *Freshwater Biol.* 63, 141–163. doi: 10.1111/fwb.13037

Viana, D. S., and Chase, J. M. (2019). Spatial scale modulates the inference of metacommunity assembly processes. *Ecology* 100:e02576. doi: 10.1002/ecy.2576

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Impacts of Urbanization on Stream Fish Assemblages: The Role of the Species Pool and the Local Environment

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Disentangling the mechanisms that determine community assembly in urban environments is a prerequisite for understanding the impacts of urbanization on the biota and for developing more effective rehabilitation strategies. Community structure in urban stream ecosystems is the sum of multiple processes, including local environmental and catchment level effects. However, the degree to which dispersal from the regional species pool influences urban stream communities still has not been rigorously examined. We studied the importance of the degree of urbanization, the local stream environment and the regional species pool on the assembly of stream fishes in the Pannon Biogeographic Region, Hungary. Correlation analyses between urbanization variables (human population size and a recently developed urbanization index) and local stream and riparian environmental variables did not show significant relationships, indicating that the examined 29 streams reacted to the degree of urbanization in a strongly individual manner. Variance partitioning in both linear regression and redundancy analyses showed that the downstream species pool was the most important determinant of fish species richness, community composition and abundance at urban stream sites. The effect of the local stream environment proved to be moderate, while purely urbanization variables explained only a very small proportion of variance in the data. The relative importance of shared fractions depended on the examined fish assemblage variable, but, in general, was also low or moderate. Additional principal component analyses indicated that community similarity between urban and associated non-urban “reference sites” varied widely, and that the sites did not separate to urban and reference fish community types. Overall, the results highlight that the degree of urbanization is not a strong determinant of local stream habitat and fish community characteristics in this region. Rather, historical species pool and stream characteristics shape fish communities with urbanization playing a rather individual role in some streams. Thus, rehabilitation of urban streams should not only focus on local habitat improvements, but rather consider how dispersal mechanisms from non- urban segments influence community organization at the urban sites.

Keywords: urban streams, fish assemblage, species pool, historical effects, habitat structure, migration, variance partitioning

INTRODUCTION

Human induced degradation of natural habitats is one of the leading factors in the decline of biodiversity worldwide (Dudgeon et al., 2006; Didham et al., 2007; Chaudhary et al., 2018). Local extinction of species and alteration of biodiversity are frequently linked to rapid human population growth and the concomitant spread of urban areas (Frissel, 1993; Czech et al., 2000; Aronson et al., 2014). Stream ecosystems are particularly vulnerable to the impacts of urbanization (Wang et al., 2000; Meyer et al., 2005; Gál et al., 2019). For example, several studies showed that urbanization could cause changes in water quality and in stream hydrology and morphology (Chadwick et al., 2006; Roy et al., 2009). In urban areas, streams are frequently confined in channels covered with impervious concrete surfaces. Combined with the alteration of the riparian zone, these modifications result channel simplification and homogenized habitat structure, which directly affect the biodiversity and ecological integrity of stream ecosystems. This process is termed the urban stream syndrome (sensu Walsh et al., 2005; Violin et al., 2011; Booth et al., 2016).

Although knowledge about the effects of urbanization on stream biota is accumulating rapidly, the complex processes of urbanization, and the relative role of interacting factors in affecting the organization of ecological assemblages are still poorly understood. In fact, recent studies reveal considerable heterogeneity in the physical and chemical characteristics of urban streams, rather than a homogenous channel type over many sites (Parr et al., 2016; Hassett et al., 2018). These studies show that the variance in assemblage structure explained by urban land cover and/or local scale instream and riparian variables can vary over a wide range (Brown et al., 2009; Engman and Ramírez, 2012; Lisi et al., 2018). Nevertheless, most studies focused only on the quantification of the effect of abiotic variables and largely neglected other potentially influencing factors in the organization of urban stream assemblages.

For example, not only catchment or local scale habitat variables likely influence the organization of assemblages in urban stream sites, but the dispersal of individual species in the stream catchment (Albanese et al., 2009) and/or the species pool of individual streams, the composition of which may be shaped by former land-use effects (Harding et al., 1998). In fact, recent studies emphasized that spatial constraints and regional species pool effects may override the importance of local habitat conditions in predicting the composition of stream assemblages (Stoll et al., 2014; Czeglédi et al., 2016). For example, Stoll et al. (2014) found that the occurrence rate of a species and species density in the regional species pool were the most important variables that explained much more proportion of the variability of species presence (34 %) and density (38 %) than local abiotic conditions (2 and 21%, respectively) in restored streams. Although dispersal has been suggested as a primary mechanism for maintaining some degree of biodiversity in urban streams (Utz et al., 2016), its relative influence, to our knowledge, still has not been determined along urbanization gradients. However, for developing more effective restoration strategies, it is important to understand not only the effects of urban development and associated physical and chemical degradation, but how dispersal mechanisms from the regional species pool interact with urban stressor variables to determine the diversity and structure of stream organisms.

The objective of this study was to quantify the importance of the degree of urbanization, the local environment and the downstream species pool on the assembly of stream fishes in the Pannon Biogeographic Region, Hungary. For stream fish, species colonization of altered reaches usually happens from downstream sites, since the species composition of fish assemblages show a strongly nested pattern along the longitudinal profile of streams (Matthews, 1998; Erős and Grossman, 2005; Grossman et al., 2010). However, abrupt changes in habitat conditions at urban sites may limit the number of fish species that can potentially colonize urban reaches. Overall, at smaller spatial scales, occurrence and abundance of species in degraded sites may be determined by the type and the extent of habitat modification and the composition of the downstream species pool (e.g., Detenbeck et al., 1992; Albanese et al., 2009). Therefore, we sampled fish assemblages and quantified instream and riparian habitat structure along an urbanization gradient, and also surveyed fish assemblages downstream from the sampled urban sites in order to characterize the potential species pool. We hypothesized that the degradation of local stream habitat will increase with the degree of urbanization, which will exert a strong effect on the structure of fish assemblages. However, we also hypothesized that species pool and associated dispersal effects would be responsible for a large proportion of variance in assemblage structure, which may be comparable with the importance of local habitat effects.

MATERIALS AND METHODS

Study Sites

The study area was located in Hungary where all the streams and rivers are tributaries of the River Danube, the second largest river in Europe (catchment area 796,250 km^2; length 2,847 km). The majority of the country's 93,036 km^2 belong to relatively lowland areas (i.e., situated below 300 m a.s.l.), with only a very small proportion being located in submontane regions. The dominant land use type in the catchments is arable fields, with vineyards, orchards, pastures, and managed deciduous forests forming a smaller proportion.

We selected 29 2nd or 3rd order wadeable streams for this study, with varying degrees of urbanization, using geoinformatic maps (**Figures 1A,B**). In selecting the stream sites we applied the following criteria: (i) streams should be situated below 350 m a.s.l. in order to decrease the effect of natural environmental variability as much as possible among sites; (ii) all selected streams should have a segment within a settlement (urban reach) and another, more natural non-urban segment (hereafter reference site) downstream from the urban ones (species pool); (iii) no insurmountable barrier (reservoir dam, high vertical drop structure, etc.) should be between the urban and the reference site, (iv) all sites should be located within a reasonable distance from the nearest road for accessibility.

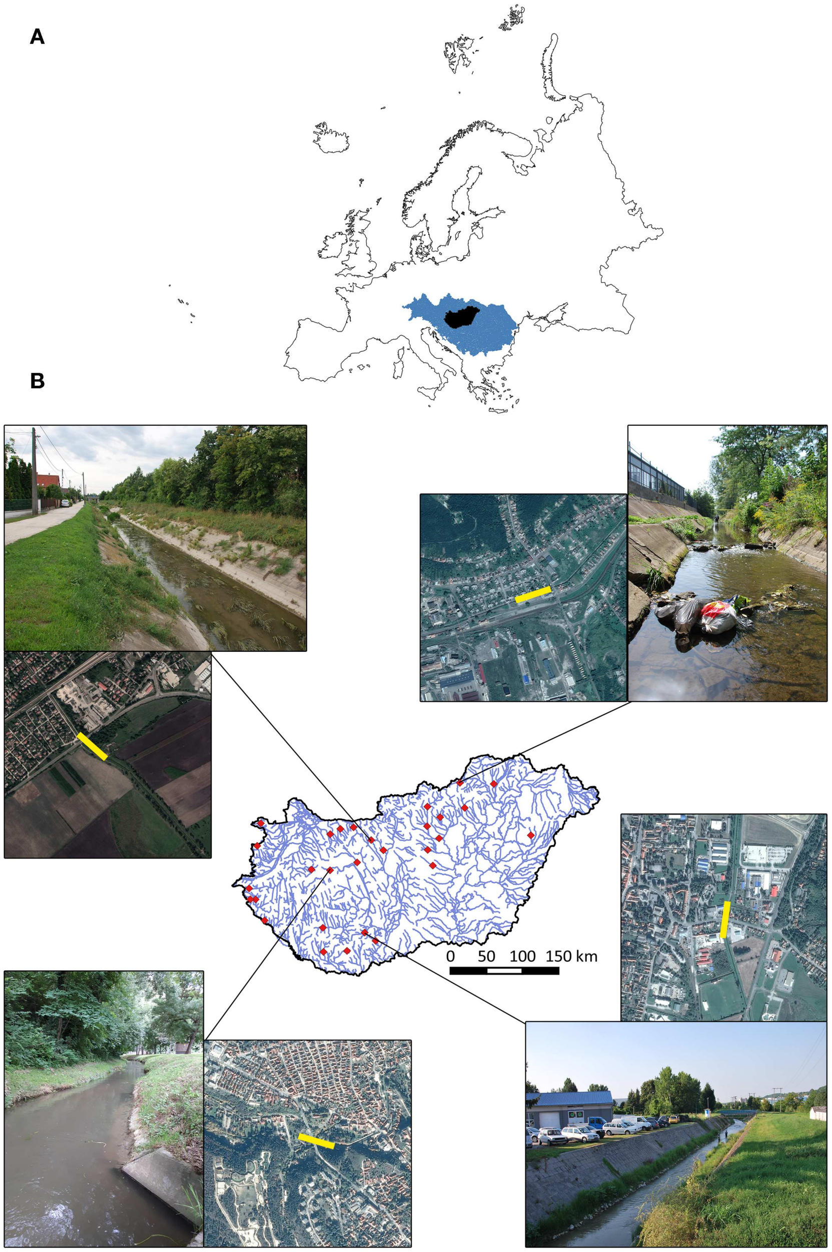

FIGURE 1 | (A) Location of Hungary (black) in the catchment of the Danube River in Europe. **(B)** Distribution of the sampling sites (red squares) in Hungary and some examples of the studied streams (photos taken during fieldwork are shown) with the satellite pictures from Google Maps. The exact locations of the sampled urbanized sections are indicated by yellow rectangles.

Fish Sampling

Fish were collected during the summer months (July–August) of 2017 and 2018. Two distinct sites were sampled on each stream, one in the urban area, and the other downstream from the urban site in a more natural area. Mean distance (measured in stream kilometers) was 5.26 ± 3.41 km S.D. between the urban and the downstream sites. At each site, we surveyed a 150 m long reach by wading, single pass electrofishing using a backpack electrofishing gear (IG200/2B, PDC, 50–100 Hz, 350–650 V, max. 10 kW; Hans Grassl GmbH, Germany). This amount of sampling effort was found to yield representative samples of fish assemblages in this study area for between-site assemblage comparisons (Sály et al., 2009), and is also comparable with those routinely used elsewhere for the sampling of fish in wadeable streams (Magalhães et al., 2002; Hughes and Peck, 2008). Fish were identified to species level, counted and released back to the stream.

Environmental Variables

We followed the methodology of Erős et al. (2012, 2016) for characterizing the environmental features of urban sites, which will be reiterated here briefly. Altogether 10 transects were placed perpendicular to the main channel at each sampling site to characterize physical features of the environment. Wetted width was measured along each transect. Water depth and current velocity (at ca. 60% depth) were measured at five equally spaced points along each transect. Visual estimates of percentage substratum cover were made at every transect point as well. Percentage substratum data of the transect points were later pooled and overall percentages of substrate categories were calculated for each site. Aquatic macrovegetation (emergent, submerged, floating) and periphyton coverage were also estimated visually for each transect point and later pooled, and the overall percentage of macrophyte categories were calculated for each site. Conductivity, dissolved oxygen content, TDS (total dissolved solids), and pH were measured with an YSI EXO2 multiparameter water quality sonde (Xylem Inc. NY, USA) before fish sampling, and the content of nitrogen forms (i.e., nitrite, nitrate, ammonium) and phosphate were measured using field kits (Visocolor ECO, Macherey-Nagel GmbH & Co. KG., Germany). The habitat structure of the stream margin (i.e., along a $\sim$10 m wide strip in both sides) was characterized by visually estimating the percentage coverage of vegetation (herbaceous and arboreal) and concrete. Altitude was measured in the field using a GPS device (Garmin Montana 650). We used these variables as they provide meaningful information on both catchment and instream level characteristics of the habitat, including possible human effects (Wang et al., 2003; Hoeinghaus et al., 2007; Erős et al., 2012).

Urbanization Variables

We used two measures for quantifying the degree of urbanization at the urban sites: (i) human population of the settlements and (ii) a recently developed urbanization index (Seress et al., 2014). Population of settlements is a widely used proxy for quantifying the degree of urbanization (e.g., Jones and Clark, 1988; Meyer et al., 2005), as it usually highly correlates with increased watershed development, area of the settlement and the amount of imperviousness per unit area (Chabaeva et al., 2009). The urbanization index scores were computed with the UrbanizationScore software[1]. Using Google Maps satellite images, this software calculates the degree of urbanization for a 1 km × 1 km area around a focal point (here: the center of a study site). To do this, the software relies on major land-cover feature data (proportion of buildings, vegetation, and impervious surfaces), and uses the PC1 score from a principal component analysis (PCA) of the estimated land-cover features. This process thus creates an urbanization gradient by providing an "urbanization score" for each study area, which is a continuous variable suitable for standard statistical analyses [for more details see Seress et al. (2014)].

Statistical Analysis

Urbanization and Habitat Features

Spearman rank correlation values were computed between the urbanization and local habitat variables to ascertain whether the degree of urbanization can be related to the degradation of the studied streams.

We used PCA on the correlation matrix of the recorded habitat data to characterize the water chemistry and the physical structure of the urban sampling sites. TDS was omitted before the analyses because it showed strong correlation with conductivity (Spearman's rho = 0.99; $p < 0.001$). Spearman correlation test was used to compute the correlation values between the environmental variables and the component scores of the sites along the first three PC axes.

Fish Assemblages and the Importance of Predictor Variables

We conducted PCAs both on species composition and abundance data to quantify and visually examine the similarity of fish assemblages between the urban and their associated reference sites. Prior to abundance-based analysis, data were Hellinger transformed (Legendre and Gallagher, 2001). In the ordination space, the shorter the distance between the urban and the corresponding reference sites, the greater the similarity between their fish assemblages. These analyses thus help to visualize the importance of the species pool in determining fish assemblage structure of the urban sites relative to other urban or reference sites.

We applied variance partitioning procedures (Borcard et al., 2018) for quantifying the importance of the degree of urbanization, the local environment and the species pool in determining the structure of fish assemblages of the urban sites. Note that prior to running the variance partitioning models, we checked for the potential effects of spatial factors on fish assemblage structure. For this, we conducted Spearman rank correlation analysis to explore the relationship between fish assemblage similarity (Euclidean distance based on abundance data) and spatial distance (km) between urban and their associated reference sites and this correlation proved to be insignificant (Spearman's rho = −0.06; $p = 0.745$). Moreover, former variance partitioning analyses indicated a statistically non-significant effect of spatial distance among sampling sites across Hungary on fish assemblages (adj. $R^2 = 0.061$; $p = 0.131$) (Tóth et al., 2019). Based on these results, we chose not to include these spatial variables in our variance partitioning models. We ran three separate analyses: (i) for the number of species, (ii) for the fish composition data and (iii) for the abundance data. We used partial multiple linear regression for partitioning the explained variation in the number of species (Borcard et al., 1992; Erős et al., 2009). Specifically, the following three sets of explanatory variables were used: (i) degree of urbanization: population of the settlements and the urban index scores; (ii) local environment: the coordinates of the urban sites along the first three principal components in the PCA applied on the local environment data (see above); (iii) species pool: number of species of the reference sites. The advantage of running a PCA on the original environmental data prior to

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[1] freely available online at: https://keplab.mik.uni-pannon.hu/en/urbanization-index

a further analysis is that it reduces the number of variables to a small number of explanatory variables (here environmental gradients, see e.g., Heino et al., 2005; Czeglédi et al., 2016). Further, we used redundancy analysis (RDA) (Peres-Neto et al., 2006; Borcard et al., 2018) to quantify the relative contribution of the three sets of explanatory variables on the composition and abundance structure of urban fish assemblages. Hellinger transformed abundance data of the species were used as response variables for the abundance-based analysis. Here, we included the same explanatory variables into the models for the degree of urbanization, and for the local environment as we did in the multiple linear regression. However, for characterizing the species pool, we conducted PCAs on the fish composition and Hellinger transformed abundance data of the reference sites and used the first, second and third components as explanatory variables. These variables explained 22.5, 14.8, 9.4, and 30.6, 18.4, 16.4% of the variance for compositional and abundance data, respectively. Variation in the number of species, fish composition, and abundance was partitioned into pure urbanization level, pure local environment and pure species pool factors, and their shared and unexplained proportions using adjusted R^2 values (Borcard et al., 2018). All statistical analyses were performed in R (R Development Core Team, 2018) using packages "vegan" (Oksanen et al., 2019), "factoextra" (Kassambara and Mundt, 2017), "FactoMineR" (Le et al., 2008), and "Hmisc" (Harrel and Dupont, 2012).

RESULTS

Urbanization and Habitat Features

The population size of the settlements varied between 128 and 204,156 (33,794 mean ± 46,775 S.D.). The urbanization index characterized an urbanization gradient, which was indicated by the increasing dominance of buildings and roads along the first principal component (**Figure 2**, positive correlation scores). The other end of the gradient (negative correlation scores) was represented by more natural surroundings with a higher proportion of forest and other vegetation types.

The population of the settlements and the urban index scores showed a significant positive correlation (**Table 1**). However, correlation values revealed only a weak relationship between the urbanization and the stream habitat variables. Only submerged aquatic vegetation showed a significantly negative correlation with the urban index scores.

PCA on environmental variables indicated high variability among the urban sites. The first principal component revealed a natural environmental gradient from stream sites with silty substrate, dense emergent aquatic macrovegetation and mainly herbaceous bank vegetation (negative correlation scores) to well-oxygenated streams with higher altitude, higher current velocity and higher proportion of coarse substrate (e.g., gravel, stone) (positive correlation scores) (**Table 2**). On the contrary, the second principal component was more related to a habitat alteration gradient from more urbanized sites with higher proportion of concrete substrate and shoreline and alkaline pH

TABLE 1 | Spearman rank correlation values between the urbanization and local habitat variables.

	Population	Urban index score
Altitude (m)	−0.09	0.16
Shoreline (herbaceous) (%)	0.08	0.02
Shoreline (arboreal) (%)	−0.11	−0.14
Shoreline (concrete) (%)	−0.02	0.07
Width (m)	0.10	−0.14
Depth (cm)	−0.09	−0.16
Current velocity (cm s^{-1})	0.31	0.33
Substrate (silt) (%)	−0.29	−0.19
Substrate (sand) (%)	0.29	−0.17
Substrate (gravel) (%)	0.06	−0.06
Substrate (stone) (%)	0.22	0.12
Substrate (rock) (%)	−0.13	0.02
Substrate (concrete) (%)	0.23	0.23
Aquatic vegetation (emerged) (%)	−0.14	−0.11
Aquatic vegetation (submerged) (%)	−0.14	−0.41*
Aquatic vegetation (floating leaved) (%)	0.05	−0.25
Aquatic vegetation (filamentous algae) (%)	0.18	0.03
Dissolved O_2 (mg l^{-1})	0.21	0.12
Conductivity (μS cm^{-1})	0.23	−0.05
pH	−0.10	0.04
NH_4 (mg l^{-1})	0.33	0.33
NO_2 (mg l^{-1})	−0.15	0.04
NO_3 (mg l^{-1})	0.02	0.05
PO_4 (mg l^{-1})	−0.21	−0.30
Population	–	0.51*

Significant ($p < 0.05$) correlations are indicated by asterisk (*).

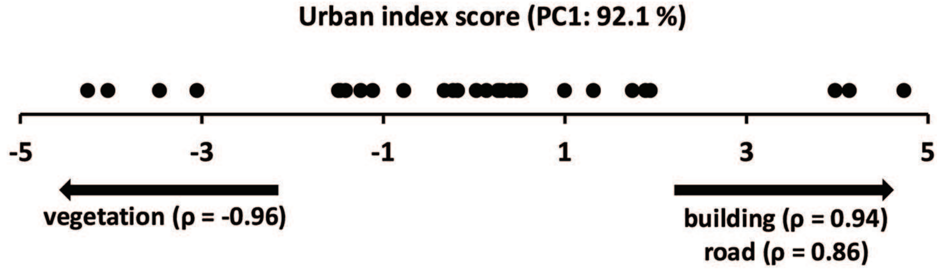

FIGURE 2 | Distribution of the urban sites along the first axis of the PCA based on the urbanization index scores. Spearman rank correlation values between the urbanization index variables and site scores are shown below the axis.

TABLE 2 | Results of the PCA conducted on the local habitat variables of the urban sites with the Spearman rank correlation values between the local habitat variables and PCA component scores of the sites.

	PC1 (21.5%)	PC2 (15.3%)	PC3 (12.2%)
Altitude (m)	0.65***	−0.04	0.33
Shoreline (herbaceous) (%)	−0.62***	−0.18	−0.25
Shoreline (arboreal) (%)	−0.01	−0.48**	0.32
Shoreline (concrete) (%)	0.46**	0.42*	0.10
Width (m)	−0.17	−0.55**	−0.24
Depth (cm)	−0.18	−0.63***	0.17
Current velocity (cm s^{-1})	0.78***	−0.17	−0.09
Substrate (silt) (%)	−0.94***	0.22	0.13
Substrate (sand) (%)	0.30	−0.48**	−0.42*
Substrate (gravel) (%)	0.59***	−0.63***	−0.12
Substrate (stone) (%)	0.51**	−0.30	−0.25
Substrate (rock) (%)	0.26	−0.41*	0.12
Substrate (concrete) (%)	0.52**	0.55**	−0.02
Aquatic vegetation (emerged) (%)	−0.82***	0.27	0.19
Aquatic vegetation (submerged) (%)	−0.17	−0.06	−0.36*
Aquatic vegetation (floating leaved) (%)	−0.33	−0.16	−0.33*
Aquatic vegetation (filamentous algae) (%)	0.16	0.24	−0.24
Dissolved O_2 (mg l^{-1})	0.62***	0.18	−0.51**
Conductivity (µS cm^{-1})	−0.21	0.14	−0.80***
pH	0.14	0.60***	0.09
NH_4 (mg l^{-1})	−0.29	0.37*	−0.62***
NO_2 (mg l^{-1})	0.01	0.17	−0.43*
NO_3 (mg l^{-1})	0.03	0.08	−0.58**
PO_4 (mg l^{-1})	0.27	−0.33	0.06

Explained variance by components is shown in parenthesis. Significant correlations are indicated by asterisks ($^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$).

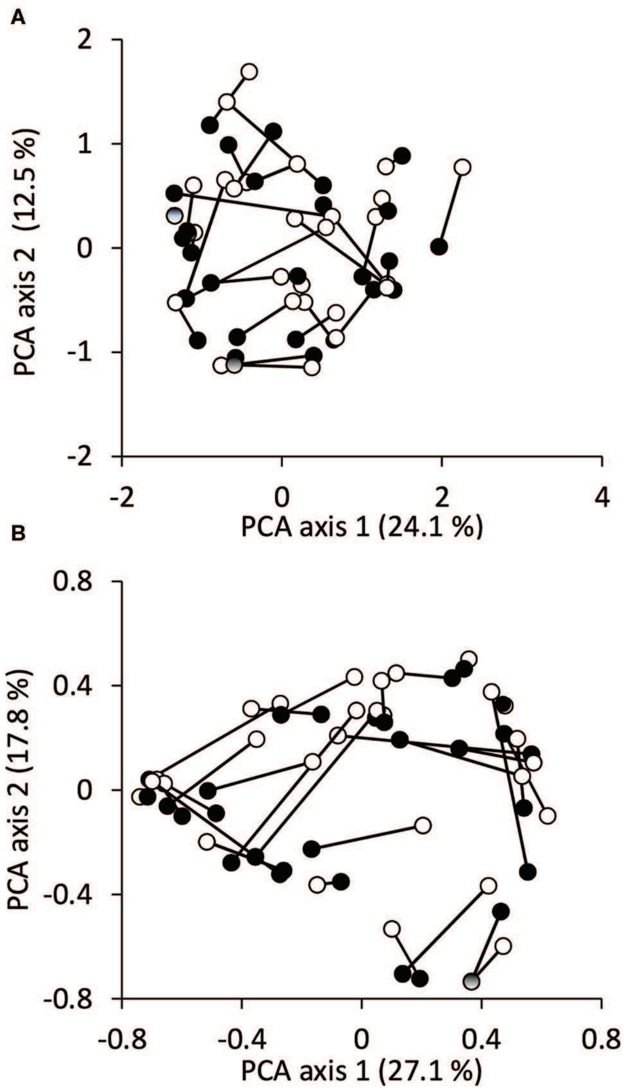

FIGURE 3 | Ordination plot of the PCA of the studied urban and their associated reference sites (linked to each other) based on **(A)** fish species composition and **(B)** abundance data. Black symbols: urban sites; white symbols: reference sites.

(positive correlation scores) to sites which showed more natural characteristics (e.g., vegetation dominated shoreline, natural substrate, wider, and deeper streambed) (negative correlation scores) (**Table 2**). Sandy substrate, submerged and floating leaved vegetation and some chemical parameters correlated significantly negatively with the third PCA axis (**Table 2**).

Fish Assemblages and the Importance of Predictor Variables

Average species richness were 6.8 ± 3.8 S.D. (min:1, max:18) and 6.2 ± 4.0 (min:1, max:15) in the reference and urban sites, respectively. The average difference in pairwise species richness between the reference and urban sites was 2.5 ± 1.8 S.D. Fish assemblage composition and abundance structure of the two types of sites did not show clear separation along the combination of the first two principal components (**Figures 3A,B**). Rather, the similarity between the urban and their associated reference sites varied widely.

The three explanatory variable groups in the variance partitioning procedures explained altogether 67.9, 32.6, and 27.1% in the number of species, fish composition and abundance data of the urban sites, respectively (**Table 3**). For the species number, the largest amount of variation was explained purely by the number of species of the reference sites ($p < 0.001$), although the unique contribution of the local environment was also significant ($p = 0.014$). For fish composition, most of the variation was explained by the pure effect variable groups. Of these, the downstream species pool was the most determining variable group, although the effects of the local stream environment and the degree of urbanization also proved to be significant (species pool: $p < 0.001$, local environment: $p = 0.030$, degree of urbanization: $p = 0.027$). For the abundance data, most of the variation was explained jointly by the local

TABLE 3 | Results of the variance partitioning analyses (% explained and residual variance) for species number, species composition, and abundance.

	Env	Urb	Spec	Env+ Urb	Env+ Spec	Urb+ Spec	Env+ Urb+ Spec	Residual
Species number	14	2.8	47.2	–	–	–	3.9	38.8
Species composition	4.8	4.6	19.8		2.9		0.5	71.6
Abundance	0.3	1.5	10.7	–	14.5	–	0.1	73.7

Env, local habitat (environmental) variables, Urb, urbanization variables, Spec, downstream species pool.

environment and species pool effects, indicating intercorrelation between these two sets of variables. Among pure variable groups, only the abundance of fish species in the reference sites explained significantly the abundance structure ($p = 0.003$).

DISCUSSION

Disentangling the mechanisms that determine community assembly in urban environments is a prerequisite for understanding the impacts of urbanization on the biota and for developing more effective rehabilitation strategies. In this study, we found that the local stream environment and the downstream species pool were more important in the assembly of urban stream fish than pure urbanization variables (urbanization index, size of the human population) which had a small, but significant effect on species composition only.

Interestingly, urbanization variables did not show relationship with local stream environmental variables, indicating that the degree of urbanization did not influence significantly the riparian and instream environmental characteristics in this region. In other words, we found relatively natural stream conditions in relatively densely populated areas and *vice versa*, relatively degraded stream conditions in less built-up areas, similarly for example to the study of Wang et al. (2001) who also found that stream habitat did not correlate well with increasing urbanization in Wisconsin, USA. In fact, PCA results of stream environmental variables suggest that natural environmental gradients were more important determinants of between stream differences than clearly anthropogenic modifications (i.e., concrete bank and substrate). However, the non-interactive effects of natural and anthropogenic factors on general stream characteristics are hard to disentangle based on multivariate field data (Erős et al., 2012). Overall, the results suggest that within stream environmental degradation was very site/stream specific. A likely explanation for this result is that, even though our study sites were distributed along a well-defined urbanization gradient, the majority of the sites were only moderately urbanized. Thus, we could characterize only a relatively short urbanization gradient, due to the lack of large metropolitan areas in Hungary, not like those found in other countries (e.g., USA). Nevertheless, documenting patterns and understanding processes in the early phase of urbanization is important to provide evidence for possible future effects, especially since urbanization processes are ongoing intensively in this region (Tóth et al., 2019).

Several studies justify the importance of habitat structure and diversity to the structure of stream fish assemblages (Gorman and Karr, 1978; Matthews, 1998). Channelization with concrete material makes both within stream habitat and the bank extremely simplified, hereby decreasing hydrologic and geomorphic diversity (Walsh et al., 2005). However, this statement is valid only if the concrete channel is regularly maintained by water management. Spading of the concrete channel by hydrologic erosion can create diverse habitat conditions for stream fish, especially if finer sediment (sand and gravel) from upstream non-urban areas fill the channel, even if at least partly. In fact, the different combinations of concrete, bank stabilizing rock, stone and finer sediment was characteristical for many urban stream sites in Hungary, which can even increase micro- and mesohabitat level hydrologic and geomorphic diversity in contrast to the sand and/or gravel substrate which is the characteristics of more natural streams. In addition, we also observed that the stream margin was differently modified and maintained by urban management practices, ranging from clearcut vegetation to totally abandoned riparian zone. These diverse, but stream specific modification effects could strongly determine why we could not find overall and clear responses to urbanization variables in the studied region neither for environmental nor for fish assemblage variables.

Fish assemblages of urban and reference sites did not clearly separate and both types showed high variability in their fish assemblage structure. Even the corresponding urban and reference site fish assemblages showed large variation, with some urban sites showing more similarity to the reference sites of other streams or reference sites to other urban sites. These results suggest the relatively low predictability of stream fish assemblages in this human-modified landscape (see also Erős et al., 2012), or at least that urbanization in itself was an insufficient predictor of fish assemblage characteristics. Our findings thus confirm other studies, which found highly variable and sometimes even weak responses of fish to land use gradients (e.g., Utz et al., 2010; Tóth et al., 2019). In contrast, most studies showed clear negative influence of increasing urbanization on fish assemblages (Helms et al., 2005; Morgan and Cushman, 2005; Slawski et al., 2008). These contradictions among the studies probably exist because of the differences in the urbanization gradient as well as the sensitivity of fish assemblages to urbanization, which can be largely different among biogeographic regions.

Local and catchment level variables, land use history and dispersal related factors can influence fish assemblage organization to a different degree in human-modified landscapes, and consequently, their interactive effects are hard to disentangle based on regional scale field observations (Wang et al., 1997; Bourassa et al., 2017). Although similarity between fish assemblages of urban and their associated reference sites varied widely, species pool of downstream sites proved to be the most important pure explanatory variable of urban fish assemblages in our variance partitioning models. These results complement recent findings, which also emphasized the role of regional species pool in shaping assemblage structure in degraded stream systems (e.g., Sundermann et al., 2011; Stoll et al., 2014). Species pool effects can prevail via dispersal processes between the urban and their associated reference sites (Utz et al., 2016) or simply by the overarching effect of historical factors over recent local habitat conditions (Harding et al., 1998; Filipe et al., 2009). In degraded stream habitats such as urbanized ones, where extinction risk is generally higher, colonization from downstream sites could be particularly important for fish populations to survive. This theory has a long history in the general ecological literature. For example, Brown and Kodric-Brown (1977) suggested that local extinction of species may be overcome by colonization from the regional species pool. However, under consecutive harsh conditions, urban streams could be population sinks (Utz et al., 2016) and the long term persistence of fish might depend on the characteristics of the downstream assemblages (e.g., species and trait composition, age structure, etc.). For example, Albanese et al. (2009) showed that the abundance and mobility of downstream fish species were key factors in colonization and population recovery processes. In this context, ensuring dispersion within and between stream segments is critically important for the long term survival of fish populations in degraded stream habitats (Bond and Lake, 2003; Brown et al., 2009).

Species richness of downstream sites was an especially good determinant of species richness of upstream urban sites and highly exceeded the predictive power of the habitat variables of urban sites. This result further confirms the role of stream history in shaping fish assemblage characteristics in this region. On the contrary, most of the variance was unexplained in the species composition and abundance-based models. This result suggests the role of other unmeasured variables (e.g., biotic interactions) in shaping the composition and abundance of species in urban sites. Environmental stochasticity (i.e., temporal variations in environmental conditions) and neutral effects could also largely contribute to the differences in the composition and species abundance between urban and their corresponding reference sites. Interestingly, local habitat variables and species pool effects intercorrelated and jointly influenced the abundance of fishes in urban sites, not like in the case of species richness, where the effect of these factors was well-separated. However, the driving of these mechanisms is difficult to interpret using a snapshot regional-scale survey, especially since the importance of individual factors in shaping population abundance can be largely different among species (Wenger et al., 2008).

There is an intense debate in the stream ecological literature whether the degree of urbanization has to attain a certain threshold until assemblage level effects can be observed (Utz et al., 2010). Studies using land cover variables suggest that impervious surface cover (ISC) has to attain at least 10–15% until significant degradation in fish assemblages occurs (Wang et al., 2000, 2001; King et al., 2005; Morgan and Cushman, 2005). Other studies, however, highlight that changes may occur even at the lowest level of land conversion (Meador et al., 2005; Utz et al., 2010). Although we did not quantify ISC directly at the catchment level, it was inherently used to calculate the urbanization index in this study (see the calculation of urbanization scores in the methods), and we found that its value varied between 22 and 98% in the vicinity of the streams. Our results thus, while support the former conclusion, also highlight that it is not enough to measure only land cover variables to understand assemblage responses to urbanization. It is at least equally important that we have detailed field data on local environmental conditions and on the regional (here stream level) species pool, because only these have the potential to reveal stream specific effects and thereby they significantly contribute to better understand the organization of ecological assemblages in human-modified landscapes.

In conclusion, we found that the local stream environment and the historical species pool of the streams were more important determinants of urban stream fish assemblages than clearly urbanization related variables. It seems that most urban streams still have the potential to recover from the degradation effects of urbanization in this region. However, rehabilitation of urban streams should not only focus on local habitat improvements, but rather consider how dispersal mechanisms from non-urban segments influence community organization at urban stream segments. Only this can ensure the long term persistence of stream fish assemblages in an increasingly urbanized world.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

All procedures described in this paper were in accordance with Hungarian laws, and were licensed by the Ministry of Agriculture of Hungary (IC permission number: HHgF/252-4/2018; TE permission number: HHgF/252-1/2018).

AUTHOR CONTRIBUTIONS

TE and IC conceived the study and analyzed the data. IC, BK, RT, and TE conducted the fieldwork. IC, TE, and GS led the writing and editing of the manuscript.

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REFERENCES

Albanese, B., Angermeier, P. L., and Peterson, J. T. (2009). Does mobility explain variation in colonisation and population recovery among stream fishes? *Freshw. Biol.* 54, 1444–1460. doi: 10.1111/j.1365-2427.2009.02194.x

Aronson, M. F. J., La Sorte, F. A., Nilon, C. H., Katti, M., Goddard, M. A., Lepczyk, C. A., et al. (2014). A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proc. R. Soc.* 281:20133330. doi: 10.1098/rspb.2013.3330

Bond, N. R., and Lake, P. S. (2003). Local habitat restoration in streams : constraints on the effectiveness of restoration for stream biota. *Ecol. Manag. Restor.* 4, 193–198. doi: 10.1046/j.1442-8903.2003.00156.x

Booth, D. B., Roy, A. H., Smith, B., and Capps, K. A. (2016). Global perspectives on the urban stream syndrome. *Freshw. Sci.* 35, 412–420. doi: 10.1086/684940

Borcard, D., Gillet, F., and Legendre, P. (2018). *Numerical Ecology With R*. New York, NY: Springer Verlag.

Borcard, D., Legendre, P., and Drapeau, P. (1992). Partialling out the spatial component of ecological variation. *Ecology* 73, 1045–1055. doi: 10.2307/1940179

Bourassa, A. L., Fraser, L., and Beisner, B. E. (2017). Benthic macroinvertebrate and fish metacommunity structure in temperate urban streams. *J. Urban Ecol.* 3, 1–14. doi: 10.1093/jue/jux012

Brown, J. H., and Kodric-Brown, A. (1977). Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58, 445–449. doi: 10.2307/1935620

Brown, L. R., Gregory, M. B., and May, J. T. (2009). Relation of urbanization to stream fish assemblages and species traits in nine metropolitan areas of the United States. *Urban Ecosyst.* 12, 391–416. doi: 10.1007/s11252-009-0082-2

Chabaeva, A., Civco, D. L., and Hurd, J. D. (2009). Assessment of impervious surface estimation techniques. *J. Hydrol. Eng.* 14, 377–387. doi: 10.1061/(ASCE)1084-0699(2009)14:4(377)

Chadwick, M. A., Dobberfuhl, D. R., Benke, A. C., Huryn, A. D., Suberkropp, K., and Thiele, J. E. (2006). Urbanization affects stream ecosystem function by altering hydrology, chemistry, and biotic richness. *Ecol. Appl.* 16, 1796–1807. doi: 10.1890/1051-0761(2006)016[1796:UASEFB]2.0.CO;2

Chaudhary, A., Pourfaraj, V., and Mooers, A. O. (2018). Projecting global land use-driven evolutionary history loss. *Divers. Distrib.* 24, 158–167. doi: 10.1111/ddi.12677

Czech, B., Krausman, P. R., and Devers, P. K. (2000). Economic associations among causes of species endangerment in the United States. *Bioscience* 50:593. doi: 10.1641/0006-3568(2000)050[0593:EAACOS]2.0.CO;2

Czeglédi, I., Sály, P., Takács, P., Dolezsai, A., Nagy, S. A., and Erős, T. (2016). The scales of variability of stream fish assemblages at tributary confluences. *Aquat. Sci.* 78, 641–654. doi: 10.1007/s00027-015-0454-z

Detenbeck, N. E., DeVore, P. W., Niemi, G. J., and Lima, A. (1992). Recovery of temperate-stream fish communities from disturbance: a review of case studies and synthesis of theory. *Environ. Manage.* 16, 33–53. doi: 10.1007/BF02393907

Didham, R. K., Tylianakis, J. M., Gemmell, N. J., Rand, T. A., and Ewers, R. M. (2007). Interactive effects of habitat modification and species invasion on native species decline. *Trends Ecol. Evol.* 22, 489–496. doi: 10.1016/j.tree.2007.07.001

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z.-I., Knowler, D. J., Lévêque, C., et al. (2006). Freshwater biodiversity: importance, threats, status and conservation challenges. *Biol. Rev.* 81, 163–182. doi: 10.1017/S1464793105006950

Engman, A. C., and Ramírez, A. (2012). Fish assemblage structure in urban streams of Puerto Rico: the importance of reach- and catchment-scale abiotic factors. *Hydrobiologia* 693, 141–155. doi: 10.1007/s10750-012-1100-6

Erős, T., and Grossman, G. D. (2005). Fish biodiversity in two Hungarian streams : a landscape-based approach. *Arch. Hydrobiol.* 162, 53–71. doi: 10.1127/0003-9136/2005/0162-0053

Erős, T., Heino, J., Schmera, D., and Rask, M. (2009). Characterising functional trait diversity and trait-environment relationships in fish assemblages of boreal lakes. *Freshw. Biol.* 54, 1788–1803. doi: 10.1111/j.1365-2427.2009.02220.x

Erős, T., Sály, P., Takács, P., Specziár, A., and Bíró, P. (2012). Temporal variability in the spatial and environmental determinants of functional metacommunity organization - stream fish in a human-modified landscape. *Freshw. Biol.* 57, 1914–1928. doi: 10.1111/j.1365-2427.2012.02842.x

Erős, T., Takács, P., Specziár, A., Schmera, D., and Sály, P. (2016). Effect of landscape context on fish metacommunity structuring in stream networks. *Freshw. Biol.* 62, 215–228. doi: 10.1111/fwb.12857

Filipe, A. F., Araújo, M. B., Doadrio, I., Angermeier, P. L., and Collares-Pereira, M. J. (2009). Biogeography of Iberian freshwater fishes revisited : the roles of historical versus contemporary constraints. *J. Biogeogr.* 36, 2096–2110. doi: 10.1111/j.1365-2699.2009.02154.x

Frissel, C. A. (1993). Topology of extinction and endangerment of native fishes in the Pacific Northwest and California (U.S.A.). *Conserv. Biol.* 7, 342–354. doi: 10.1046/j.1523-1739.1993.07020342.x

Gál, B., Szivák, I., Heino, J., and Schmera, D. (2019). The effect of urbanization on freshwater macroinvertebrates – knowledge gaps and future research directions. *Ecol. Indic.* 104, 357–364. doi: 10.1016/j.ecolind.2019.05.012

Gorman, O. T., and Karr, J. R. (1978). Habitat structure and stream fish communities. *Ecology* 59, 507–515. doi: 10.2307/1936581

Grossman, G. D., Ratajczak, R. E., Farr, M. D., Wagner, C. M., and Petty, J. T. (2010). Why there are fewer fish upstream?. in *Community Ecology of Stream Fishes: Concepts, Approaches, and Techniques* (Bethesda: American Fisheries Society), 73, 63–81.

Harding, J. S., Benfield, E. F., Bolstad, P. V., Helfman, G. S., and Jones, E. B. D. (1998). Stream biodiversity: the ghost of land use past. *Proc. Natl. Acad. Sci.U.S.A.* 95, 14843–14847. doi: 10.1073/pnas.95.25.14843

Harrel, F. E., and Dupont, M. C. (2012). *Package 'Hmisc'. R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Hassett, B. A., Sudduth, E. B., Somers, K. A., Urban, D. L., Violin, C. R., Wang, S.-Y., et al. (2018). Pulling apart the urbanization axis : patterns of physiochemical degradation and biological response across stream ecosystems. *Freshw. Sci.* 37, 653–672. doi: 10.1086/699387

Heino, J., Paavola, R., Virtanen, R., and Muotka, T. (2005). Searching for biodiversity indicators in running waters: do bryophytes, macroinvertebrates, and fish show congruent diversity patterns? *Biodivers. Conserv.* 14, 415–428. doi: 10.1007/s10531-004-6064-z

Helms, B. S., Feminella, J. W., and Pan, S. (2005). Detection of biotic responses to urbanization using fish assemblages from small streams of western Georgia, USA. *Urban Ecosyst.* 8, 39–57. doi: 10.1007/s11252-005-1418-1

Hoeinghaus, D. J., Winemiller, K. O., and Birnbaum, J. S. (2007). Local and regional determinants of stream fish assemblage structure: inferences based on taxonomic vs. functional groups. *J. Biogeogr.* 34, 324–338. doi: 10.1111/j.1365-2699.2006.01587.x

Hughes, R. M., and Peck, D. V. (2008). Acquiring data for large aquatic resource surveys: the art of compromise among science, logistics, and reality. *J. North Am. Benthol. Soc.* 27, 837–859. doi: 10.1899/08-028.1

Jones, R. C., and Clark, C. C. (1988). Impact of watershed urbanization on stream insect communities. *J. Am. Water Resour. Assoc.* 23, 1047–1055. doi: 10.1111/j.1752-1688.1987.tb00854.x

Kassambara, A., and Mundt, F. (2017). *Factoextra: Extract and Visualize the Results of Multivariate Data Analyses*. R package version 1.0.5. Available online at: https://CRAN.R-project.org/package=factoextra (accessed September 27, 2020).

King, R. S., Baker, M. E., Whigham, D. F., Weller, D. E., Jordan, T. E., Kazyak, P. F., et al. (2005). Spatial considerations for linking watershed land cover to ecological indicators in streams. *Ecol. Appl.* 15, 137–153. doi: 10.1890/04-0481

Le, S., Josse, J., and Husson, F. (2008). FactoMineR : an R package for multivariate analysis. *J. Stat. Softw.* 25, 1–18. doi: 10.18637/jss.v025.i01

Legendre, P., and Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia* 129, 271–280. doi: 10.1007/s004420100716

Lisi, P. J., Childress, E. S., Gagne, R. B., Hain, E. F., Lamphere, B. A., Walter, R. P., et al. (2018). Overcoming urban stream syndrome: trophic flexibility confers resilience in a Hawaiian stream fish. *Freshw. Biol.* 63, 492–502. doi: 10.1111/fwb.13091

Magalhães, M. F., Batalha, D. C., and Collares-Pereira, M. J. (2002). Gradients in stream fish assemblages across a Mediterranean landscape: contributions of environmental factors and spatial structure. *Freshw. Biol.* 47, 1015–1031. doi: 10.1046/j.1365-2427.2002.00830.x

Matthews, W. J. (1998). *Patterns in Freshwater Fish Ecology*. Norwell, MA: Chapman and Hall.

Meador, M. R., Coles, J. F., and Zappia, H. (2005). Fish assemblage responses to urban intensity gradients in contrasting metropolitan areas: Birmingham, Alabama and Boston, Massachusetts. *Am. Fish. Soc. Symp.* 47, 409–423. doi: 10.1049/iet-cvi.2013.0217

Meyer, J. L., Paul, M. J., and Taulbee, W. K. (2005). Stream ecosystem function in urbanizing landscapes. *J. North Am. Benthol. Soc.* 24, 602–612. doi: 10.1899/04-021.1

Morgan, R. P., and Cushman, S. F. (2005). Urbanization effects on stream fish assemblages in Maryland, USA. *J. North Am. Benthol. Soc.* 24, 643–655. doi: 10.1899/04-019.1

Oksanen, J., Guillaume Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., et al. (2019). *Vegan: Community Ecology Package*. R package version 2.5-6. Available online at: https://CRAN.R-project.org/package=vegan (accessed September 27, 2020).

Parr, T. B., Smucker, N. J., Bentsen, C. N., and Neale, M. W. (2016). Potential roles of past, present, and future urbanization characteristics in producing varied stream responses. *Freshw. Sci.* 35, 436–443. doi: 10.1086/685030

Peres-Neto, P. R., Legendre, P., Dray, S., and Borcard, D. (2006). Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* 87, 2614–2625. doi: 10.1890/0012-9658(2006)87[2614:VPOSDM]2.0.CO;2

R Development Core Team (2018). *A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Available online at: https://www.R-project.org

Roy, A. H., Dybas, A. L., Fritz, K. M., and Lubbers, H. R. (2009). Urbanization affects the extent and hydrologic permanence of headwater streams in a midwestern US metropolitan area. *J. North Am. Benthol. Soc.* 28, 911–928. doi: 10.1899/08-178.1

Sály, P., Erős, T., Takács, P., Specziár, A., Kiss, I., and Bíró, P. (2009). Assemblage level monitoring of stream fishes: the relative efficiency of single-pass vs. double-pass electrofishing. *Fish. Res.* 99, 226–233. doi: 10.1016/j.fishres.2009.06.010

Seress, G., Lipovits, Á., Bókony, V., and Czúni, L. (2014). Quantifying the urban gradient: a practical method for broad measurements. *Landsc. Urban Plan.* 131, 42–50. doi: 10.1016/j.landurbplan.2014.07.010

Slawski, T. M., Veraldi, F. M., Pescitelli, S. M., and Pauers, M. J. (2008). Effects of tributary spatial position, urbanization, and multiple low-head dams on warmwater fish community structure in a midwestern stream. *North Am. J. Fish. Manag.* 28, 1020–1035. doi: 10.1577/M06-186.1

Stoll, S., Kail, J., Lorenz, A. W., Sundermann, A., and Haase, P. (2014). The importance of the regional species pool, ecological species traits and local habitat conditions for the colonization of restored river reaches by fish. *PLoS ONE* 9:e84741. doi: 10.1371/journal.pone.0084741

Sundermann, A., Stoll, S., and Haase, P. (2011). River restoration success depends on the species pool of the immediate surroundings. *Ecol. Appl.* 21, 1962–1971. doi: 10.1890/10-0607.1

Tóth, R., Czeglédi, I., Kern, B., and Erős, T. (2019). Land use effects in riverscapes: diversity and environmental drivers of stream fish communities in protected, agricultural and urban landscapes. *Ecol. Indic.* 101, 742–748. doi: 10.1016/j.ecolind.2019.01.063

Utz, R. M., Hilderbrand, R. H., and Raesly, R. L. (2010). Regional differences in patterns of fish species loss with changing land use. *Biol. Conserv.* 143, 688–699. doi: 10.1016/j.biocon.2009.12.006

Utz, R. M., Hopkins, K. G., Beesley, L., Booth, D. B., Hawley, R. J., Baker, M. E., et al. (2016). Ecological resistance in urban streams : the role of natural and legacy attributes. *Freshw. Sci.* 35, 380–397. doi: 10.1086/684839

Violin, C. R., Cada, P., Sudduth, E. B., Hassett, B. A., Penrose, D. L., and Bernhardt, E. S. (2011). Effects of urbanization and urban stream restoration on the physical and biological structure of stream ecosystems. *Ecol. Appl.* 21, 1932–1949. doi: 10.1890/10-1551.1

Walsh, C. J., Roy, A. H., Feminella, J. W., Cottingham, P. D., Groffman, P. M., Morgan, I. I., et al. (2005). The urban stream syndrome: current knowledge and the search for a cure. *J. North Am. Benthol. Soc.* 24, 706–723. doi: 10.1899/04-028.1

Wang, L., Lyons, J., and Kanehl, P. (2001). Impacts of urbanization on stream habitat and fish across multiple spatial scales. *Environ. Manage.* 28, 255–266. doi: 10.1007/s002670010222

Wang, L., Lyons, J., Kanehl, P., Bannerman, R., and Emmons, E. (2000). Watershed urbanization and changes in fish communities in southeastern Wisconsin streams. *J. Am. Water Resour. Assoc.* 36, 1173–1189. doi: 10.1111/j.1752-1688.2000.tb05719.x

Wang, L., Lyons, J., Kanehl, P., and Gatti, R. (1997). Influences of watershed land use on habitat quality and biotic integrity in Wisconsin streams. *Fisheries* 22, 6–12.

Wang, L., Lyons, J., Rasmussen, P., Seelbach, P., Simon, T., Wiley, M., et al. (2003). Watershed, reach, and riparian influences on stream fish assemblages in the Northern Lakes and Forest Ecoregion, U.S.A. *Can. J. Fish. Aquat. Sci.* 60, 491–505. doi: 10.1139/F03-043

Wenger, S. J., Peterson, J. T., Freeman, M. C., Freeman, B. J., and Homans, D. D. (2008). Stream fish occurrence in response to impervious cover, historic land use, and hydrogeomorphic factors. *Can. J. Fish. Aquat. Sci.* 1264, 1250–1264. doi: 10.1139/F08-046

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Environmental Factors Override Dispersal-Related Factors in Shaping Diatom and Macroinvertebrate Communities Within Stream Networks in China

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Metacommunity theory provides a useful framework to describe the underlying factors (e.g., environmental and dispersal-related factors) influencing community structure. The strength of these factors may vary depending on the properties of the region studied (e.g., environmental heterogeneity and spatial location) and considered biological groups. Here, we examined environmental and dispersal-related controls of stream macroinvertebrates and diatoms in three regions in China using the distance-decay relationship analysis. We performed analyses for the whole stream network and separately for two stream network locations (headwater and downstream sites) to test the network position hypothesis (NPH), which states that the strength of environmental and dispersal-related controls varies between headwater and downstream communities. Community dissimilarities were significantly related to environmental distances, but not geographical distances. These results suggest that communities are structured strongly by environmental filtering, but weakly by dispersal-related factors such as dispersal limitation. More importantly, we found that, at the whole network scale, environmental control was the highest in the regions with highest environmental heterogeneity. Results further showed that the influence of environmental control was strong in both headwaters and downstream sites, whereas spatial control was generally weak in all sites. This suggests a lack of consistent support for the NPH in our studied stream networks. Moreover, we found that local-scale variables relative to basin-scale variables better explained community dissimilarities for diatoms than for macroinvertebrates. This indicates that diatoms and macroinvertebrates responded to environment at different scales. Collectively, these results suggest that the importance of drivers behind the metacommunity assembly varied among regions with different level of environmental heterogeneity and between organism groups, potentially indicating context dependency among stream systems and taxa.

Keywords: environmental filtering, distance-decay, dispersal, spatial scale, environmental heterogeneity, dendritic networks

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INTRODUCTION

The assembly rules of biotic communities are among the leading concerns of community ecology. Metacommunity theory suggests that the assembly of local communities results from a combination of dispersal, environmental filtering, stochastic colonization and extinction events, and biological interactions (Leibold et al., 2004). Based on these assembly processes, Leibold et al. (2004) suggested four paradigms or archetypes of metacommunities: species sorting, mass effects, neutral model and patch dynamics. Recent studies suggest that metacommunities form a continuum structured by different assembly mechanisms varying in their relative importance, rather than a typological classification based on four accurately bordered archetypes (Winegardner et al., 2012; Brown et al., 2017; Leibold and Chase, 2017). The assembly processes within metacommunities might vary among different study systems and this variability may be related to the environmental and spatial characteristics of the study region (Heino et al., 2012, 2015a).

Environmental heterogeneity prevailing in the study region is typically one of the main factors affecting metacommunity assembly (but see Bini et al., 2014). For example, the importance of environmental filtering is expected to vary among regions that cover different levels of environmental heterogeneity (Leibold et al., 2004). Such an effect would be more likely to be found when studying metacommunities that show intermediate among-site dispersal and intermediate spatial extent (e.g., within a river basin, Heino et al., 2015b). This is because the "true" effect of environmental filtering can be masked by limited or excessive dispersal, which likely occur at large or small spatial scales, respectively (Ng et al., 2009; Heino et al., 2015c). However, empirical support for such an expectation (i.e., the importance of environmental filtering on community composition is expected to be greater within regions that have higher environmental heterogeneity) is relatively weak, particularly in stream ecosystems (Landeiro et al., 2012; Grönroos et al., 2013; Heino et al., 2015a).

Spatial location of a site may also affect metacommunity organization. In an influential study on stream macroinvertebrates, Brown and Swan (2010) predicted that headwater metacommunities are strongly determined by environmental filtering because headwaters are more isolated and more environmentally heterogeneous, whereas downstream metacommunities are potentially more influenced by mass effects due to a surplus of dispersal across well-connected downstream sites and the likely strong influence of movements from headwaters to downstream. These predictions were described as the network position hypothesis (NPH) by Schmera et al. (2018). However, recent studies found that the relative roles of environmental and dispersal-related factors on community composition are likely to depend on network level differences in environmental heterogeneity and connectivity configurations, rather than simply on headwater-downstream differences in environmental and connectivity variables (Eros, 2017; Schmera et al., 2018; Eros and Lowe, 2019; Henriques-Silva et al., 2019). For example, Henriques-Silva et al. (2019) found a lack of general support for the NPH predictions across multiple catchments and suggested that catchment properties (e.g., network connectivity) generated considerable context dependency in NPH predictions. These findings thus underline the need for testing the core predictions of the NPH in different regions.

Previous studies suggest that the relative roles of environmental and dispersal-related factors could also differ between biological groups with different traits such as body size (De Bie et al., 2012; Farjalla et al., 2012), dispersal ability (Grönroos et al., 2013), environmental tolerance and environmental optima. Diatoms are unicellular organisms and could be expected to be stronger dispersers than larger sized macroinvertebrates due to their small size and high abundance (Astorga et al., 2012; Heino et al., 2012). They may thus be better able to track environmental variation and show a stronger degree of environmental control than macroinvertebrates (Astorga et al., 2012). This is because diatoms can disperse passively via air and animal vectors (Kristiansen, 1996) and may overcome dispersal barriers more easily than macroinvertebrates restricted to dispersal via watercourses (Shurin et al., 2009; De Bie et al., 2012; Tonkin et al., 2017). However, some studies observed that the level of environmental control was surprisingly weaker for diatoms when compared with macroinvertebrates (Heino et al., 2012; Soininen, 2014). We note though that these studies considered the whole environment in only one single model without making distinction between different scales (e.g., local scale and basin scale). However, organisms with different biological traits may respond environmental variables at multiple scales differently (Johnson et al., 2007; Liu et al., 2016; Heino et al., 2017). For example, (Liu et al., 2016) found that catchment-level variables (e.g., land use diversity) explained a larger amount of variation in macroinvertebrate community composition than small-scale variables (e.g., substrates). In contrast, Pan et al. (1996) suggested that local variables (e.g., pH) played a more important role in structuring diatom communities than broad-scale variables (e.g., climatic variables). Recognition of such scale-related responses implies the need for simultaneous disentangling of multi-scale (e.g., local scale vs. basin scale) environmental effects on diatom and macroinvertebrate communities.

Here we aimed at addressing the role of environmental filtering and dispersal-related processes (e.g., dispersal limitation and mass effect) in structuring communities of stream diatoms and macroinvertebrates from the same set of sites at three intermediate-sized regions in China. The three regions differed in the level of environmental heterogeneity and were located spatially distant from each other. Stream assemblages across a set of sites within a region were defined here as a metacommunity. We performed independent analyses at different spatial hierarchies using data from the whole stream network and separately from headwater and downstream sites. We hypothesized that (H_1) the effect of environmental filtering would be the highest in the region with highest environmental variation and (H_2) the NPH predictions would receive inconsistent support across three regions and between two organismal groups. As (i) previous studies found a mixture of outcomes for the differences in environmental and dispersal-related controls between diatoms and macroinvertebrates, and (ii) only few studies have examined the differences in local-scale and basin-scale environmental controls between these two biological groups, we did not form a specific hypothesis regarding the differences in assembly processes between diatoms and macroinvertebrates.

MATERIALS AND METHODS

Study Area

In this study, we used a data set containing three geographically distant (minimum distance between regions is ∼2,000 km) regions: the Irtysh River (ITR) in Xijiang autonomous region, the middle section of Qiantang River (QTR) in Zhejiang Province, and the upper section of the Mekong River (MKR) in Xishuangbanna prefecture in China (**Figure 1**). These regions are ideal intermediate-sized systems (i.e., within a drainage basin) for our study with spatial extent ranging between 168 and 311 km. The study regions located in different climate zones: ITR, QTR and MKR in temperate arid climate, subtropical monsoon climate and tropical monsoon climate, respectively (Wang et al., 2012; Ding et al., 2017; Chen et al., 2019). They are also evidently different in human land use characteristics. We focus our investigation on streams ranging from first to fourth Strahler orders. We classified orders 1–2 as headwater (mean geographical distances between sites were 130, 72, and 85 km in the ITR, QTR, and MKR regions, respectively) sites and orders 3-4 as downstream (mean geographical distances between sites were 115, 80, and 79 km in the ITR, QTR, and MKR regions, respectively), sites (Henriques-Silva et al., 2019). We selected the same number of headwater ($n = 15$) and downstream ($n = 15$) sites within each region based on two restrictions: (1) we included sites where both macroinvertebrates and diatoms were collected, and (2) we included headwater sites that had the highest position in the river network, and downstream sites that had the lowest position in the river network to distinguish between different-sized streams as well as possible. For example, in the QTR region, we included all ($n = 14$) orders 1, and the order 2 with the narrowest wetted width. After the selection procedure, headwater sites were significantly ($p < 0.0001$) narrower and shallower than downstream sites within each region (**Table 1**). We conducted all analyses using only the selected sites in each region (**Figure 1**).

Environmental Variables

Chemical and physical data – We measured physical habitat and water chemical data from local scale for each site. These environmental data were measured simultaneously with the collection of macroinvertebrates and diatoms. We used a METTLER TOLEDO meter (model SG23, Mettler) to measure water temperature (WT), pH, total dissolved solids (TDS) and conductivity (Cond) *in situ*. We used a portable meter HI93752 (Hanna, Italy) to measure calcium (Ca^{2+}) and magnesium (Mg^{2+}) concentrations. We measured mean channel width and water depth on transects with equal distance interval across channel sections (Song et al., 2009). We also estimated the percentages of different substrate categories (i.e., % sands, % gravels, % cobbles and % boulders) (Wolman, 1954; Kondolf, 1997). Prior to the field measurements and biotic sampling, we collected one 500 ml water sample at each riffle and stored them in a portable refrigerator at < 4°C. In the laboratory, we analyzed these samples for total nitrogen (TN), total phosphorus (TP), ammonia nitrogen (NH_4-N), phosphate (PO_4-P) contents and determined the potassium permanganate index (COD_{Mn}).

Land use and climate data - We followed Chen et al. (2015) to delineate the watershed boundaries for each site using the Multi-Watershed Delineation Tool and ArcGIS 9.3 software (Esri, Redlands, CA, USA) with 30-m resolution digital elevation models provided by the Chinese Academy of Sciences (http://www.cnic.cn/). We then included a digital land-use raster layer provided by GLOBELAND30 (http://www.globallandcover.com/) to estimate the percentages of three land-use types (i.e., % forest, % farmland, and % urban) within each watershed. We also used 19 bioclimatic variables available in the WorldClim database (http://www.worldclim.org/), at a resolution of 2.5' (∼25 km^2). These variables included data about annual trends (e.g., mean annual temperature and annual precipitation), seasonality (e.g., annual range in temperature and precipitation) and climatic extremes (e.g., temperature of the coldest and warmest month). In addition, because elevation is closely related to annual mean temperature (Pearson coefficients were 0.92, 0.89, and 0.84 in the ITR, QTR and MKR regions, respectively), we considered elevation as a climate variable. Elevation was documented with a Garmin eTrex GPS device. We considered human land use and natural climatic variables as "basin-scale" variables comparatively, relative to the "local-scale" variables. All environmental variables are provided in the **Supplementary Material Data Sheet 1**.

Biotic Sampling

Benthic macroinvertebrates and diatoms were collected simultaneously from a 100 m-long reach at each sampling site in ITR in March 2013, in QTR in April 2010 and in MKR in June 2013. We collected macroinvertebrates using a Surber-net (30 × 30 cm, 250 μm mesh size) from three riffles and two pools with a total of 0.45 m^2 sampling area (Chen et al., 2019). All Surber net samples were combined into one composite sample and preserved in 10% buffered formalin. In the laboratory, macroinvertebrate individuals were sorted, counted and identified to the lowest practical taxonomic level, in most case to genus (>75% of taxa, Morse et al., 1994). Presence-absence data for macroinvertebrates are provided in the **Supplementary Material Data Sheet 2.**

We collected diatoms from nine transects at each site. Diatoms were scraped off from one coarse substrate particle from a defined area (10.17 cm^2) with a toothbrush and an area delimiter (PVC tube) at each transect. We washed and combined the nine subsamples into a single composite sample, and added distilled water to a constant volume of 500 ml. We then extracted 50 ml out of the 500 ml to a specimen bottle for taxonomic analysis and preserved the sample by adding two ml of 10% formalin. In the laboratory, a total of 500 frustules per sample were identified and counted with a light microscope (Olympus BX41TF) at 1,000 × magnification. All diatom individuals were identified to the

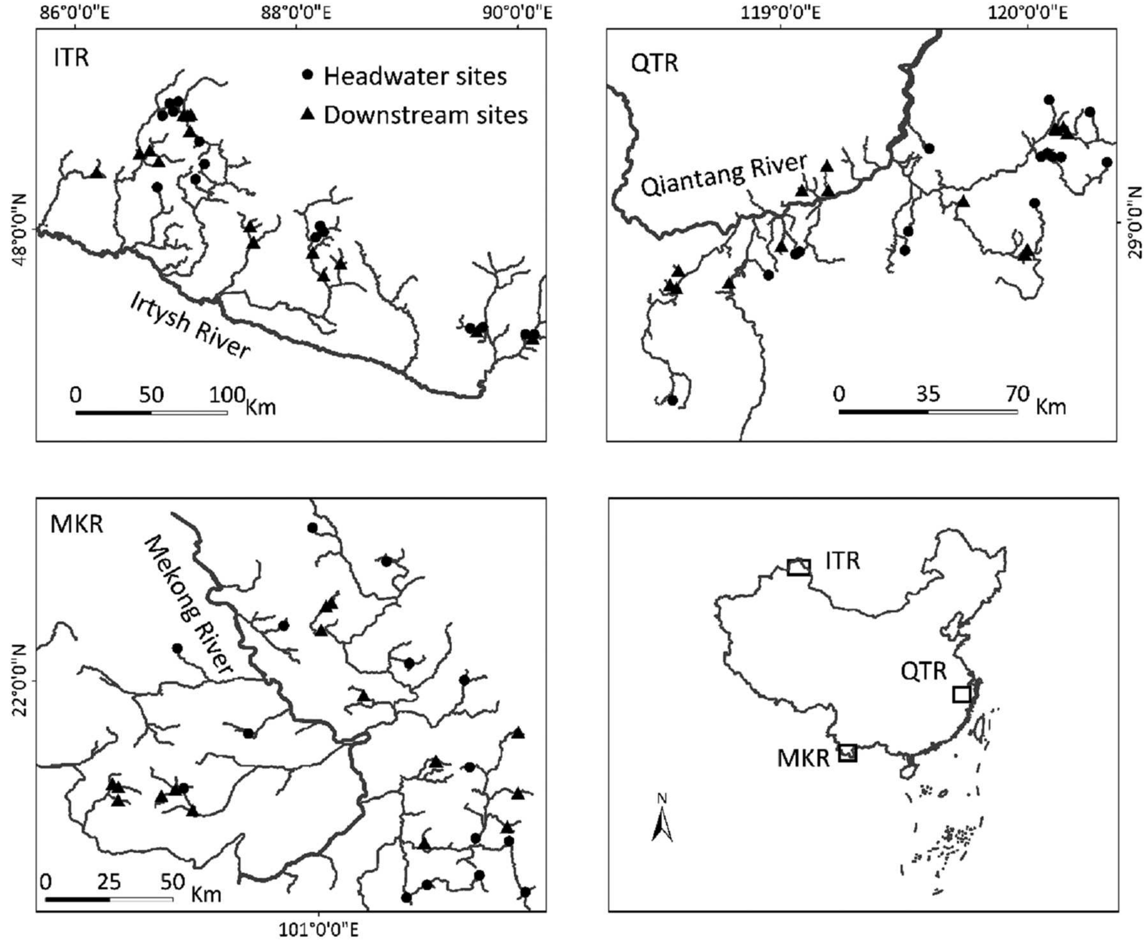

FIGURE 1 | Geographic locations of sampling site in three regions in China: the Irtysh River (ITR) in Xijiang autonomous region, the middle section of Qiantang River (QTR) in Zhejiang Province, and the upper section of the Mekong River (MKR) in Xishuangbanna prefecture.

TABLE 1 | Comparison of wetted width and water depth (mean ± standard deviation) between headwater and downstream sites in three regions in China: the Irtysh River (ITR) in Xijiang autonomous region, the middle section of Qiantang River (QTR) in Zhejiang Province, and the upper section of the Mekong River (MKR) in Xishuangbanna prefecture.

Variable	Region	Headwater	Downstream	Test
Wetted width (m)	ITR	1.53 (± 1.09)	5.35 (± 2.97)	$t = 6.07$, $p < 0.0001$
	QTR	1.52 (± 0.65)	6.58 (± 5.05)	$t = 5.07$, $p < 0.0001$
	MKR	1.63 (± 0.66)	5.99 (± 2.47)	$t = 7.34$, $p < 0.0001$
Water depth (cm)	ITR	12.54 (± 5.46)	22.52 (± 10.85)	$t = 9.42$, $p < 0.0001$
	QTR	15.64 (± 7.58)	36.58 (± 15.42)	$t = 8.94$, $p < 0.0001$
	MKR	9.81 (± 5.17)	16.66 (± 8.60)	$t = 9.30$, $p < 0.0001$

species level (Krammer and Lange-Bertalot, 1986, 1988, 1991a,b; Krammer, 2003). Presence-absence data for diatoms are provided in the **Supplementary Material Data Sheet 3**.

Spatial Distance Metrics

We calculated geographical distances using straight-line distances between each pair of sites in two-dimensional space. The geographical distances were calculated using the Analysis/Proximity/Point distance tool in ArcGIS 9.3 software. However, some studies have recommended for the use of other spatial distances, such as watercourse and topographic distances instead of geographical distances in stream ecosystem (e.g., Brown and Swan, 2010; Cañedo-Argüelles et al., 2015). But, as these different distances were highly correlated (e.g., Mantel coefficients of geographical distances on watercourse distances are 0.81, 0.92, and 0.78 in the ITR, QTR, and MKR regions, respectively), in each of three basins of our study, we opted to use simple horizontal geographical distance here.

Environmental Heterogeneity

We used an analysis of homogeneity of group dispersions (PERMDISP; Anderson, 2006) to test the possible differences in the degree of environmental heterogeneity among the three river regions. We calculated mean dispersions of environmental variables across streams within a region (mean distances of sites (streams) to group (a region) centroid) as a measure of environmental variability. Prior to PERMDISP analysis, we standardized each environmental variable to mean = 0 and standard deviation = 1 using the "scale" function in R. We tested for among-group differences in the distance from the observations to their group centroid using ANOVA F-statistic with 1,000 permutations and, where significant, tested for between-group differences with Tukey's HSD test (R function Tukey-HSD). Analyses were conducted for the environment as a whole and separately for each of three environmental groups (local environmental variables, land use and climate). We conducted the PERMDISP analysis using the "betadisper" function in vegan R package (Oksanen et al., 2013; R. Core Team, 2018).

Distance-Decay Relationships

We applied distance-decay relationships (DDRs) to reveal which drivers of metacommunity assembly are most associated with macroinvertebrates and diatoms in headwater and downstream sites and the whole network. If the NPH was clearly supported, we would find significant relationship between community dissimilarity and environmental distance in both headwater and downstream sites, but significant relationship between community dissimilarity and geographical distance only in downstream sites due to mass effect (Brown and Swan, 2010). We calculated the dissimilarity index using Sørensen coefficients (Legendre and Legendre, 2012) based on presence-absence data. We also calculated the dissimilarity index using Bray-Curtis coefficients based on abundance data (see results in **Table S1**). Although we also separated total dissimilarities into replacement and nestedness components (Baselga, 2010), we showed only results from using total dissimilarities as replacement components were the dominant ones in our data. We calculated the environmental Euclidean distance between each pair of sites using the best subset of explanatory variables (e.g., local environmental, climatic and land use variables) selected in BIO-ENV analysis (Clarke and Ainsworth, 1993; Astorga et al., 2012). The BIO-ENV analysis provides predictors that decrease random variation in environmental distance calculation and produce the highest correlation between environmental distance matrix and community dissimilarity matrix. We conducted the BIO-ENV analysis using the vegan package (Oksanen et al., 2013). We normalized all environmental variables (except pH) using log, square-root or centered log ratio (i.e., land-use and substrata data) transformations if necessary. Prior to BIO-ENV analysis, we removed variables that were highly correlated with other variables (Pearson $r > 0.8$). We then used the multiple regression on distance matrices (MRM) to test the relative importance of the environmental and geographical distances on biological community dissimilarities using ecodist package (Goslee and Urban, 2007). MRM analysis is a highly useful modeling approach in analyzing community variation because it can be used to investigate multiple relationships (e.g., linear or non-linear) between distance-based matrices (Lichstein, 2007). We used a backward selection procedure to progressively eliminate non-significant ($P > 0.05$) matrices from the models (see Tonkin et al., 2017 for a similar approach) and tested the significance of R^2 values with 10,000 permutations. Because MRM analysis may not be efficient to account for the collinearity between environmental and geographical distances, we used the linear mixed effect model (LME) to address such a potential problem (Sarremejane et al., 2017; He et al., 2020). However, the determination coefficients (R^2_β) obtained from LME analysis (**Table S2**) and the standardized coefficients obtained from MRM analysis (**Table 2**) are highly similar. A more detailed description of the LME analysis is provided in the **Supplementary Material Text S1**. Finally, to evaluate the relative importance of local-scale vs. basin-scale environmental control, we calculated the ratio between local R^2_β and basin R^2_β (that is, local-scale environmental/basin-scale environmental effect ratio) rather than their absolute values. Here, basin R^2_β equals the sum of land use R^2_β and climate R^2_β.

RESULTS

Taxa Richness

We identified a total of 219 macroinvertebrate and 206 diatom taxa from three regions (Supporting material data). Macroinvertebrate richness pattern across three basins differed notably from diatoms as ITR had the lowest total macroinvertebrate taxa richness of 60 with a mean of 17 (± 5, standard deviation) per site, whereas both QTR and MKR had two times greater total richness of 146 and 153 taxa with averages of 31 (± 21) and 40 (± 17) per site, respectively. For diatoms, the QTR had the lowest total richness of 78 with a mean of 15 (± 7) taxa per site, whereas both MKR and ITR had higher richness of 108 taxa with a mean of 19 (± 11) per site and 107 taxa with average 21 (± 10) per site, respectively.

Environmental Heterogeneity

Environmental heterogeneity varied significantly among the three regions based on PERMDISP analysis (the whole environment, local environment, land use and climate, **Figure 2**). The whole environmental heterogeneity, local environmental heterogeneity and land-cover heterogeneity were the highest in the QTR region, intermediate in the MKR region and the lowest in the ITR region (**Figure 2**). However, climatic heterogeneity was the highest in the ITR region, intermediate in the QTR region and the lowest in the MKR region (**Figure 2**).

Distance-Decay Relationships

At the whole network level, the relationships between community dissimilarities and environmental distances were significant, but differed in their strength among regions (**Table 2**, **Figure 3**). The QTR had the highest values of the coefficients of determination

TABLE 2 | Final modeling results of multiple regression of distance matrices (MRM) analyses between community dissimilarity and explanatory distance matrices (environmental and geographical distance) for stream macroinvertebrates and diatoms in the ITR, QTR, and MKR regions, based on 10,000 permutations.

Taxon	Region	Stream type	Standardized Coefficients					Full model	
			Intercept	Local environment	Climate	Land use	Geographical	R^2	F
Macroinvertebrates	ITR	Whole network	0.32	0.34***	0.32***	–	–	0.29	89.85***
		Headwater	0.26	0.38***	0.33**	–	–	0.31	22.60**
		Downstream	0.32	0.55***	–	–	–	0.30	44.54**
	QTR	Whole network	0.34	0.17**	0.20***	0.58***	–	0.73	383.58***
		Headwater	0.30	0.41**	0.44 **	–	–	0.58	71.42***
		Downstream	0.27	0.58***	–	–	–	0.36	58.27***
	MKR	Whole network	0.35	0.43***	–	0.34**	–	0.49	210.09***
		Headwater	0.33	0.28*	–	0.64***	–	0.76	161.93***
		Downstream	0.41	–	–	–	0.38***	0.14	17.46***
Diatoms	ITR	Whole network	0.39	0.34**	0.17**	–	–	0.18	47.27**
		Headwater	0.33	0.41***	0.46***	–	–	0.37	30.12***
		Downstream	0.40	0.59**	–	–	–	0.35	55.94**
	QTR	Whole network	0.39	0.41***	–	0.32***	–	0.47	189.20***
		Headwater	0.30	0.60***	–	–	–	0.36	58.44**
		Downstream	0.33	0.41**	–	–	–	0.18	21.85**
	MKR	Whole network	0.43	0.34***	–	–	0.28***	0.21	58.02***
		Headwater	0.56	–	0.39**	–	–	0.15	18.50**
		Downstream	0.45	0.52***	–	–	–	0.27	38.29***

*Analyses were conducted for the whole network and separately for headwater and downstream sites. - represents matrix not included in the final model. Four explanatory matrices are local environmental, climatic, land use, and geographical distance matrices. ***P < 0.001; **P < 0.01; *P < 0.05.*

(R^2_β), followed by MKR and ITR (**Figure 3**). Geographical distance was important for diatoms only in the MKR region (**Table 2**). The environmental effects were generally higher in macroinvertebrates than diatoms (**Figure 3**), and significantly higher at the basin scale (ANOVA, $F_{1,6} = 14.636$, $P = 0.009$, **Table S3**).

Environmental distances were related with community dissimilarities in both headwater and downstream sites (except the case of macroinvertebrates in MKR downstream sites, see **Table 2**), thus generally agreeing with NPH prediction about environmental control. However, significant relationship between geographical distance and community dissimilarity was found in downstream sites only in the MKR region and for macroinvertebrates. Thus, these results partly disagree with the general predictions of NPH as we did not find consistent support for spatial distance decay in downstream sites for both taxa groups and for all regions.

The Relative Role of Local-Scale Environmental and Basin-Scale Environmental Controls

The ratios between local-scale environmental effect and basin-scale environmental effect were consistently higher in diatom communities regardless of the region (9.7 in ITR, 1.7 in QTR, 3.8 in MKR) than in macroinvertebrate communities (1.1 in ITR, 0.1 in QTR, 1.2 in MKR, **Figure 4**).

DISCUSSION

We found that the relative role of environmental control on community variation differed among three regions. These among-region differences were likely related to the variation in the degree of environmental heterogeneity. We further found that communities were exclusively controlled by environment in both headwater and downstream sites (except for one case), giving no consistent support for the general predictions of the NPH. Moreover, our results showed that diatom communities were more influenced by local-scale relative to basin-scale environmental filtering while the opposite was true for macroinvertebrate communities. This suggests that the difference in the ability to track environmental variation between macroinvertebrates and diatoms was most probably scale-dependent.

Comparison of Environmental Filtering Among Regions

In this study, the level of environmental control on community variation was the highest in the region with the highest environmental heterogeneity. We also found that the QTR region exhibited the highest and most significant land-cover control, whereas the ITR region exhibited the most significant climatic control. Such a finding may arise because the degree of land use heterogeneity was the highest in the QTR region, while the degree of climatic heterogeneity was the highest in the ITR region. Because the QTR region has experienced

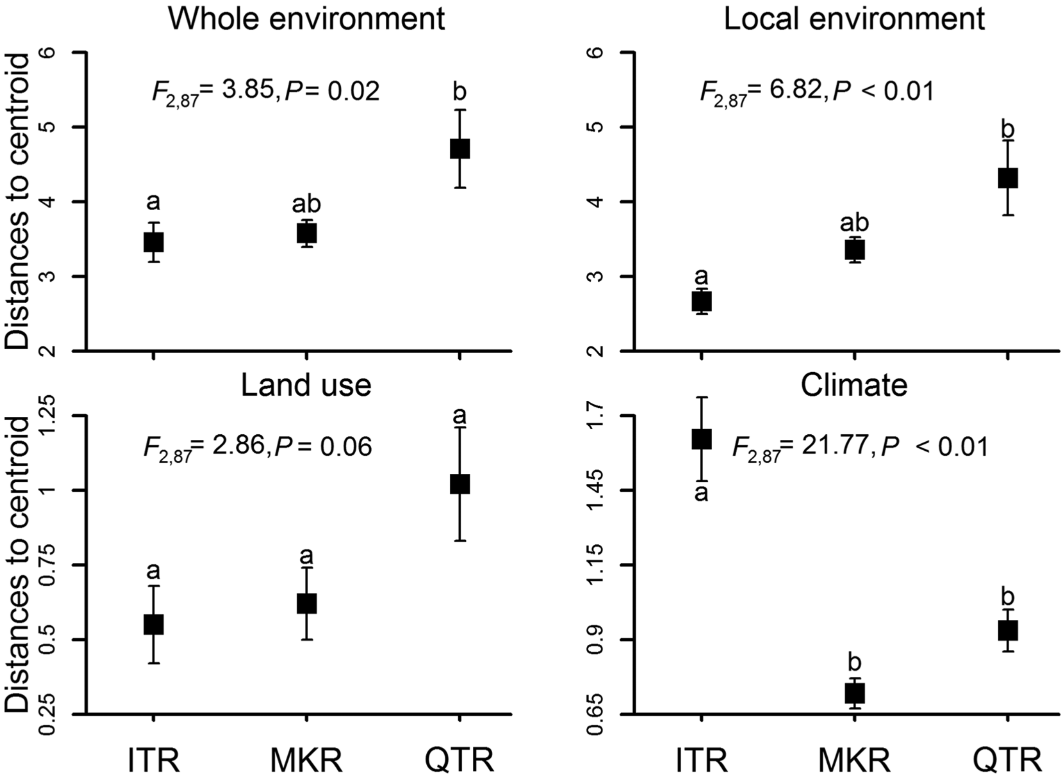

FIGURE 2 | Average distances to centroid for sampled stream sites for the three study regions. Analyses were conducted for the environment as a whole and separately for each of three environmental groups (local environment, land use and climate) at the whole network level. Square symbols represent averages and error bars denote the standard error. Different letters represent significant differences between regions according to the Tukey's HSD test.

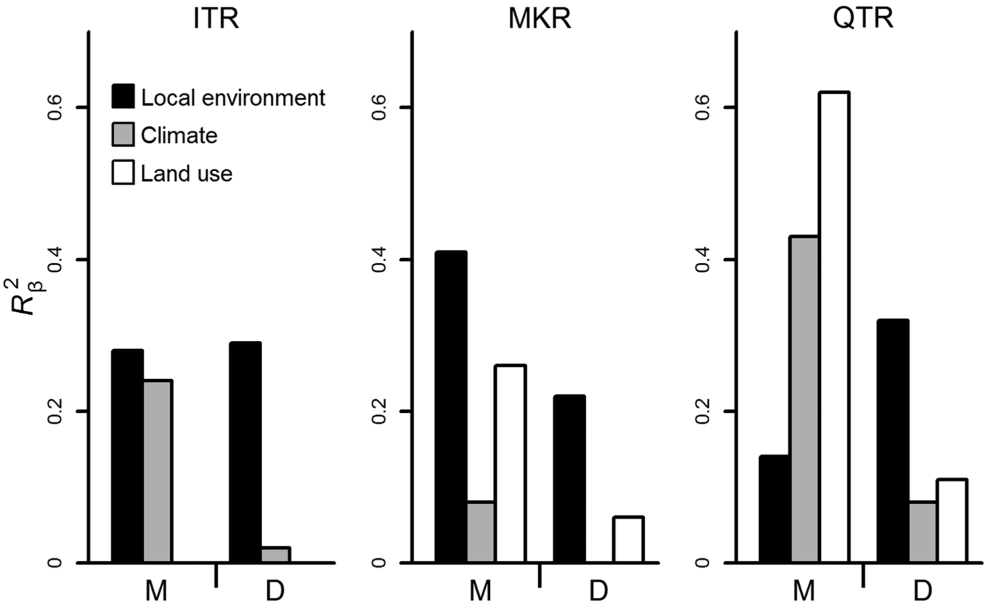

FIGURE 3 | Strength of relationship between community dissimilarities and environmental (local environmental, climatic, and land use) distances calculated using the coefficient of determination (R^2_β, y axis) for diatoms and macroinvertebrates in the three regions. Analyses were conducted at the whole network level. Abbreviations below axis are as follows. ITR, the Irtysh River in Xijiang autonomous region; QTR, the middle section of Qiantang River in Zhejiang Province; MKR, the upper section of the Mekong River in Xishuangbanna prefecture; M, Macroinvertebrates; D, Diatoms.

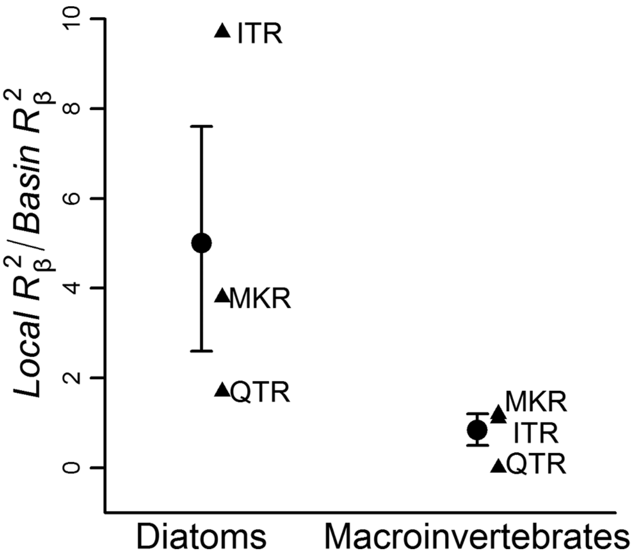

FIGURE 4 | The ratio between local-scale environmental effect and basin-scale environmental effect (Local R_β^2/Basin R_β^2, on y axis) for diatom vs. macroinvertebrate communities in the three regions. Analyses were conducted at the whole network level. Triangles represent individual regions; circular symbols represent averages and error bars denote the standard error. For region abbreviations, see **Figure 3**.

significant changes in land-use such as a dramatic decline in forests and an increase in farmland and urban land use during the last several decades (Wang et al., 2012), the QTR region covered large within-watershed land use gradients (e.g., 24–100% forested watershed land use). However, compared with the QTR and MKR regions, the ITR region covered larger spatial extent, and consequently, had higher climatic heterogeneity. Therefore, our results indicated that the importance of environmental filtering varied among regions with different level of environmental heterogeneity. Generally, heterogeneous environmental conditions offer more niche opportunities for species, thus elevating local and regional diversity if species dispersal is not limiting diversity (Heino et al., 2015b). Therefore, such environmental heterogeneity increases the role of environmental filtering (Leibold et al., 2004; Heino et al., 2015b).

Several studies have indicated only a weak influence of the level of environmental heterogeneity on environmental filtering (Landeiro et al., 2012; Grönroos et al., 2013; Bini et al., 2014; Heino et al., 2015a). However, the fact that we found a difference in the degree of environmental control among regions with different environmental heterogeneity may be related to at least two unique features of our study design: (1) In contrast to most studies that capture few environmental variables, our suite of 40 explaining variables including local environmental, climatic and land use factors (**Tables S4**, **S5**) may perhaps better reflect the true differences in environmental heterogeneity faced by the stream biota. (2) Unlike other studies that use an ecoregion (e.g., across multiple basins, Bini et al., 2014) as the metacommunity unit, we used a drainage basin as the unit of observation. In a relative sense, dispersal rates generally decrease with spatial extent (stream > basin > ecoregion). Dispersal rate among sites within a basin was probably adequate for species to track environmental variation across sites, resulting in strong environmental filtering but weak dispersal-related controls (Heino et al., 2015b,c). This was implied by the fact that the relationship between community dissimilarity and geographical distance was non-significant in most cases (**Table 2**), suggesting a generally weak effect of dispersal limitation but also that mass effects were not influential.

NPH Predictions

Consistent with recent stream studies (Schmera et al., 2018; Henriques-Silva et al., 2019), our results indicated that the NPH predictions cannot be regarded as general hypotheses in stream networks. We found that community dissimilarities in both headwater and downstream sites were significantly related solely to environmental distances, but not geographical distances. Therefore, general support for NPH predictions was basically lacking because mass effects were not strong enough in downstream sites. There are several reasons and evidence for a lack of mass effects on downstream metacommunities here. First, dispersal rate among sites was most probably relatively modest in our study regions due to intermediate extent, which resulted in strong environmental filtering (Ng et al., 2009; Heino et al., 2015c). Second, in half of the cases, downstream metacommunities were less connected than headwater metacommunities (**Table S5**), which decreases the importance of mass effects on downstream metacommunities. Third, only in half of the cases, community turnover was significantly ($p < 0.001$) higher at downstream sites than at headwater sites (**Table S6**), suggesting that beta diversity of downstream communities was only relatively weakly influenced by mass effects that should generally homogenize communities across sites (Jamoneau et al., 2018).

Environmental Control of Macroinvertebrates vs. Diatoms

Our MRM analyses showed that the level of environmental control was in general higher for macroinvertebrates than diatoms. Such a difference between macroinvertebrates and diatoms in the relative roles of environment in shaping communities across the same set of stream sites was also observed by Heino et al. (2012). Diatoms are more likely to have higher dispersal rates among sites than macroinvertebrates due their short life cycles and to being easily transported by a wide variety of vectors (e.g., wind, stream flow and animals, Kristiansen, 1996). Thus, diatoms can be often present in environmentally sub-optimal sites due to intense dispersal from environmentally suitable sites (mass effects). This may lead to a lower importance of environmental controls and a higher importance of spatial controls (Rouquette et al., 2013; Vilmi et al., 2017). Concordantly, in the MKR region, spatial control was significantly important for diatoms but not for macroinvertebrates.

An alternative explanation for this pattern is that most of macroinvertebrates (e.g. aquatic insects) can often actively select environmentally suitable habitats via dispersal (Heino, 2013). Therefore, macroinvertebrates may be able to track environmental variation well-through active dispersal within our studied regions (e.g., in the ITR and QTR regions) and show stronger environmental filtering than diatoms (Farjalla et al., 2012).

However, when analyzing environmental factors more closely, we found diatom assemblages to be more related with local-scale environmental factors relative to basin-scale environmental factors while the opposite was true for macroinvertebrates. These findings indicate that diatoms are possibly better able to track local environmental variation e.g., in nutrients or water pH than macroinvertebrates, whereas macroinvertebrates are better able to track environmental variability at larger basin scale (e.g., climatic or land cover variables, physical stream variables) than diatoms. This result is congruent with earlier stream studies (Urban et al., 2006; Soininen, 2007; Liu et al., 2016). We recommend that further research aiming to compare environmental structuring of different organism groups should encompass multi-scale (e.g., local scale and basin scale) environmental variables, particularly at intermediate or large spatial extents (e.g., within a basin and across basin extents, Jyrkänkallio-Mikkola et al., 2017). Our results may thus have practical implications for stream monitoring programmes. For example, if alterations in watershed land use by agriculture or forestry are the main stressors, then macroinvertebrates might be recommended as the biological indicators. This is especially true if such land use effects modify physical structure of the streams via habitat modification or increased sediment load, for example.

Possible Caveats

Our results may have been affected also by some other factors such as biotic interactions not directly considered here. For example, we found that diatom community composition was significantly linked to macroinvertebrate community composition when correcting for both environmental and geographical distances in the QTR and MKR regions (**Figure S1**). This result suggests that in the QTR and MKR regions, availability of diatoms as prey may have influenced macroinvertebrate communities and grazing by macroinvertebrates may have influenced diatom communities.

A second factor may stem from seasonal and interannual biases in communities and community-environment relationships as three data sets were collected in different months. To facilitate the identification to the lowest possible level, we collected macroinvertebrates in spring season in the MKR and QTR regions as spring is the time when most macroinvertebrates are still in the larval stage but close to their maximum size. However, because of icebound waters during the spring season in the ITR region, sampling was conducted in summer season in the ITR region. Moreover, because of the large geographical extent among three regions, sampling of three regions was not possible in single year due to limited resources. However, metacommunity assembly is expected to be temporally relatively stable in perennial river systems (Sarremejane et al., 2017; Csercsa et al., 2019), such as in streams studied here. We thus believe that our main conclusions of macroinvertebrate metacommunity assembly may have been only little affected by the seasonal effects.

CONCLUSIONS

Our study suggested that environmental filtering generally overrode dispersal-related factors in stream networks and was most important in the regions characterized with high environmental heterogeneity. However, as the number of regions in our study was limited, future studies should include more regional datasets to obtain more general conclusions. Additionally, we found only weak evidence of the NPH predictions across different regions and organisms suggesting that environmental filtering prevailed throughout the river networks. Finally, we showed that diatoms and macroinvertebrates perceive their environment at different scales most probably because of their fundamental biological differences. To summarize, even if environmental filtering is generally strong on stream metacommunities, these results support a view suggesting that metacommunity assembly is relatively context-dependent, potentially related to the degree of environmental heterogeneity, biological characteristics of the focal organismal group and spatial extent.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary materials, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

SH and BW conceived the ideas. SH, KC, and BW analyzed the data. SH, JS, and BW led the writing. All authors contributed to the writing of the paper.

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REFERENCES

Anderson, M. J. (2006). Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* 62, 245–253. doi: 10.1111/j.1541-0420.2005.00440.x

Astorga, A., Oksanen, J., Luoto, M., Soininen, J., Virtanen, R., and Muotka, T. (2012). Distance decay of similarity in freshwater communities: do macro- and microorganisms follow the same rules? *Global Ecol. Biogeogr*. 21, 365–375. doi: 10.1111/j.1466-8238.2011.00681.x

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecol. Biogeogr*. 19, 134–143. doi: 10.1111/j.1466-8238.2009.00490.x

Bini, L. M., Landeiro, V. L., Padial, A. A., Siqueira, T., and Heino, J. (2014). Nutrient enrichment is related to two facets of beta diversity for stream invertebrates across the United States. *Ecology* 95, 1569–1578. doi: 10.1890/13-0656.1

Brown, B. L., Sokol, E. R., Skelton, J., and Tornwall, B. (2017). Making sense of metacommunities: dispelling the mythology of a metacommunity typology. *Oecologia* 183, 643–652. doi: 10.1007/s00442-016-3792-1

Brown, B. L., and Swan, C. M. (2010). Dendritic network structure constrains metacommunity properties in riverine ecosystems. *J. Anim. Ecol*. 79, 571–580. doi: 10.1111/j.1365-2656.2010.01668.x

Cañedo-Argüelles, M., Boersma, K. S., Bogan, M. T., Olden, J. D., Phillipsen, I., Schriever, T. A., et al. (2015). Dispersal strength determines meta-community structure in a dendritic riverine network. *J. Biogeogr*. 42, 778–790. doi: 10.1111/jbi.12457

Chen, K., Hughes, R. M., and Wang, B. (2015). Effects of fixed-count size on macroinvertebrate richness, site separation, and bioassessment of Chinese monsoonal streams. *Ecol. Indic*. 53, 162–170. doi: 10.1016/j.ecolind.2015.01.011

Chen, K., Sun, D., Rajper, A. R., Mulatibieke, M., Hughes, R. M., Pan, Y., et al. (2019). Concordance in biological condition and biodiversity between diatom and macroinvertebrate assemblages in Chinese arid-zone streams. *Hydrobiologia* 829, 245–263. doi: 10.1007/s10750-018-3836-0

Clarke, K. R., and Ainsworth, M. (1993). A Method of linking multivariate community structure to environmental variables. *Mar. Ecol. Prog. Ser*. 92, 205–219. doi: 10.3354/meps092205

Csercsa, A., Krasznai, E. Á., Várbíró, G., Szivák, I., Tóth, M., et al. (2019). Seasonal changes in relative contribution of environmental control and spatial structuring on different dispersal groups of stream macroinvertebrates. *Hydrobiologia* 828, 101–115. doi: 10.1007/s10750-018-3806-6

De Bie, T., De Meester, L., Brendonck, L., Martens, K., Goddeeris, B., Ercken, D., et al. (2012). Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. *Ecol. Lett*. 15, 740–747. doi: 10.1111/j.1461-0248.2012.01794.x

Ding, N., Yang, W., Zhou, Y., Gonzalez-Bergonzoni, I., Zhang, J., Chen, K., et al. (2017). Different responses of functional traits and diversity of stream macroinvertebrates to environmental and spatial factors in the Xishuangbanna watershed of the upper Mekong River Basin, China. *Sci. Total Environ*. 574, 288–299. doi: 10.1016/j.scitotenv.2016.09.053

Eros, T. (2017). Scaling fish metacommunities in stream networks: synthesis and future research avenues. *Commun. Ecol*. 18, 72–86. doi: 10.1556/168.2017.18.1.9

Eros, T., and Lowe, W. H. (2019). The landscape ecology of rivers: from patch-based to spatial network analyses. *Curr. Landsc. Ecol. Rep*. 4, 103–112. doi: 10.1007/s40823-019-00044-6

Farjalla, V. F., Srivastava, D. S., Marino, N. A., Azevedo, F. D., Dib, V., Lopes, P. M., et al. (2012). Ecological determinism increases with organism size. *Ecology* 93, 1752–1759. doi: 10.1890/11-1144.1

Goslee, S. C., and Urban, D. L. (2007). The ecodist package for dissimilarity-based analysis of ecological data. *J. Stat. Softw*. 22, 1–19. doi: 10.18637/jss.v022.i07

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.00141/full#supplementary-material

Grönroos, M., Heino, J., Siqueira, T., Landeiro, V. L., Kotanen, J., and Bini, L. M. (2013). Metacommunity structuring in stream networks: roles of dispersal mode, distance type, and regional environmental context. *Ecol. Evol*. 3, 4473–4487. doi: 10.1002/ece3.834

He, S. W., Soininen, J., Deng, G. P., and Wang, B. X. (2020). Metacommunity structure of stream insects across three hierarchical spatial scales. *Ecol. Evol*. 10, 2874–2884. doi: 10.1002/ece3.6103

Heino, J. (2013). Environmental heterogeneity, dispersal mode, and co-occurrence in stream macroinvertebrates. *Ecol. Evol*. 3, 344–355. doi: 10.1002/ece3.470

Heino, J., Grönroos, M., Soininen, J., Virtanen, R., and Muotka, T. (2012). Context dependency and metacommunity structuring in boreal headwater streams. *Oikos* 121, 537–544. doi: 10.1111/j.1600-0706.2011.19715.x

Heino, J., Melo, A. S., and Bini, L. M. (2015b). Reconceptualising the beta diversity-environmental heterogeneity relationship in running water systems. *Freshw. Biol*. 60, 223–235. doi: 10.1111/fwb.12502

Heino, J., Melo, A. S., Bini, L. M., Altermatt, F., Al-Shami, S. A., Angeler, D. G., et al. (2015a). A comparative analysis reveals weak relationships between ecological factors and beta diversity of stream insect metacommunities at two spatial levels. *Ecol. Evol*. 5, 1235–1248. doi: 10.1002/ece3.1439

Heino, J., Melo, A. S., Siqueira, T., Soininen, J., Valanko, S., and Bini, L. M. (2015c). Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. *Freshw. Biol*. 60, 845–869. doi: 10.1111/fwb.12533

Heino, J., Soininen, J., Alahuhta, J., Lappalainen, J., and Virtanen, R. (2017). Metacommunity ecology meets biogeography: effects of geographical region, spatial dynamics and environmental filtering on community structure in aquatic organisms. *Oecologia* 183, 121–137. doi: 10.1007/s00442-016-3750-y

Henriques-Silva, R., Logez, M., Reynaud, N., Tedesco, P. A., Brosse, S., Januchowski-Hartley, S. R., et al. (2019). A comprehensive examination of the network position hypothesis across multiple river metacommunities. *Ecography* 42, 284–294. doi: 10.1111/ecog.03908

Jamoneau, A., Passy, S. I., Soininen, J., Leboucher, T., and Tison-Rosebery, J. (2018). Beta diversity of diatom species and ecological guilds: response to environmental and spatial mechanisms along the stream watercourse. *Freshw. Biol*. 63, 62–73. doi: 10.1111/fwb.12980

Johnson, R. K., Furse, M. T., Hering, D., and Sandin, L. (2007). Ecological relationships between stream communities and spatial scale: implications for designing catchment-level monitoring programs. *Freshw. Biol*. 52: 939–958. doi: 10.1111/j.1365-2427.2006.01692.x

Jyrkänkallio-Mikkola, J., Meier, S., Heino, J., Laamanen, T., Pajunen, V., Tolonen, K. T., et al. (2017). Disentangling multi-scale environmental effects on stream microbial communities. *J. Biogeogr*. 44, 1512–1523. doi: 10.1111/jbi.13002

Kondolf, G. M. (1997). Application of the pebble count: notes on purpose, method, and variants. *J. Am. Water Resour. Assoc*. 33, 79–87. doi: 10.1111/j.1752-1688.1997.tb04084.x

Krammer, K. (2003). "Cymbopleura, delicata, navicymbula, gomphocymbellopsis, afrocymbella," in *Diatoms of Europe, Diatoms of the European Inland Waters and Comparable Habitats, vol. 4*. ed H. Lange-Bertalot (Rugell: A.R.G.Gantner Verlag K.G.), 1–529.

Krammer, K., and Lange-Bertalot, H. (1986). *Bacillariophyceae, Teil 1 Naviculaceae*. Heidelberg: Spektrum Akademischer Verlag.

Krammer, K., and Lange-Bertalot, H. (1988). *Bacillariophyceae, Teil 2 Epithemiaceae, Bacillariophyceae, Surirellaceae*. Heidelberg: Spektrum Akademischer Verlag.

Krammer, K., and Lange-Bertalot, H. (1991a). *Bacillariophyceae, Teil 3. Centrales, Fragilariaceae, Eunotiaceae, Achnanthaceae*. Heidelberg: Spektrum Akademischer Verlag.

Krammer, K., and Lange-Bertalot, H. (1991b). *Bacillariophyceae, Teil 4. Achnanthaceae, Kritische ErganzungenzuNavicula (lineolate) Und Gomphonema*. Heidelberg: Spektrum Akademischer Verlag.

Kristiansen, J. (1996). Dispersal by freshwater algae—a review. *Hydrobiologia* 336, 151–157. doi: 10.1007/BF00010829

Landeiro, V. L., Bini, L. M., Melo, A. S., Pes, A. M. O., and Magnusson, W. E. (2012). The roles of dispersal limitation and environmental conditions in controlling caddisfly (Trichoptera) assemblages. *Freshw. Biol.* 57, 1554–1564. doi: 10.1111/j.1365-2427.2012.02816.x

Legendre, P., and Legendre, L. F. J. (2012). *Numerical Ecology*. Boston, MA: Elsevier.

Leibold, M. A., and Chase, J. M. (2017). *Metacommunity Ecology*. Princeton, NJ: Princeton University Press.

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., et al. (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.* 7, 601–613. doi: 10.1111/j.1461-0248.2004.00608.x

Lichstein, J. W. (2007). Multiple regression on distance matrices: a multivariate spatial analysis tool. *Plant Ecol.* 188, 117–131. doi: 10.1007/s11258-006-9126-3

Liu, S., Xie, G., Wang, L., Cottenie, K., Liu, D., and Wang, B. (2016). Different roles of environmental variables and spatial factors in structuring stream benthic diatom and macroinvertebrate in Yangtze River Delta, China. *Ecol. Indic.* 61: 602–611. doi: 10.1016/j.ecolind.2015.10.011

Morse, J. C., Yang, L. F., and Tian, L. X. (1994). *Aquatic Insects of China Useful for Monitoring Water Quality*. Nanjing: Hohai University Press.

Ng, I. S. Y., Carr, C. M., and Cottenie, K. (2009). Hierarchical zooplankton metacommunities: distinguishing between high and limiting dispersal mechanisms. *Hydrobiologia* 619, 133–143. doi: 10.1007/s10750-008-9605-8

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'hara, R. B., et al. (2013). Package 'vegan'. *Community Ecology Package, Version*.

Pan, Y., Stevenson, R. J., Hill, B. H., Herlihy, A. T., and Collins, G. B., (1996). Using diatoms as indicators of ecological conditions in lotic systems: a regional assessment. *J. N. Am. Benthol. Soc.* 15, 481–495.

R. Core Team (2018). *R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing*. (Vienna). Available online at: https://www.R-project.org/

Rouquette, J. R., Dallimer, M., Armsworth, P. R., Gaston, K. J., Maltby, L., and Warren, P. H. (2013). Species turnover and geographic distance in an urban river network. *Divers Distrib.* 19, 1429–1439. doi: 10.1111/ddi.12120

Sarremejane, R., Cañedo-Argüelles, M., Prat, N., Mykrä, H., Muotka, T., and Bonada, N. (2017). Do metacommunities vary through time? Intermittent rivers as model systems. *J. Biogeogr.* 44, 2752–2763. doi: 10.1111/jbi.13077

Schmera, D., Árva, D., Boda, P., Bódis, E., Bolgovics, Á., Borics, G., et al. (2018). Does isolation influence the relative role of environmental and dispersal-related processes in stream networks? An empirical test of the network position hypothesis using multiple taxa. *Freshw. Biol.* 63, 74–85. doi: 10.1111/fwb.12973

Shurin, J. B., Cottenie, K., and Hillebrand, H. (2009). Spatial autocorrelation and dispersal limitation in freshwater organisms. *Oecologia* 159, 151–159. doi: 10.1007/s00442-008-1174-z

Soininen, J. (2007). Environmental and spatial control of freshwater diatoms - A review. *Diatom Res.* 22, 473–490. doi: 10.1080/0269249X.2007.970572

Soininen, J. (2014). A quantitative analysis of species sorting across organisms and ecosystems. *Ecology* 95, 3284–3292. doi: 10.1890/13-2228.1.sm

Song, M. Y., Leprieur, F., Thomas, A., Lek-Ang, S., Chon, T. S., and Lek, S. (2009). Impact of agricultural land use on aquatic insect assemblages in the Garonne river catchment (SW France). *Aquatic Ecol.* 43, 999–1009. doi: 10.1007/s10452-008-9218-3

Tonkin, J. D., Tachamo Shah, R. D., Shah, D. N., Hoppeler, F., Jähnig, S. C., and Pauls, S. U. (2017). Metacommunity structuring in Himalayan streams over large elevational gradients: the role of dispersal routes and niche characteristics. *J. Biogeogr.* 44, 62–74. doi: 10.1111/jbi.12895

Urban, M. C., Skelly, D. K., Burchsted, D., Price, W., and Lowry, S. (2006). Stream communities across a rural–urban landscape gradient. *Divers. Distrib.* 12: 337–350. doi: 10.1111/j.1366-9516.2005.00226.x

Vilmi, A., Tolonen, K. T., Karjalainen, S. M., and Heino, J. (2017). Metacommunity structuring in a highly-connected aquatic system: effects of dispersal, abiotic environment and grazing pressure on microalgal guilds. *Hydrobiologia* 790, 125–140. doi: 10.1007/s10750-016-3024-z

Wang, B. X., Liu, D. X., Liu, S. R., Zhang, Y., Lu, D. Q., and Wang, L. Z. (2012). Impacts of urbanization on stream habitats and macroinvertebrate communities in the tributaries of Qiangtang River, China. *Hydrobiologia* 680, 39–51. doi: 10.1007/s10750-011-0899-6

Winegardner, A. K., Jones, B. K., Ng, I. S. Y., Siqueira, T., and Cottenie, K. (2012). The terminology of metacommunity ecology. *Trends Ecol. Evol.* 27, 253–254. doi: 10.1016/j.tree.2012.01.007

Wolman, M. G. (1954). A method of sampling coarse river-bed material. *Eos Trans. AGU* 35, 951–956. doi: 10.1029/TR035i006p00951

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Spatial and Temporal Ecological Uniqueness of Andean Diatom Communities Are Correlated With Climate, Geodiversity and Long-Term Limnological Change

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High-elevation tropical lakes are excellent sentinels of global change impacts, such as climate warming, land-use change, and atmospheric deposition. These effects are often correlated with temporal and spatial beta diversity patterns, with some local communities contributing more than others, a phenomenon known as local contribution to beta diversity (LCBD) or ecological uniqueness. Microorganisms, such as diatoms, are considered whole-ecosystem indicators, but little is known about their sensitivity and specificity in beta diversity studies mostly because of the lack of large spatial and temporal datasets. To fill this gap, we used a tropical South American diatom database comprising modern (144 lakes) and paleolimnological (6 sediment cores) observations to quantify drivers of spatial and temporal beta diversity and evaluated implications for environmental change and regional biodiversity. We used methods of beta diversity partitioning (replacement and richness components) by determining contributions of local sites to these components (LCBDrepl and LCBDrich), and studied how they are related to environmental, geological, and historical human variables using Generalized Additive Models (GAM). Beta replacement time series were also analyzed with GAM to test whether there is widespread biotic homogenization across the tropical Andes. Modern lake ecological uniqueness was jointly explained by limnological (pH), climatic (mean annual precipitation), and historical human density. Local lake (conductivity) and regional geodiversity variables (terrain ruggedness, soil variability) were inversely correlated to replacement and richness components of LCBD, suggesting that not all lakes contributing to broad-scale diversity are targets for conservation actions. Over millennial time scales, decomposing temporal trends of beta diversity components showed different trajectories of lake diatom diversity as response of environmental change: i) increased hydroclimatic variability (as inferred by decreased temperature seasonality) mediating higher contribution of richness to local beta diversity patterns *ca.* 1000 years ago in Ecuador Andean lakes and ii) lake-specific temporal beta diversity trends for the last *ca*. 200 years, indicating that biotic homogenization is not widespread across the tropical Andes. Our approach for unifying diatom ecology, metacommunity, and paleolimnology can facilitate the understanding of future responses of tropical Andean lakes to global change impacts.

Keywords: diatoms, biotic homogenization, metacommunity, beta diversity components, GAM

INTRODUCTION

Human activities have caused in the past and are currently causing diverse and long-lasting changes in freshwater ecosystems (Vitousek et al., 1997). In mountainous areas, high-elevation lakes are excellent sentinels of current global change and some of the most comparable ecosystems across the world (Catalan and Rondón, 2016). It is widely recognized that predicting how high-elevation lakes will respond to ongoing and future global changes requires a long-term perspective to evaluate recent (last *ca.* 150 years) human-driven impacts and to characterize background natural variability (Mills et al., 2017; Dubois et al., 2018). Biological assemblages accumulate with lake sediments as natural archives, which can be used to understand temporal dynamics of biodiversity and provide insights into the organization of ecological communities and their responses to natural and human-induced drivers (e.g., habitat loss, human impacts, eutrophication) (Willis et al., 2010; Heino et al., 2016). Because lakes are not isolated in the landscape (rather they form a continuum embedded in a terrestrial matrix), researchers have also examined the role of spatial variables in determining biodiversity patterns using paleolimnological approaches (Castillo-Escrivà et al., 2017; Benito et al., 2019). However, contemporary and paleolimnological studies still remain largely disconnected in biodiversity and environmental change research (Gregory-Eaves and Beisner, 2011). One reason for this may be that the application of the metacommunity concept (i.e., set of local communities potentially connected by dispersal of multiple interacting species, Leibold et al., 2004), has so far seldomly been applied over long time scales. Understanding broad-scale biodiversity patterns is necessary, because many environmental pressures operate at large spatial and long temporal scales but interactions with high-elevation lakes at smaller scales (Catalan et al., 2013) are still mostly unexplored.

Spatial variability in species composition between sites (i.e., spatial beta diversity) is particularly well suited for exploring metacommunity structuring, because its components: species replacement and richness difference (species gain and loss), are often correlated with climatic, geological, and limnological gradients (Winegardner et al., 2017; Castro et al., 2019; Szabó et al., 2019). With an index of local contribution to beta diversity (LCBD) it is possible to examine each site's disproportionate contribution to maintaining regional diversity. High LCBD values flag ecologically unique sites where regionally rare taxa, exceptional species richness or unusual combinations of taxa are present (Legendre and De Cáceres, 2013). Both niche-based (i.e., species sorting) and dispersal-based community assembly processes may influence beta diversity patterns, either independently or in combination (Heino, 2013). Thus, it is important to include different metrics of beta diversity and their environmental and spatial correlates to assess biodiversity changes across ecological gradients in a more nuanced way.

In aquatic ecosystems, comparisons of temporal beta diversity between localities may be a fingerprint of environmental variation, for instance, as a measure of acidity changes in boreal lakes (Angeler, 2013) or forest cover in United States lakes (Winegardner et al., 2017). Recent meta-analyses have linked beta diversity loss, increasing trends between assemblages' similarities to reduced environmental heterogeneity due to human actions (Cardinale et al., 2012; McGill et al., 2015). Other studies further indicated that ecosystem function and services, such as carbon storage and food production, could be severely jeopardized by biotic homogenization (Van der Plas et al., 2016). However, patterns prior to intense human occupation remain largely unknown, and a time interval spanning the last 1000 to 2000 years is most appropriate for evaluating the magnitude of recent changes in biodiversity and environmental conditions at regional and global scales (Pages 2k Consortium, 2013).

The tropical Andes is one of the world's richest biodiversity hotspot (Myers et al., 2000). Lakes are ecologically important regional features and also serve as a crucial source of freshwater for millions of people living in the Andes and the adjacent Amazon lowlands (Buytaert et al., 2006). Historically, humans have been an integral part of Andean lake-catchment systems, shaping cultural landscapes by means of agriculture, pastoralism, and deforestation (Sarmiento, 2002). Andean lakes in tropical South America are valuable model systems for examining spatial and temporal beta diversity patterns for several reasons. First, they are well-defined ecosystems, many of which have persisted over long geological time-scales such as lakes Titicaca and Umayo, allowing evolutionary processes (speciation, extinction) to affect biota (Fritz et al., 2012). Second, despite contrasts in the climatic and evolutionary history of various regions, broadly similar ecoregions and communities are present due to the relative tectonic stability of the Andes throughout much of the Neogene (Baker and Fritz, 2015). Third, they are in a topographically diverse landscape characterized by notable spatial variability in geological, geomorphological, soil, and hydrological features, also known as geodiversity (Killeen et al., 2007; Gray, 2008). In the tropical Andes many geodiversity variables are available for studying their influence on biological communities (Antonelli et al., 2018). However, very little is known about how geodiversity and other macroscale environmental gradients, such as climate, relate to beta diversity and its replacement and richness components in mountain lakes.

Biodiversity studies of Neotropical macroorganisms have historically recognized the roles of environmental, climatic, and geological factors in structuring communities at different spatial and temporal scales (Banda et al., 2016), but their influences on microorganisms are not well characterized (Benito and Fritz, 2020). Diatoms, unicellular siliceous algae, are a very species-rich biological group that disperses widely, responds to local (e.g., limnological) and regional (e.g., climatic) variables, has different traits for resource use and resistance to disturbance, and their remains preserve in lake sediments. In addition to their role as whole-ecosystem indicators, diatoms are also particularly useful for evaluating relationships between spatial and temporal beta diversity (Winegardner et al., 2017). Yet, additional exploration of their use in identifying ecologically unique sites and the mechanisms behind spatial and temporal beta diversity is still needed for tropical Andean lakes. This information is crucial as global change intensifies in the Neotropics (Vuille et al., 2003), including local (e.g., agriculture, fish stocking) and regional (e.g., deforestation, damming, land-use) environmental impacts (Van Colen et al., 2017). Hence, studies comparing modern and paleolimnological records are needed to assess which high-elevation lake ecosystems are most sensitive to environmental changes and to evaluate their resilience.

To start filling these knowledge gaps, we used a database of lake diatoms that spans large gradients of latitude, limnology, climate, and topography in the tropical Andes. We estimated LCBD and applied beta diversity partitioning methods, including species replacement and richness difference and the contributions of sites to these components (LCBDrich and LCBDrepl). LCBDrich and LCBDrepl describe how each individual sample contributes to richness gradients and to replacement gradients (Ruhí et al., 2017). To identify spatial beta diversity trends through time, we analyzed diatom paleolimnological assemblages that span the last ∼2000 years using the same partitioning methods with Generalized Additive Models (GAM). Finally, using diatom beta replacement time series we tested the hypothesis that broad-scale environmental changes have an homogenizing effect across large, disconnected lakes; to provide a regional long-term limnological change perspective in the tropical Andes.

MATERIALS AND METHODS

Study Area

Our study lakes are distributed across the tropical Andes (8°N–30°S and 58–79°W) (**Figure 1**). This region encompasses a wide range of physiographic and climatic settings that produce diverse limnological conditions. The investigated lakes occupy a range of high elevations (2500–4500 m a.s.l) and are mostly formed by glacial and/or volcanic processes. The study area has a north-south orientation and is characterized by varied degrees of topographic heterogeneity. Both local and regional climates are influenced by the topographic profile, which creates distinct conditions at both eastern and western flanks (Valencia et al., 2016). Northern Andean lakes in Ecuador and Colombia lie in montane forests, inter-Andean valleys, and páramo ecosystems. Above the tree line (páramo), climatic conditions are characterized by the lack of seasonal changes and cold mean annual temperature. More dry and wet climatic conditions are characteristic of the interandean valleys and montane forests, respectively. In the central Andean Cordillera of Perú and Bolivia, most of the study lakes are in montane grassland or shrubland. In the Altiplano plateau (central Andes), the northern region is characterized by cold and relatively humid conditions. Lakes are mainly freshwater and lie in extensive interconnected hinterland basins (Cohen et al., 2014). The southern Altiplano is drier, and most lakes are isolated and saline due to the basin geology and high evaporation rates (Blanco et al., 2013). Lakes in the south-central Chilean Andes are located at lower elevation (<2500 m a.s.l) and are surrounded by steppe vegetation; climatic conditions are semi-arid to temperate (Carrevedo et al., 2015).

Diatom Database

We used diatom abundance data from 144 lakes comprising sediment surface samples (n = 215) from a newly created tropical South American diatom database available in the Dryad repository (Benito et al., 2018b) (**Figure 1A** and **Supplementary Table 1**) and GitHub[1]. Briefly, the database comprises published and unpublished studies from lentic and lotic environments collected by different authors under different objectives (e.g., paleoclimatic reconstructions, taxonomy, biodiversity). When possible, diatoms were identified to the species level. The samples were collected in the period 1999–2017. Detailed information about sample processing, taxonomic harmonization, and identification of diatom taxa can be found in Benito et al. (2018b).

In addition, we used sedimentary cores from six lakes located in Ecuador (Piñan, Yahuarcocha, Fondococha, Llaviucu), Peru (Umayo), and Bolivia (Titicaca) for temporal beta diversity analyses (**Figure 1A**). Sediment cores from the Ecuador lakes were collected in summer 2014 (Llaviucu and Fondococha) and July 2017 (Piñan and Yahuarcocha). Cores (mean core length = 61 cm) were retrieved using a UWITEC gravity corer near the center of each lake when possible; lake Piñan was cored at the south-west shallow platform. Sediment cores were sliced in the field at 1 cm intervals. In the laboratory, samples were processed for diatom analyses following standard methods (Battarbee et al., 2002). At least 300 valves were counted per sample and identified using diatom regional floras (Metzeltin and Lange-Bertalot, 1998, 2007; Rumrich et al., 2000; Metzeltin et al., 2005). Core chronologies were established using ^{210}Pb and ^{14}C dating techniques. For Lake Fondococha, details about the ^{210}Pb-chronology can be found in Bandowe et al. (2018) and information about the age-depth model is described in Arcusa et al. (2020) and Schneider et al. (2018). Instantly deposited event layers (e.g., tephra layers and flood layers) were masked for the age calculations and reinserted in the combined age-depth model. The list of ^{14}C and ^{210}Pb dates and associated age-depth models for the lakes Piñan, Yahuarcocha, Fondococha and Llaviucu can be found in **Supplementary Material**. Diatom core assemblages of Lakes Umayo and Titicaca (Ekdahl et al., 2008; Weide et al., 2017) and from Piñan and Fondococha in Ecuador (Luethje, 2020) are published. Altogether, diatom records span the last 1102 (Piñan), 1815 (Yahuarcocha), 2598 (Fondococha), ∼2250

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[1] https://github.com/xbenitogranell/diatoms-biogeography-southamerica

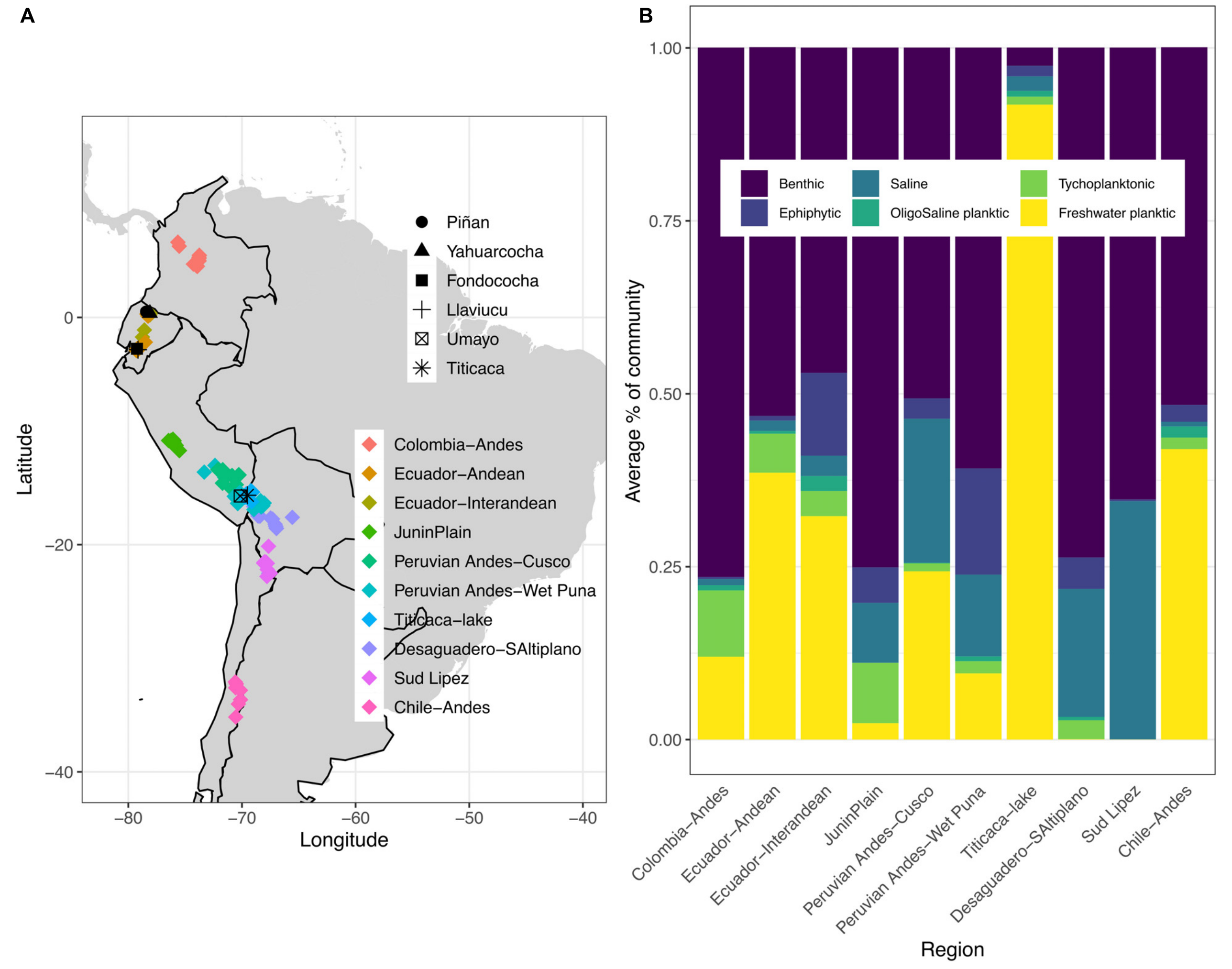

FIGURE 1 | (A) Geographical location of the modern investigated lakes (*n* = 144) colored by regions within the tropical Andes of South America (see **Supplementary Table 1** for individual lakes information in each region); the location of the six lake cores are also shown with different symbols; **(B)** Proportion of diatom ecological groups for each lake region. Samples represent sediment surface habitats.

(Llaviucu), ∼6500 (Umayo), and ∼6000 (Titicaca) cal years BP (cal year BP = years before 1950), with a median temporal resolution of 20.8 years (range 8–44 years).

Predictor Variables

We extracted different datasets from several sources to characterize local (limnological) and regional (climatic and geological) environmental characteristics, as well as historical effects of the investigated lakes. Lake water-chemistry variables were collected simultaneously with the modern diatom samples and included water temperature (°C), pH, conductivity (μS/cm), cations (Ca^{2+}, Mg^{2+}, K^{+}, Na^{+}; mg/L) and anions (Cl^{-}, $SO_4{}^{2-}$; mg/L). Nutrient data (N, P) are not included here, because the database has a very high number of missing values. However, our prior analyses indicate that nutrient conditions are strongly correlated with landscape factors—total phosphorus decreases with elevation—and also that geo-climatic factors are more highly correlated with diatom diversity than limnological conditions in most of the Andean lake regions (Benito et al., 2018b). Elevation (m) and lake area (km^2) were extracted using ArcGIS from the STRM 90 m Digital Elevation Model (Jarvis et al., 2008) and using ESRI World Imagery layer as a basemap, respectively. In equal grids of 50 km^2, the Global Lakes and Wetlands Database (GLWD at ∼ 1 km resolution; Lehner and Döll, 2004) was used to extract the surface area occupied by fresh waters. The percentage of aquatic systems in the surface area acts as a proxy for hydrological connectivity. Climatic variables included mean annual air temperature (MAT; °C), mean annual precipitation (MAP; mm), temperature seasonality (SD; °C), and precipitation seasonality (coefficient of variation; mm). These variables were extracted from the WorldClim 1.4 database (Hijmans et al., 2005). WorldClim contains averaged monthly climate data for the period 1950 to 2000 at 1 km of spatial resolution and falls well within the temporal window of the analyzed diatom samples. To account for the effect of geodiversity, for each lake we extracted geological [soil variability (number of soil types per grid cell), long-term erosion (km/Ma)] and topographic (terrain ruggedness index) variables from Antonelli et al. (2018) within 1° × 1° rid cell (~80 km^2 at the equator). Soil variability is the number of soil types in each grid cell derived from Hengl et al. (2014), while long-term erosion is derived from termochronometric data using the Herman's method which accounts for topography and isotopic data to generate maps of averaged erosion rates over time (Fox et al., 2014). Finally, to estimate the human historical footprint in the lakes, we obtained human density and cropland area from the HYDE 3.2 database (Goldewijk et al., 2011). We extracted human density (inhabitants/km^2 grid cell) and cropland area (km^2/grid cell) values for the last 300 years at 10 years timesteps and averaged over three estimate scenarios (baseline, lower, and upper) for each investigated lake within a spatial resolution of ~80km^2.

Statistical Analyses

All statistical analyses were performed using the R software version 3.6.2 (R Development Team, 2016).

Prior to running statistical analyses, predictor variables were checked and transformed accordingly [log10(x + 0.25) or square root] to meet assumptions of linearity and homogeneity of variances. In both modern and fossil diatom matrices, those species having >3% relative abundance in at least one sample were selected.

Hellinger-transformed diatom relative abundances were used for estimating beta diversity indices. First, we calculated beta diversity for each lake and partitioned it into components, namely replacement and richness difference, with the Podani decomposition family of indices using Bray-Curtis dissimilarity (Podani et al., 2013) with the *beta.div.comp* function of the *adespatial* package (Dray et al., 2016). The replacement component refers to simultaneous species loss and gain along ecological gradients (in space or time), whereas the species richness component means that one sample contains more unique taxa than another (Podani et al., 2013). Second, to further investigate mechanisms behind beta diversity patterns across space (144 lakes) and time (paleolimnological time series from six lake cores), we estimated the local contribution of each sample (sediment surface and 1-cm sample slice for space and time, respectively) to the total beta diversity (LCBD) using the *beta.div* function. The significance of each LCBD value was assessed by 999 permutations, and the p-values were corrected for multiple testing using Holm's procedure (Dray et al., 2016). We also calculated site-specific diatom richness and related with LCBD using Spearman correlation. Third, from the initial richness and replacement matrices, we decomposed LCBD to richness (LCBDrich) and replacement (LCBDrepl) components to assess how each individual sample (in space and time) contributes to richness and to replacement gradients, respectively, in the diatom communities using the *LCBD.comp* function.

To aid interpretation of local contributions to beta diversity, we calculated mean percentages of diatom ecological groups in each of the regions of study (**Figure 1A**). We placed diatom species into the following groups: freshwater planktic (e.g., *Discostella stelligera*, *Cyclostephanos andinus*), oligosaline planktic (*Cyclotella meneghiniana*), tychoplanktonic (e.g., *Fragilaria capucina*, *Aulacoseira alpigena*), freshwater benthic (e.g., *Achnanthidium minutissimum*), epiphytic (e.g., *Cocconeis placentula*), and saline (e.g., *Craticula halophila*, *Navicula salinicola*), following regional diatom floristic studies (Steinitz-Kannan et al., 1993; Metzeltin and Lange-Bertalot, 1998, 2007; Weide et al., 2017).

We ran GAM to model the relationship between LCBD and its replacement (LCBDrepl) and richness (LCBDrich) components and local, regional, and historical predictors. GAMs are a non-parametric extension of the Generalized Linear Models and allow fitting linear and non-linear relationships between the response and explanatory variables when there is no *a priori* reason for choosing a particular function (i.e., linear, quadratic) (Wood, 2017). Only variables that had Variation Inflation Factor (VIF) values <10 were included in the GAMs. We estimated the linear effect of each predictor, accounted for spatial autocorrelation by including smooth splines of geographical coordinates, and included lake region (as in **Figure 1**) as a random factor (*bs* = *'re'*). Both statistically significant predictors and the level of complexity of the response shapes to each variable were selected with Restricted Maximum Likelihood (REML) using the *mgcv* package (Wood, 2011). Finally, we checked residuals for any deviation from normality and linearity using diagnostic plots (**Supplementary Figure 2**).

To determine if statistically significant change in temporal beta diversity trends at millennial time scales could be identified, we modeled the beta replacement time series using a Hierarchical GAM (HGAM) (Pedersen et al., 2019). Here, we were interested in comparing spatial patterns in temporal beta diversity. We used the vector of beta replacement values that resulted from the *beta.div.comp* function as a response variable. We tested the hypothesis that variations in temporal beta diversity are homogenous across the landscape (biotic homogenization) or whether temporal changes differed from lake to lake. For this, we built two HGAMs separately: (a) a global smoother and lake-level smoothers having different wiggliness (i.e., individual curves), hence allow for inter-lake variability (HGAM GI model type in Pedersen et al., 2019) and (b) a global smoother and lake-level smoothers that have the same wiggliness (i.e., shared curves), hence do not allow for inter-lake variability (HGAM GS model type in Pedersen et al., 2019). In all models, we accounted for the different amount of time each sediment core sample represents (difference between ages at the top and bottom of each sediment slice) by including these values as weights in the model (Simpson, 2018). Since the beta diversity replacement range from 0 to 1 in the form of relative values, a gaussian link function was applied. We applied two methods for model selection: (a) AIC values using a cut-off level of two units or less from the lowest AIC model (Burnham and Anderson, 2004), and (b) out-of-sample deviance performance, where each model was compared to a null model (intercept-only model with only lake-level random effects intercepts included). We fitted all the models using the *gam* function in the *mgcv* package.

RESULTS

Ecological Uniqueness and Its Components

Freshwater benthic diatoms dominate across the study regions, except for Lake Titicaca with dominance of freshwater planktic species (**Figure 1B**). Freshwater planktic diatoms are the second most abundant ecological group, followed by saline-tolerant and epiphytic benthic species. Among the freshwater benthic taxa, *Achnanthidium minutissimum* s.l., *Amphora veneta*, *Cymbella cistula*, and *Staurosira construens* var. *venter* made up the majority of the sediment surface diatom flora (**Supplementary Figure 1**). These taxa are indicative of a wide range of limnological conditions, ranging from acidic, low nutrient to high conductivity waters. Freshwater planktic diatoms characteristic of low nutrient conditions were dominated by *Cyclostephanos andinus*, whereas *Aulacoseira ambigua*, *Aulacoseira granulata*, *Discostella stelligera*, and *Tabellaria flocculosa* strain IV may respond to increased nutrients. Saline-tolerant and epiphytic benthic diatoms included the endemic *Amphora carvajaliana*, *Epithemia adnata*, *Navicula salinicola*, and *Cocconeis placentula* var. *placentula*, respectively.

Local contribution to beta diversity did not show statistically significant variation across the study lakes according to corrected *p*-values for multiple testing. Without correcting for multiple testing, 24 lakes (13% of total) had significant LCBDs, mostly concentrated in the south-central Andes of Chile (**Supplementary Figure 2**).

There was a significant negative relationship between LCBD and species richness (Spearman rho = −0.58; $p < 0.01$) (**Supplementary Figure 3**). GAM results showed that modern LCBD decreased with increasing pH, MAP, and historical footprint (**Figure 2A**). The full model explained 38.1% of the deviance. When analyzing the replacement and richness components of LCBD, the effects of environmental predictors were generally inverse (**Figures 2B,C**), as supported by the negative relationship between LCBDrepl and LCBDrich components (**Supplementary Figure 4**). A consistent set of variables representative of local (limnological), and regional (climatic and geological) conditions explained variation in

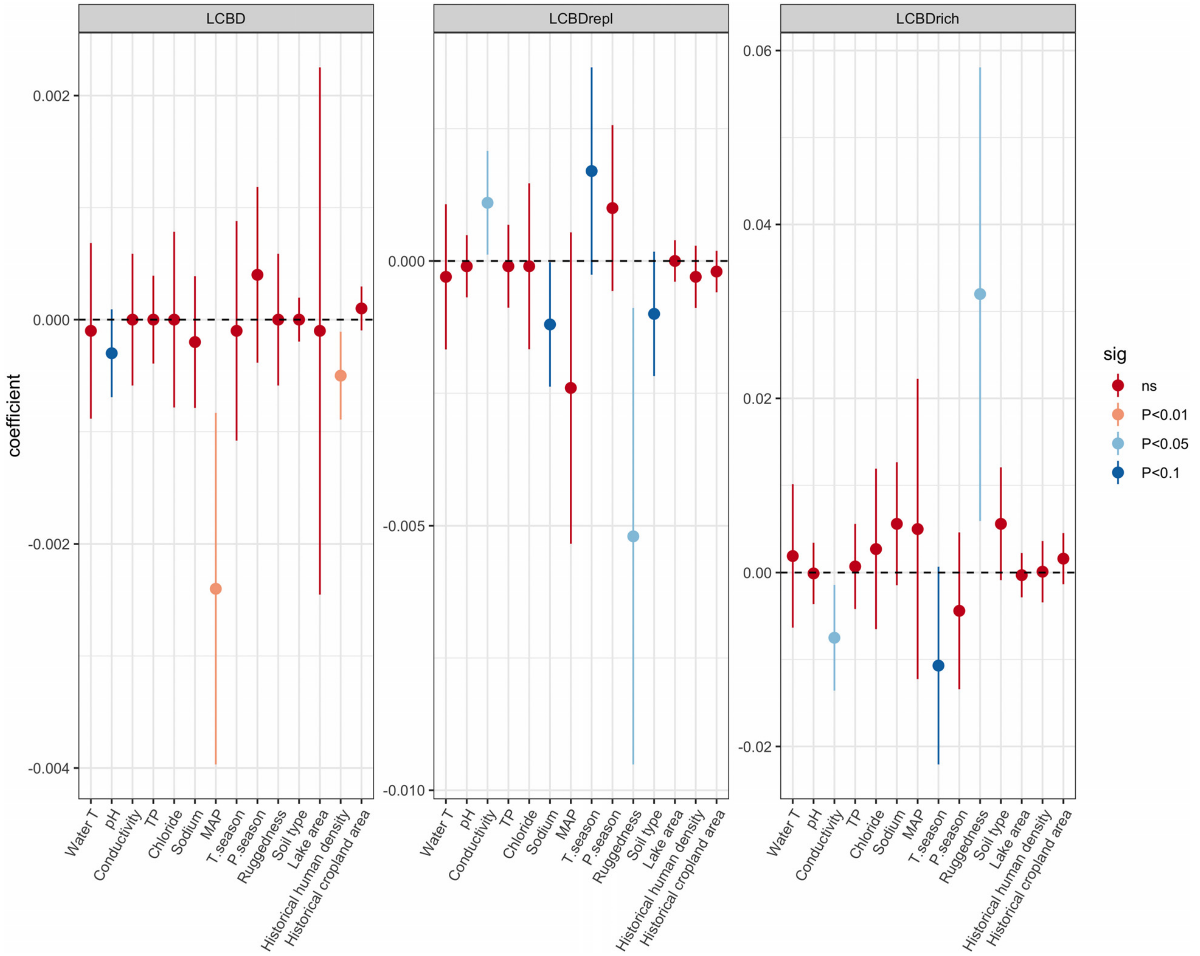

FIGURE 2 | Effect of predictors on local contributions to beta diversity (LCBD) and to the replacement (LCBDrepl) and richness (LCBDrich) components, estimated as linear coefficients from Generalized Additive Models. Errors bars are ±95% confidence intervals. Colors indicate the significance level α = 0.05.

LCBD indices. LCBDrepl increased with increasing conductivity and seasonality in temperature, and decreased with increasing terrain ruggedness, soil variability, and Na^+ (full model % deviance explained = 37.7). LCBDrich increased with decreasing conductivity and seasonality in temperature, and increased with higher terrain ruggedness (full model % deviance explained = 31.4).

Temporal Trends of Beta Diversity Components

As expected, the temporal trends of LCBDrepl and LCBDrich components fluctuated over millennial-time scales (**Figure 3**). In general, LCBDrich fluctuated more and was comparatively higher than LCBDrepl across lakes, especially in the two-deep freshwater Altiplano lakes, Umayo and Titicaca. These two lakes also showed increased trend in LCBDrepl since *ca* 1000 cal years BP. Replacement and richness fluctuated more similarly in the two remote Ecuadorean páramo lakes (Piñan [Spearman rho: -0.17, $p = 0.22$] and Fondococha [Spearman rho: 0.51; $p < 0.01$]) than the two lakes located closer to human settlements (Yahuarcocha and Llaviucu [Spearman rho range: 0.02–0.09, $p > 0.05$]). Interestingly, LCBDrich and LCBDrepl time series of Piñan, Yahuarcocha and Fondococha showed a peak at *ca*. 1000 cal years BP. The main diatom stratigraphic changes and dominant taxa for each lake are summarized in the supplementary material (**Supplementary Figures 10–15**).

All the HGAMs models fitted to the beta replacement time series predicted better than the null models (**Supplementary Table 2**). The best HGAMs included a global smoother plus lake-specific smoothers having different wiggliness (GI model) according to the AIC models. These results suggest that allowing for lake-specific variation explained more variation in beta replacement trends. The shape of the fitted HGAMs differed across lakes. Beta replacement increased in the last *ca* 500 cal years BP in the deep Altiplano lakes (Umayo and Titicaca) (**Figure 4**). More coherent trends of beta replacement were observed in the Ecuadorean lakes, which were characterized by

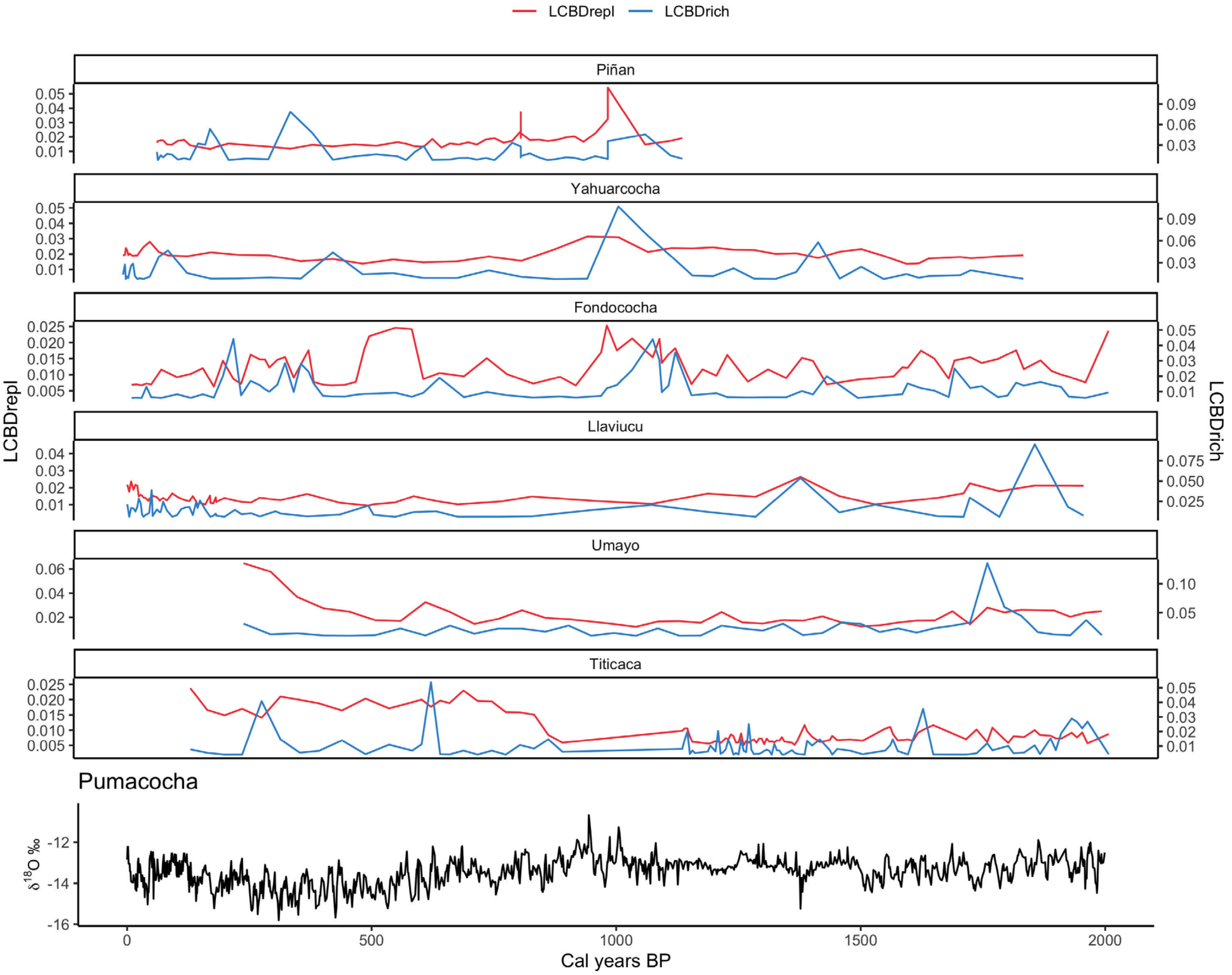

FIGURE 3 | Contribution of replacement (LCBDrepl) and richness (LCBDrich) components to beta diversity for the six investigated lake cores (arranged by increased latitude). Isotopic $\delta^{18}O$ measurements from Pumacocha lake (Bird et al., 2011) are interpreted as dry periods with enriched values. Note the two y-axes for replacement and richness components of beta diversity time series.

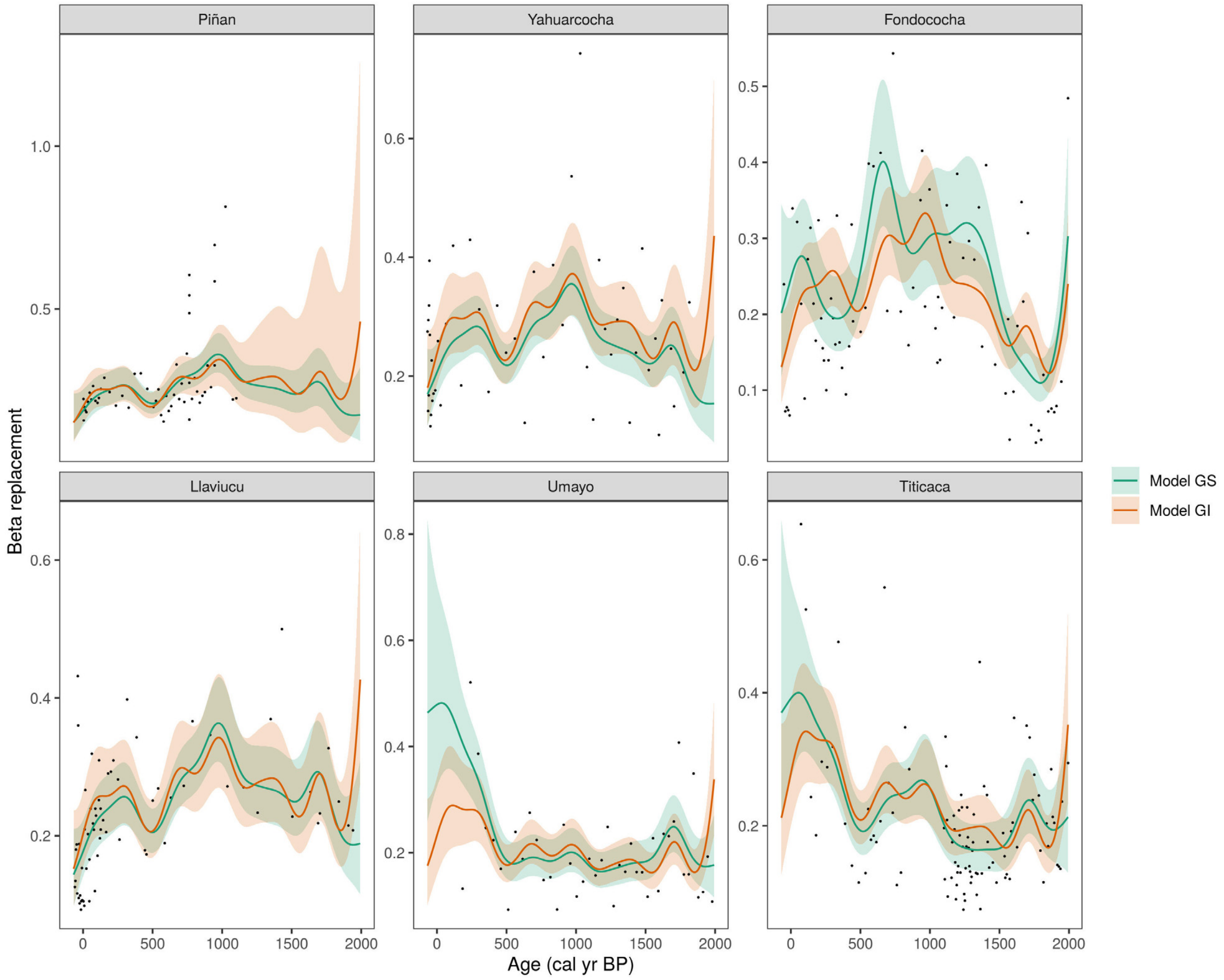

FIGURE 4 | Temporal trends of Hierarchical GAM-fitted beta replacement for the six Andean lakes investigated in this study (arranged by increased latitude). Model GS (green line) indicates a global curve and inter-lake variation having similar smoothness. Model GI (orange line) indicates a global curve allowing for varied smoothness among lakes. Points are original beta replacement values. Ribbons indicate ±2 standard errors around the mean (green and orange lines for GS and GI models respectively).

slight increases at *ca*. 1000 and 500 cal years BP and a decrease over the last *ca*. 200 years (**Figure 4**).

DISCUSSION

Previous studies have demonstrated that species composition and taxonomic richness of lake diatom communities in the tropical South America are jointly structured by the local (water chemistry) and regional environmental factors (aquatic connectivity and climate) (Benito et al., 2018b,a). Moreover, biogeographic patterns emerge after determining latitudinal gradients of species richness and estimating the role of dispersal dynamics on diatom community structure (Benito and Fritz, 2020). In the analyses presented here, the calculation of LCBD introduced an additional biodiversity metric for Neotropical diatom metacommunities and biogeography studies. Our results identified a set of local and regional ecological gradients that explained patterns in LCBD, including its replacement and richness components. We found that LCBD was related to pH, MAP, and historical human density. The effect of pH and MAP are not surprising given the relatively high variance displayed across the study lakes (Steinitz-Kannan et al., 1983; Michelutti et al., 2019) and the known direct role of pH in affecting physiological process in diatoms (Van Dam et al., 1994). Precipitation indirectly affects catchment-lake linkages through, for instance, biochemical processes and resource supply (Passy, 2010). Here, we found that high-elevation lakes lying in drier areas are ecologically more unique than lakes receiving more precipitation. Vilmi et al. (2020) showed a distinction between dry/cold and wet/warm conditions related to the assembly processes of high-elevation stream invertebrates and bacteria, reinforcing the role of climate in mountainous aquatic biodiversity patterns.

We found more ecologically unique lakes (i.e., lakes with high LCBD values) in areas with a history of low human impact.

Indeed, human impacts can have a homogenizing effect on aquatic communities (Olden et al., 2004). In our case, low LCBD values in lakes with higher human impact may be a result of, for instance, alteration of communities by hydrological modifications and external impacts (e.g., cattle grazing) in the Andean lakes since prehistoric times (Sarmiento, 2002; Van Colen et al., 2018). Although we did not observe statistically significant geographic patterns in the distribution of LCBD when the p-values were corrected for multiple testing, lakes located in the central-south Chilean Andes displayed higher LCBDs (without correcting for multiple testing). A correlation between LCBD and latitude also gave the significant negative relationships (Spearman rho = -0.47, $p < 0.05$), suggesting a decreasing latitudinal gradient of LCBDs. This may be partially associated with the onset and legacy of historical occupation in the continent of the southern portions of our latitudinal gradient (Gayo et al., 2015; Goldberg et al., 2016).

Partitioning LCBD into replacement and richness components provided further insights into the mechanisms underlying changes in spatial beta diversity of diatoms in South America. Most significant environmental correlates for each of the LCBD indices, i.e., LCBDrepl and LCBDrich, were fundamentally different from the ones observed for total LCBD. For instance, LCBD components are responding inversely to the same water chemistry correlates (e.g., conductivity), supporting previous research on lake communities analyzing turnover and nestedness components (Angeler, 2013). Other studies also highlight that finding consistent predictor variables among beta diversity components is challenging in lentic systems in general, and on tropical aquatic communities in particular, including diatom and invertebrate communities (Jyrkänkallio-Mikkola et al., 2018; Castro et al., 2019). Nonetheless, when the replacement component of LCBD dominates, a regional approach focusing on multiple sites might be needed to conserve ecologically unique diatom metacommunities (Wright and Reeves, 1992). In our study, regional environmental variables for conservation purposes are terrain ruggedness and soil variability. In contrast, a dominating richness component of LCBD suggests the need to focus on a few species-rich lakes and local limnological correlates (Ramos-Jiliberto et al., 2009). In this context, conductivity could be a variable to ensure conservation of diatom metacommunities in certain tropical Andean lakes that are naturally salty such as Southern Altiplano regions (**Figure 1** and **Supplementary Figure 1**).

We found that ecological uniqueness in terms of replacement and richness gradients responded to climate (i.e., seasonality in temperature) and geology (soil variability, terrain ruggedness). The influences of diverse climatic conditions and geodiversity on freshwater biodiversity have recently gained attention (Kärnä et al., 2018; Toivanen et al., 2019). In a study on boreal stream and lake diatoms, Vilmi et al. (2017) found a strong association between LCBD and bed rock, soil, and ecoregion characteristics. Studies relating geodiversity-biodiversity in freshwaters suggest an incipient tight coupling between regional catchment characteristics and local biological dynamics, and are in line with studies from high-elevation lakes (Zaharescu et al., 2016). In the Andes of Ecuador, northern páramo lakes differ in SO_4^{2-} content compared with their southern páramo lake counterparts, which have much higher Ca^{2+} concentrations (Luethje, 2020). Interestingly, Andean lakes located in high-elevation rugged basins harbor ecologically unique diatom communities in terms of richness. We found a negative relationship between LCBD and species richness (Spearman rho = -0.58, $p < 0.01$), indicating that lakes with exceptional ecological uniqueness are usually the ones with lower numbers of species. Similar negative relationships have been reported in other contexts as well (Legendre and De Cáceres, 2013; da Silva and Hernández, 2014; Mimouni et al., 2015; Heino et al., 2017). High terrain rugosity promotes lake isolation from the surrounding landscape (Valencia et al., 2016), which may result in more dispersal-limited conditions, even for organisms with high dispersal capabilities, like diatoms (Kristiansen, 1996; Benito et al., 2018b). From a biogeographical perspective, identifying topographically diverse mountain regions that harbor ecologically unique lakes may complement research on evolutionary processes, such as diatom endemism (Spanbauer et al., 2018) and climatic microrefugia (de Novaes Nascimento et al., 2019).

Diatom community structure differs among lake habitats, thereby highlighting the relevance of species sorting due to substrate type (e.g., mud, plants, rocks), and dispersal between different lake habitats (pelagic versus benthic communities) as a result of the fluid aquatic environment (Wetzel et al., 2012; Cantonati and Lowe, 2014). We can assume that each study region operates as a metacommunity (Benito et al., 2018b) and hence hypothesize on mechanisms driving LCBD patterns by considering the variability of lake diatom habitats (**Figure 1B**). We suggest that it is the diversity from the peripheral (benthic) communities that eventually determines between-lake diversity of diatoms and ultimately the ecological uniqueness of the lakes compared to other sites in the region. For instance, in the Peruvian Andes (Cusco and Wet Puna regions), the presence of heterogenous benthic diatom groups (saline, epiphytic, benthic) may account for the high LCBD values (**Supplementary Figure 1**). In contrast, the homogenous pattern in terms of lake habitat diatoms in the Sud Lipez and Desaguadero regions of Bolivia could arise because of limited opportunities for dispersal. These Bolivian regions are cold and arid, with a low density and small number of suitable aquatic environments, most of which are shallow hypersaline lakes and wetlands (Servant-Vildary and Roux, 1990). In the Chilean Andean lakes, the higher local contributions to beta diversity could be a function of their relatively poor pelagic diatom community compared with richer-than-average planktic dominated diatom regions, such as Lake Titicaca or the Ecuadorian Andes. Diatom diversity often increases in deeper lake zones, because benthic diatoms are transported from other lake habitats and mixed with pelagic taxa associated with seasonal changes (Pla-Rabés and Catalan, 2018). However, we cannot discard the possibility that the observed relationships between LCBD values and ecological groups in each diatom metacommunity were influenced by the temporal variability in our modern database, as the data do not correspond to the same time point among regions. More research is needed to unveil the effect of benthic area on diatom communities' structure in deep tropical lakes.

The term metacommunity can also be used to define the diatom community of the whole lake for each sedimentary sequence (Leibold et al., 2004). Sediment samples integrate the local species richness and the beta diversity (replacement) of the lake habitats and the variability in composition among them (Pla-Rabés and Catalan, 2018). Thus, local contributions to beta diversity may differ over time in response to lake habitat changes driven by limnological change. We observed a consistent pattern of more variability in LCBDrich than LCBDrepl time series. This is expected given the role of sediment samples acting as a sink by accumulating different entities (species) from other lake habitats (i.e., source) (Logue et al., 2011). Three lakes in the Andes of Ecuador (Piñan, Yahuarcocha and Fondococha) experienced a coincident peak in LCBDrich, but less in LCBrepl, at *ca* 1000 cal years BP, likely responding to dry/warm conditions centered around the Medieval Climate Anomaly (MCA). The MCA triggered lower lake levels based on many tropical Andean paleolimnological records (**Figure 3**; Lüning et al., 2019 and references therein). Despite different conditions in water chemistry and lake depths, our findings suggest that the relatively high synchronous compositional uniqueness at that time may be a fingerprint of regional-scale limnological variation in these three lakes. This is partly supported by the fact that high modern LCBDrich values are explained by low temperature seasonality and conductivity (**Figure 2**). In this application, however, methodological issues, such as time-averaging processes and the partial representation of the entire population abundance, may introduce bias in beta diversity estimates from paleolimnological assemblages (Birks et al., 2016). To the best of our knowledge, our study is the first to investigate the ecological uniqueness in terms of richness and replacement using sediment diatom assemblages, which hampers comparisons with similar works. Further research in other tropical Andean lakes with available contemporary time series data is necessary to assess the generality of this finding.

Our GAM time series models (HGAMs) further delineate temporal beta diversity patterns in tropical Andean lakes of varied size, limnology, and climatic conditions that can provide a regional, long-term perspective of biodiversity changes (Dornelas et al., 2014; McGill et al., 2015). A decreasing trend in beta diversity over time (biotic homogenization) has been assumed to be a result of increased human impacts (Olden and Rooney, 2006). In our case, we found signs of long-term biotic homogenization of diatom assemblages, as measured by decreasing trends of beta replacement over the past *ca*. 200 years across the four lakes investigated from Ecuador (**Figure 4**). Nonetheless, beta replacement values fluctuate around a long-term mean for the whole time series, and no periods with substantial increases or decreases in beta diversity arose. In contrast, biotic differentiation (i.e., increase of beta replacement over time) was found in the two deep freshwater lakes of the Altiplano. Admittedly, the low sample density for the most recent period of these two lakes is not captured well by the GAM models (as in Piñan before *ca* 900 cal. years BP), resulting in wide confidence intervals, like with any other smooth regression approach (Simpson, 2018).

A high context dependency exists among studies that investigate biotic homogenization and its explanatory factors at varied spatial and temporal scales in aquatic ecosystems. In the case of lake sediment diatoms, Winegardner et al. (2017) did not find patterns of biotic homogenization across the conterminous United States between *ca*. 150 years ago and modern times. In a study on tropical reservoirs affected by eutrophication, Wengrat et al. (2018) found a decreasing trend of spatial beta diversity over the past 100 years. Eutrophication-driven homogenization was also reported by Salgado et al. (2018) using macrophyte paleoecological assemblages. These observations highlight the usefulness of the HGAM models used here for detecting temporal beta diversity trends across space: as this approach does not assume any specific dynamics in the time series, it is possible to determine if broad-scale environmental change (e.g. climate change) led to uniform diversity patterns across the landscape, or if lake-specific dynamics decouple from the regional signal. The latter could be the case here, indicating no widespread biotic homogenization across the tropical Andes. Additionally, HGAM models allow to circumvent the issue of harmonization among lake samples (e.g., binning), which is problematic given the differences in temporal resolution and length. We suggest that this approach can also be applied to other aquatic systems that may or may not have well-defined boundaries and monitoring time series data but that are subject to strong environmental disturbances (e.g., temporary rivers, wetlands) (Ruhí et al., 2017).

CONCLUSION

Our approach for investigating ecological uniqueness (i.e., LCBD) has the potential to generate new opportunities to integrate modern ecology and paleolimnology for biodiversity and metacommunity studies. In this context, we emphasize several aspects of our results. First, ecological uniqueness of tropical Andean lakes was linked to local and regional environmental variables and showed an inverse pattern for the replacement and richness components of LCBD. Specifically, mean precipitation and the historical human impact mediated how ecologically unique the lakes were, whereas geodiversity (soil variability, terrain ruggedness), temperature seasonality and conductivity mediated, in an opposite manner, its replacement and richness components. We suggest this finding has different management and conservation measures. For instance, individual lakes characterized by high terrain ruggedness and low conductivity are clear management targets if local diatom richness is a conservation goal; if the goal is to conserve lake-catchment systems within a given spatial context (beta diversity), lakes with low soil variability and low Na^+ content may be suitable management targets. Second, by identifying diatom richness contributions to beta diversity over time, we were able to observe a shared limnological response to warm/dry climatic changes centered around the MCA driven by decreased temperature seasonality and conductivity. However, diatom sedimentary assemblages should not be interpreted as a unique response to environmental change because, for instance, temperature seasonality might have a stronger effect on planktic communities than on the benthos via thermal structure impacts as a result of warming or drying. If environmental variation mediates the relationship between replacement and richness components of beta diversity, then increasing limnological changes due to climate change and human impacts will likely destabilize long-term metacommunity stability; this could be the case in páramo lakes of Ecuador as seen by higher correlations between both LCBD components over time. Finally, we have provided a broader perspective of aquatic biodiversity change over the Common Era (last 2000 years) with beta replacement trends to test the hypothesis of recent biotic homogenization. Considering diatoms are one of the most sensitive groups of organisms, situated at the base of aquatic food webs, the decreasing trends in temporal beta diversity across lakes in the Ecuadorean Andes, albeit being lake-specific and not unprecedented, may cause unexpected effects in the structure and functioning of these ecological and climatic sensors in vulnerable tropical high-elevation ecosystems.

DATA AVAILABILITY STATEMENT

Diatom and environmental datasets, and R code to perform the analyses are available from GitHub (https://github.com/xbenitogranell/LCBD-diatoms).

AUTHOR CONTRIBUTIONS

XB and AV conceived the idea. XB constructed the database, performed the statistical analysis, and led the writing. XB, SF, and MLu conducted the fieldwork in Ecuador. MLu performed the diatom analysis for Piñan and Fondococha, and XB for Yahuarcocha. MC performed the diatom analyses from modern Chilean lakes. All authors contributed to writing of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.00260/full#supplementary-material

REFERENCES

Angeler, D. G. (2013). Revealing a conservation challenge through partitioned long-term beta diversity: increasing turnover and decreasing nestedness of boreal lake metacommunities. *Divers. Distribut.* 19, 772–781. doi: 10.1111/ddi.12029

Antonelli, A., Kissling, W. D., Flantua, S. G., Bermúdez, M. A., Mulch, A., Muellner-Riehl, A. N., et al. (2018). Geological and climatic influences on mountain biodiversity. *Nat. Geosci.* 11:718. doi: 10.1038/s41561-018-0236-z

Arcusa, S. H., Schneider, T., Mosquera, P. V., Vogel, H., Kaufman, D., Szidat, S., et al. (2020). Late Holocene tephrostratigraphy from Cajas National Park, southern Ecuador. *Andean Geol.* 47, doi: 10.5027/andgeoV47n3-3301

Baker, P., and Fritz, S. C. (2015). Nature and causes of quaternary climate variation of tropical South America. *Quat. Sci. Rev.* 124, 31–47. doi: 10.1016/j.quascirev.2015.06.011

Banda, K. A. M., Delgado-Salinas, A., Dexter, K., Linares-Palomino, R., Oliveira-Filho, A., Prado, D., et al. (2016). Plant diversity patterns in neotropical dry forests and their conservation implications. *Science* 353, 1383–1387.

Bandowe, B., Fränkl, L., Grosjean, M., Tylmann, W., Mosquera, P. V., Hampel, H., et al. (2018). A 150-year record of polycyclic aromatic compound (PAC) deposition from high Andean Cajas National Park, southern Ecuador. *Sci. Total Environ.* 621, 1652–1663. doi: 10.1016/j.scitotenv.2017.10.060

Battarbee, R. W., Jones, V. J., Flower, R. J., Cameron, N. G., Bennion, H., Carvalho, L., et al. (2002). "Diatoms," in *Tracking Environmental Change Using Lake Sediments*, eds W. M. Last and J. P. Smol (Berlin: Springer), 155–202.

Benito, X., Feitl, M., Fritz, S. C., Mosquera, P. V., Schneider, T., Hampel, H., et al. (2019). Identifying temporal and spatial patterns of diatom community change in the tropical Andes over the last ˜150 years. *J. Biogeogr.* 46, 1889–1900. doi: 10.1111/jbi.13561

Benito, X., and Fritz, S. C. (2020). "Diatom diversity and biogeography across tropical South America," in *Neotropical Diversification: Patterns and Processes Fascinating Life Sciences*, eds V. Rull and A. C. Carnaval (Cham: Springer International Publishing), 121–143. doi: 10.1007/978-3-030-31167-4_7

Benito, X., Fritz, S. C., Steinitz-Kannan, M., Tapia, P., Kelly, M. A., and Lowell, T. V. (2018a). Geo-climatic factors drive diatom community distribution in tropical South American freshwaters. *J. Ecol.* 106, 1660–1672. doi: 10.1111/1365-2745.12934

Benito, X., Fritz, S. C., Steinitz−Kannan, M., Vélez, M. I., and McGlue, M. M. (2018b). Lake regionalization and diatom metacommunity structuring in tropical South America. *Ecol. Evol.* 8, 7865–7878. doi: 10.1002/ece3.4305

Bird, B. W., Abbott, M. B., Vuille, M., Rodbell, D. T., Stansell, N. D., and Rosenmeier, M. F. (2011). A 2,300-year-long annually resolved record of the South American summer monsoon from the Peruvian Andes. *PNAS* 108, 8583–8588. doi: 10.1073/pnas.1003719108

Birks, H. J. B., Felde, V. A., Bjune, A. E., Grytnes, J.-A., Seppä, H., and Giesecke, T. (2016). Does pollen-assemblage richness reflect floristic richness? A review of recent developments and future challenges. *Rev. Palaeobot. Palynol.* 228, 1–25. doi: 10.1016/j.revpalbo.2015.12.011

Blanco, S., Álvarez-Blanco, I., Cejudo-Figueiras, C., De Godos, I., Bécares, E., Muñoz, R., et al. (2013). New diatom taxa from high-altitude Andean saline lakes. *Diatom Res.* 28, 13–27. doi: 10.1080/0269249x.2012.734528

Burnham, K., and Anderson, D. (2004). Multimodel inference understanding AIC and BIC in model selection. *Sociol. Methods Res.* 33, 261–304. doi: 10.1177/0049124104268644

Buytaert, W., Célleri, R., De Bièvre, B., Cisneros, F., Wyseure, G., Deckers, J., et al. (2006). Human impact on the hydrology of the Andean páramos. *Earth Sci. Rev.* 79, 53–72. doi: 10.1016/j.earscirev.2006.06.002

Cantonati, M., and Lowe, R. L. (2014). Lake benthic algae: toward an understanding of their ecology. *Freshw. Sci.* 33, 475–486. doi: 10.1086/676140

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., et al. (2012). Biodiversity loss and its impact on humanity. *Nature* 486, 59–67. doi: 10.1038/nature11148

Carrevedo, M. L., Frugone, M., Latorre, C., Maldonado, A., Bernárdez, P., Prego, R., et al. (2015). A 700-year record of climate and environmental change from a high Andean lake: laguna del Maule, central Chile (36 S). *Holocene* 25, 956–972. doi: 10.1177/0959683615574584

Castillo-Escrivà, A., Valls, L., Rochera, C., Camacho, A., and Mesquita-Joanes, F. (2017). Disentangling environmental, spatial, and historical effects on ostracod communities in shallow lakes. *Hydrobiologia* 787, 61–72. doi: 10.1007/s10750-016-2945-x

Castro, E., Siqueira, T., Melo, A. S., Bini, L. M., Landeiro, V. L., and Schneck, F. (2019). Compositional uniqueness of diatoms and insects in subtropical streams is weakly correlated with riffle position and environmental uniqueness. *Hydrobiologia* 842, 219–232. doi: 10.1007/s10750-019-04037-8

Catalan, J., Pla-Rabés, S., Wolfe, A. P., Smol, J. P., Rühland, K. M., Anderson, N. J., et al. (2013). Global change revealed by palaeolimnological records from remote lakes: a review. *J. Paleolimnol.* 49, 513–535. doi: 10.1007/s10933-013-9681-2

Catalan, J., and Rondón, J. C. D. (2016). Perspectives for an integrated understanding of tropical and temperate high-mountain lakes. *J. Limnol.* 75, 215–234.

Cohen, A., McGlue, M. M., Ellis, G. S., Zani, H., Swarzenski, P. W., Assine, M. L., et al. (2014). Lake formation, characteristics, and evolution in retroarc deposystems: a synthesis of the modern Andean orogen and its associated basins. *Geol. Soc. Am. Mem.* 212, 212–216.

da Silva, P. G., and Hernández, M. I. M. (2014). Local and regional effects on community structure of dung beetles in a Mainland-Island Scenario. *PLoS One* 9:e111883. doi: 10.1371/journal.pone.0111883

de Novaes Nascimento, M., Laurenzi, A. G., Valencia, B. G., Van, R., and Bush, M. (2019). A 12,700-year history of paleolimnological change from an Andean microrefugium. *Holocene* 29, 231–243. doi: 10.1177/0959683618810400

Dornelas, M., Gotelli, N. J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., et al. (2014). Assemblage time series reveal biodiversity change but not systematic loss. *Science* 344, 296–299. doi: 10.1126/science.1248484

Dray, S., Blanchet, G., Borcard, D., Guenard, G., Jombart, T., Larocque, G., et al. (2016). *adespatial: Multivariate Multiscale Spatial Analysis. R package version 0.0-4*.

Dubois, N., Saulnier-Talbot, É, Mills, K., Gell, P., Battarbee, R., Bennion, H., et al. (2018). First human impacts and responses of aquatic systems: a review of palaeolimnological records from around the world. *Anthropocene Rev.* 5, 28–68. doi: 10.1177/2053019617740365

Ekdahl, E. J., Fritz, S. C., Baker, P. A., Rigsby, C. A., and Coley, K. (2008). Holocene multidecadal-to millennial-scale hydrologic variability on the South American Altiplano. *Holocene* 18, 867–876. doi: 10.1177/0959683608093524

Fox, M., Herman, F., Willett, S. D., and May, D. A. (2014). A linear inversion method to infer exhumation rates in space and time from thermochronometric data. *Earth Surf. Dyn.* 2, 47–65. doi: 10.5194/esurf-2-47-2014

Fritz, S. C., Baker, P. A., Tapia, P., Spanbauer, T., and Westover, K. (2012). Evolution of the Lake Titicaca basin and its diatom flora over the last ∼370,000 years. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 317–318, 93–103. doi: 10.1016/j.palaeo.2011.12.013

Gayo, E. M., Latorre, C., and Santoro, C. M. (2015). Timing of occupation and regional settlement patterns revealed by time-series analyses of an archaeological radiocarbon database for the South-Central Andes (16–25 S). *Quat. Int.* 356, 4–14. doi: 10.1016/j.quaint.2014.09.076

Goldberg, A., Mychajliw, A. M., and Hadly, E. A. (2016). Post-invasion demography of prehistoric humans in South America. *Nature* 532:232. doi: 10.1038/nature17176

Goldewijk, K. K., Beusen, A., van Drecht, G., and de Vos, M. (2011). The HYDE 3.1 spatially explicit database of human-induced global land-use change over the past 12,000 years. *Glob. Ecol. Biogeogr.* 20, 73–86. doi: 10.1111/j.1466-8238.2010.00587.x

Gray, M. (2008). Geodiversity: developing the paradigm. *Proc. Geol. Assoc.* 119, 287–298. doi: 10.1016/s0016-7878(08)80307-0

Gregory-Eaves, I., and Beisner, B. E. (2011). Palaeolimnological insights for biodiversity science: an emerging field. *Freshw. Biol.* 56, 2653–2661. doi: 10.1111/j.1365-2427.2011.02677.x

Heino, J. (2013). The importance of metacommunity ecology for environmental assessment research in the freshwater realm. *Biol. Rev.* 88, 166–178. doi: 10.1111/j.1469-185x.2012.00244.x

Heino, J., Bini, L. M., Andersson, J., Bergsten, J., Bjelke, U., and Johansson, F. (2017). Unravelling the correlates of species richness and ecological uniqueness in a metacommunity of urban pond insects. *Ecol. Indic.* 73, 422–431. doi: 10.1016/j.ecolind.2016.10.006

Heino, J., Soininen, J., Alahuhta, J., Lappalainen, J., and Virtanen, R. (2016). Metacommunity ecology meets biogeography: effects of geographical region, spatial dynamics and environmental filtering on community structure in aquatic organisms. *Oecologia* 183, 121–137. doi: 10.1007/s00442-016-3750-y

Hengl, T., de Jesus, J. M., MacMillan, R. A., Batjes, N. H., Heuvelink, G. B., Ribeiro, E., et al. (2014). SoilGrids1kmlGrids1km., ogeography: effects of geographical regio. *PLoS One* 9:e105992. doi: 10.1371/journal.pone.0105992

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., and Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25, 1965–1978. doi: 10.1002/joc.1276

Jarvis, A., Reuter, H. I., Nelson, A., and Guevara, E. (2008). *Hole-filled SRTM for the globe Version 4. available from the CGIAR-CSI SRTM 90m Database (http://srtm.csi.cgiar.org)*. Available online at: http://www.cgiar-csi.org/data/srtm-90m-digital-elevation-database-v4-1 (accessed June 5, 2017)

Jyrkänkallio-Mikkola, J., Siljander, M., Heikinheimo, V., Pellikka, P., and Soininen, J. (2018). Tropical stream diatom communities – The importance of headwater streams for regional diversity. *Ecol. Indic.* 95, 183–193. doi: 10.1016/j.ecolind.2018.07.030

Kärnä, O.-M., Heino, J., Grönroos, M., and Hjort, J. (2018). The added value of geodiversity indices in explaining variation of stream macroinvertebrate diversity. *Ecol. Indic.* 94, 420–429. doi: 10.1016/j.ecolind.2018.06.034

Killeen, T. J., Douglas, M., Consiglio, T., Jørgensen, P. M., and Mejia, J. (2007). Dry spots and wet spots in the Andean hotspot. *J. Biogeogr.* 34, 1357–1373. doi: 10.1111/j.1365-2699.2006.01682.x

Kristiansen, J. (1996). Dispersal of freshwater algae—a review. *Hydrobiologia* 336, 151–157. doi: 10.1007/978-94-017-0908-8_15

Legendre, P., and De Cáceres, M. (2013). Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. *Ecol. Lett.* 16, 951–963. doi: 10.1111/ele.12141

Lehner, B., and Döll, P. (2004). Development and validation of a global database of lakes, reservoirs and wetlands. *J. Hydrol.* 296, 1–22. doi: 10.1016/j.jhydrol.2004.03.028

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., et al. (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.* 7, 601–613. doi: 10.1111/j.1461-0248.2004.00608.x

Logue, J. B., Mouquet, N., Peter, H., Hillebrand, H., and Metacommunity Working Group (2011). Empirical approaches to metacommunities: a review and comparison with theory. *Trends Ecol. Evol.* 26, 482–491. doi: 10.1016/j.tree.2011.04.009

Luethje, M. (2020). *Identifying the Resilience of Andean Lakes to Climatic and Anthropogenic Impacts on Varying Temporal and Spatial Scales*. Ph.D. Dissertation. University of Nebraska-Lincoln.

Lüning, S., Gałka, M., Bamonte, F. P., Rodríguez, F. G., and Vahrenholt, F. (2019). The medieval climate anomaly in South America. *Quat. Int.* 508, 70–87. doi: 10.1016/j.quaint.2018.10.041

McGill, B. J., Dornelas, M., Gotelli, N. J., and Magurran, A. E. (2015). Fifteen forms of biodiversity trend in the Anthropocene. *Trends Ecol. Evol.* 30, 104–113. doi: 10.1016/j.tree.2014.11.006

Metzeltin, D., and Lange-Bertalot, H. (1998). *Tropical Diatoms of South America I.* Königstein: A.R.G. Gantner Verlag K.G.

Metzeltin, D., and Lange-Bertalot, H. (2007). in *Tropical Diatoms of South America II*, ed. H. Lange-Bertalot Königstein: Iconographia Diatomologica 18 A.R.G. Gantner Verlag K.G.

Metzeltin, D., Lange-Bertalot, H., and Garcia-Rodriguez, F. (2005). "Diatoms of Uruguay," in *Iconographia diatomologica* 15, 1ologic, (Königstein: A.R.G. Gantner Verlag K.G).

Michelutti, N., Tapia, P. M., Labaj, A. L., Grooms, C., Wang, X., and Smol, J. P. (2019). A limnological assessment of the diverse waterscape in the Cordillera Vilcanota, Peruvian Andes. *Inland Waters* 9, 395–407. doi: 10.1080/20442041.2019.1582959

Mills, K., Schillereff, D., Saulnier−Talbot, É, Gell, P., Anderson, N. J., Arnaud, F., et al. (2017). Deciphering long-term records of natural variability and human impact as recorded in lake sediments: a palaeolimnological puzzle. *Wiley Interdiscip. Rev. Water* 4:e1195. doi: 10.1002/wat2.1195

Mimouni, E.-A., Pinel-Alloul, B., and Beisner, B. E. (2015). Assessing aquatic biodiversity of zooplankton communities in an urban landscape. *Urban Ecosyst.* 18, 1353–1372. doi: 10.1007/s11252-015-0457-5

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A. B., and Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858. doi: 10.1038/35002501

Olden, J. D., Poff, N. L., Douglas, M. R., Douglas, M. E., and Fausch, K. D. (2004). Ecological and evolutionary consequences of biotic homogenization. *Trends Ecol. Evol.* 19, 18–24. doi: 10.1016/j.tree.2003.09.010

Olden, J. D., and Rooney, T. P. (2006). On defining and quantifying biotic homogenization. *Glob. Ecol. Biogeogr.* 15, 113–120. doi: 10.1111/j.1466-822x.2006.00214.x

Pages 2k Consortium (2013). Continental-scale temperature variability during the past two millennia. *Nat. Geosci.* 6, 339–346. doi: 10.1038/ngeo1797

Passy, S. I. (2010). A distinct latitudinal gradient of diatom diversity is linked to resource supply. *Ecology* 91, 36–41. doi: 10.1890/09-0545.1

Pedersen, E. J., Miller, D. L., Simpson, G. L., and Ross, N. (2019). Hierarchical generalized additive models in ecology: an introduction with mgcv. *PeerJ* 7:e6876. doi: 10.7717/peerj.6876

Pla-Rabés, S., and Catalan, J. (2018). Diatom species variation between lake habitats: implications for interpretation of paleolimnological records. *J. Paleolimnol.* 60, 169–187. doi: 10.1007/s10933-018-0017-0

Podani, J., Ricotta, C., and Schmera, D. (2013). A general framework for analyzing beta diversity, nestedness and related community-level phenomena based on abundance data. *Ecol. Complex.* 15, 52–61. doi: 10.1016/j.ecocom.2013.03.002

R Development Team (2016). *R: A Language and Environment for Statistical Computing*. Vienna: R Development Team.

Ramos-Jiliberto, R., Pablo Oyanedel, J., Vega-Retter, C., and Valdovinos, F. S. (2009). Nested structure of plankton communities from Chilean freshwaters. *Limnologica* 39, 319–324. doi: 10.1016/j.limno.2009.06.005

Ruhí, A., Datry, T., and Sabo, J. L. (2017). Interpreting beta-diversity components over time to conserve metacommunities in highly dynamic ecosystems. *Conserv. Biol.* 31, 1459–1468. doi: 10.1111/cobi.12906

Rumrich, U., Lange-Bertalot, H., and Rumrich, M. (2000). *Diatoms of the Andes, from Venezuela to Patagonia/Tierra del Fuego, and Two Additional Contributions*. Königstein: Iconographia diatomologica 9 ARG Gartner Verlag KG.

Salgado, J., Sayer, C. D., Brooks, S. J., Davidson, T. A., Goldsmith, B., Patmore, I. R., et al. (2018). Eutrophication homogenizes shallow lake macrophyte assemblages over space and time. *Ecosphere* 9:e02406. doi: 10.1002/ecs2.2406

Sarmiento, F. O. (2002). Anthropogenic change in the landscapes of highland Ecuador. *Geogr. Rev.* 92, 213–234. doi: 10.1111/j.1931-0846.2002.tb00005.x

Schneider, T., Hampel, H., Mosquera, P. V., Tylmann, W., and Grosjean, M. (2018). Paleo-ENSO revisited: Ecuadorian Lake Pallcacocha does not reveal a conclusive El Niño signal. *Glob. Planet. Change* 168, 54–66. doi: 10.1016/j.gloplacha.2018.06.004

Servant-Vildary, S., and Roux, M. (1990). Multivariate analysis of diatoms and water chemistry in Bolivian saline lakes. *Hydrobiologia* 197, 267–290. doi: 10.1007/978-94-009-0603-7_23

Simpson, G. L. (2018). Modelling palaeoecological time series using generalized additive models. *Front. Ecol. Evol.* 6:149. doi: 10.3389/fevo.2018.00149

Spanbauer, T. L., Fritz, S. C., and Baker, P. A. (2018). Punctuated changes in the morphology of an endemic diatom from Lake Titicaca. *Paleobiology* 44, 89–100. doi: 10.1017/pab.2017.27

Steinitz-Kannan, M., Colinvaux, P., and Kannan, R. (1983). Limnological studies in Ecuador: 1. A survey of chemical and physical properties of Ecuadorian lakes. *Arch. Hydrobiol.* 65, 61–105.

Steinitz-Kannan, M., Nienaber, M. A., and Riedinger-Whitmore, M. A. (1993). The fossil diatoms of Lake Yambo, Ecuador: a 2500 year record of intense El Niño events. *Bull. Inst. Fr. Etudes Andines* 22, 227–241.

Szabó, B., Lengyel, E., Padisák, J., and Stenger-Kovács, C. (2019). Benthic diatom metacommunity across small freshwater lakes: driving mechanisms, β-diversity and ecological uniqueness. *Hydrobiologia* 828, 183–198. doi: 10.1007/s10750-018-3811-9

Toivanen, M., Hjort, J., Heino, J., Tukiainen, H., Aroviita, J., and Alahuhta, J. (2019). Is catchment geodiversity a useful surrogate of aquatic plant species richness? *J. Biogeogr.* 46, 1711–1722. doi: 10.1111/jbi.13648

Valencia, B. G., Matthews-Bird, F., Urrego, D. H., Williams, J. J., Gosling, W. D., and Bush, M. (2016). Andean microrefugia: testing the Holocene to predict the Anthropocene. *New Phytol.* 212, 510–522. doi: 10.1111/nph.14042

Van Colen, W., Mosquera, P. V., Hampel, H., and Muylaert, K. (2018). Link between cattle and the trophic status of tropical high mountain lakes in páramo grasslands in Ecuador. *Lakes Reserv. Res. Manag.* 23, 303–311. doi: 10.1111/lre.12237

Van Colen, W. R., Mosquera, P., Vanderstukken, M., Goiris, K., Carrasco, M.-C., Decaestecker, E., et al. (2017). Limnology and trophic status of glacial lakes in the tropical Andes (Cajas National Park, Ecuador). *Freshw. Biol.* 62, 458–473. doi: 10.1111/fwb.12878

Van Dam, H., Mertens, A., and Sinkeldam, J. (1994). A coded checklist and ecological indicator values of freshwater diatoms from the Netherlands. *Netherland J. Aquat. Ecol.* 28, 117–133. doi: 10.1007/bf02334251

Van der Plas, F., Manning, P., Soliveres, S., Allan, E., Scherer-Lorenzen, M., Verheyen, K., et al. (2016). Biotic homogenization can decrease landscape-scale forest multifunctionality. *Proc. Natl. Acad. Sci. U.S.A.* 113, 3557–3562.

Vilmi, A., Karjalainen, S. M., and Heino, J. (2017). Ecological uniqueness of stream and lake diatom communities shows different macroecological patterns. *Diver. Distribut.* 23, 1042–1053. doi: 10.1111/ddi.12594

Vilmi, A., Zhao, W., Picazo, F., Li, M., Heino, J., Soininen, J., et al. (2020). Ecological processes underlying community assembly of aquatic bacteria and macroinvertebrates under contrasting climates on the Tibetan Plateau. *Sci. Total Environ.* 702:134974. doi: 10.1016/j.scitotenv.2019.134974

Vitousek, P. M., Mooney, H. A., Lubchenco, J., and Melillo, J. M. (1997). Human domination of Earth's ecosystems. *Science* 277, 494–499. doi: 10.1126/science.277.5325.494

Vuille, M., Bradley, R. S., Werner, M., and Keimig, F. (2003). 20th century climate change in the tropical Andes: observations and model results. *Clim. Change* 59, 75–99. doi: 10.1007/978-94-015-1252-7_5

Weide, D. M., Fritz, S. C., Hastorf, C. A., Bruno, M. C., Baker, P. A., Guedron, S., et al. (2017). A∼ 6000 yr diatom record of mid-to late Holocene fluctuations in the level of Lago Wiñaymarca, Lake Titicaca (Peru/Bolivia). *Quat. Res.* 88, 179–192. doi: 10.1017/qua.2017.49

Wengrat, S., Padial, A. A., Jeppesen, E., Davidson, T. A., Fontana, L., Costa-Böddeker, S., et al. (2018). Paleolimnological records reveal biotic homogenization driven by eutrophication in tropical reservoirs. *J. Paleolimnol.* 60, 299–309. doi: 10.1007/s10933-017-9997-4

Wetzel, C. E., de Bicudo, D. C., Ector, L., Lobo, E. A., Soininen, J., Landeiro, V. L., et al. (2012). Distance decay of similarity in neotropical diatom communities. *PLoS One* 7:e45071. doi: 10.1371/journal.pone.0045071

Willis, K. J., Bailey, R. M., Bhagwat, S. A., and Birks, H. J. B. (2010). Biodiversity baselines, thresholds and resilience: testing predictions and assumptions using palaeoecological data. *Trends Ecol. Evol.* 25, 583–591. doi: 10.1016/j.tree.2010.07.006

Winegardner, A. K., Legendre, P., Beisner, B. E., and Gregory-Eaves, I. (2017). Diatom diversity patterns over the past c. 150 years across the conterminous United States of America: identifying mechanisms behind beta diversity. *Glob. Ecol. Biogeogr.* 26, 1303–1315. doi: 10.1111/geb.12640

Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J. R. Stat. Soc. Ser. B* 73, 3–36. doi: 10.1111/j.1467-9868.2010.00749.x

Wood, S. N. (2017). *Generalized Additive Models: An Introduction with R*. Boca Raton, FL: CRC press.

Wright, D. H., and Reeves, J. H. (1992). On the meaning and measurement of nestedness of species assemblages. *Oecologia* 92, 416–428. doi: 10.1007/bf00317469

Zaharescu, D. G., Hooda, P. S., Burghelea, C. I., and Palanca-Soler, A. (2016). A multiscale framework for deconstructing the ecosystem physical template of high-altitude lakes. *Ecosystems* 19, 1064–1079. doi: 10.1007/s10021-016-9987-9

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REVIEW
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Integrating Disturbance, Seasonality, Multi-Year Temporal Dynamics, and Dormancy Into the Dynamics and Conservation of Metacommunities

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The metacommunity framework has rapidly become a dominant concept used by ecologists to understand community assembly. By emphasizing extinction-colonization dynamics, dispersal, and species' niche requirements in determining community structure, metacommunity theory unifies local and regional processes as integral to species distributions across landscapes. Metacommunity structure has traditionally been treated as static. However, habitat characteristics and community composition can shift through time because of factors like seasonal dynamics, ecosystem disturbance, multi-year climate variation (e.g., El Niño Southern Oscillation), and production and emergence of dormant propagules. In most systems, the relevance of such temporal variation for the structure and persistence of metacommunities is an open question that is of potential importance for conservation and management. We evaluate and synthesize the theory and concepts relevant to four major forms of temporal dynamics that are pertinent to metacommunities: disturbance, seasonality, multi-year climate variation, and dormancy. For each type of dynamic we review the theoretical underpinnings and empirical evidence to evaluate how the dynamic drives temporal variation in metacommunity structure. We also consider how major forms of anthropogenic change further influence these patterns. Our survey highlights that seasonal climatic differences can modify the distribution and availability of resources and connectivity, with consequences for species' use of the landscape and species interactions. Disturbance and multi-year climate cycles can increase the importance of dispersal, but implications for environmental filtering and species interactions remain unresolved. Dormant life stages serve to anchor habitat patches and species pools in space and highlight the importance of dispersal-dormancy tradeoffs and environmental variation for metacommunity structure. Temporal variability in biotic and abiotic conditions associated with these drivers can modify the relative strengths of dispersal, environmental filtering, and species interactions, three biological processes that drive metacommunity structure. Inclusion of spatiotemporal drivers creates patterns

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of species diversity that differ from traditional metacommunity ideas. We use these insights to highlight research needs, suggest a reconceptualization of metacommunities as undergoing continuous change, and discuss the implications of temporal dynamism for the conservation and management of metacommunities.

Keywords: environmental filtering, dispersal, species interactions, species diversity, anthropogenic change, species sorting, mass effects

INTRODUCTION

In their original conception, metacommunities were largely viewed as occupying a temporally invariant stochastic environment. The metacommunity concept depicts idealized types of metacommunity dynamics in such temporally static environments (Leibold et al., 2004; Holyoak et al., 2005). Metapopulations and metacommunities have focused on "ecology at the mesoscale," reflecting timescales shorter than those required for speciation (<1–100 generations) and spatial scales between those of local populations/communities and biogeography (Holt, 1993). However, systems may have extrinsic temporal dynamics (e.g., Jabot et al., 2020). These may either coincide with timescales over which metapopulation and metacommunity dynamics occur or happen over longer time periods and potentially cause shifts in metacommunity dynamics. Consequently, several forms of extrinsic temporal dynamics are potentially relevant to metacommunities, including disturbance regimes, seasonality, multi-year temporal dynamics such as El Niño cycles, and dormancy. We review relevant theoretical and empirical work that relates to temporal dynamics of metacommunities as well as the consequences of global change for such dynamics. Considering our findings, we make recommendations about how to progress in studying temporal metacommunity dynamics and for the conservation of metacommunities.

A hierarchy of spatial and temporal scales are relevant to how temporal dynamics affect metacommunities and biodiversity (Hart et al., 2017). The original metacommunity paradigm was based on the idea that populations can colonize or go extinct from local habitat patches, or be rescued from extinction by immigration, but the habitat and environment are static (Leibold et al., 2004). This implies a relatively constant resource supply, environmental conditions amenable to individual survival, and patches always present. Such temporal stasis implicitly assumes that there is a fixed per unit time probability of individual birth, death, and movement due to environmental conditions (e.g., Chave, 2004). Another common scenario is that habitat patches are temporary ecosystems that come and go through time, such as tidal pools (Kolasa and Romanuk, 2005), temporary seasonal wetlands (Boudell and Stromberg, 2008), temporary streams (Resh et al., 1988), water-filled tree holes (Ellis et al., 2006), and water-filled pitcher plant leaves (Kneitel and Miller, 2002). Patch formation and destruction might occur stochastically, through external environmental drivers (e.g., seasonal weather, tidal cycles), or through an internal patch process (e.g., succession, aging of individual pitcher plant leaves or tree branches that can hold water). Simplified models typically assume constant probabilities of patch formation and destruction through time (e.g., Hastings, 2003), but patches may have their own temporal dynamics. Temporal environmental variation could cause local extinctions of species or affect population growth rates more generally (Drake and Lodge, 2004), including through seasonal fluctuations, disturbances, or multi-annual climate variation, which we review in this paper.

Temporal variation could be considered in three ways. First, if variation is stochastic and unpredictable but frequent in occurrence, it may be within the norm to which an organism is adapted and, consequently, such organisms may buffer against this variability through existing plasticity (behavior, physiology, etc.) or demographic responses (West-Eberhard, 1989). Conversely, temporally predictable variation (e.g., seasonality) might be overcome by life-history evolution or some form of plasticity in behavior, morphology, or physiology (Boyce, 1979). Disturbance events were originally thought of as unpredictable (Resh et al., 1988), but later were pointed out to be quite predictable in some systems (e.g., Poff, 1992; Tonkin et al., 2017). Recurrent periods of low resources or otherwise stressful conditions within habitat patches that remain in the same places could select for dormancy (McPeek and Kalisz, 1998; Wisnoski et al., 2019) or hibernation (e.g., Bieber et al., 2014). Finally, other temporal variation may be both stochastic and infrequent such as rare, extreme and often large disturbance events including hurricanes, droughts, volcanic eruptions, and some floods or fires (e.g., Foster et al., 1998). Rare events or changes in systems that are observed at a short timescale may appear as shifts in dynamical regimes (Folke et al., 2004), or as transient dynamics, and thus may not be reflective of dynamics that occur over longer timescales (e.g., Hastings, 2004). At spatial scales up to entire continents, organisms may also deal with or benefit from spatially and temporally unpredictable rare events by being extremely mobile and itinerant or nomadic in their movements (Andersson, 1980; Ydenberg, 1987).

We explore how temporal and spatiotemporal variation affect metacommunity dynamics through three separate biological drivers: dispersal, environmental filtering, and species interactions (Biswas and Wagner, 2012; Marrec et al., 2018). Dispersal (in contrast with migration or general movement) is defined as a one-way, permanent movement of individuals from one population to another (Jacobson and Peres-Neto, 2010) and has a well-established role in metacommunity theory (Mouquet and Loreau, 2002). Environmental filtering has been defined as the selection of species that can survive and persist given the environmental conditions at a location (Emerson and Gillespie, 2008; Kraft et al., 2015; Cadotte and Tucker, 2017), and can be understood in a metacommunity context as the environmental conditions that govern species' occurrence (Biswas and Wagner, 2012). Species interactions in a metacommunity context influence species' occurrence through interspecific competition and predation (Cottenie, 2005; Biswas and Wagner, 2012), and is an often overlooked but key driver (García-Girón et al., 2020). Thompson et al. (2020) used dispersal, "density-independent responses to abiotic conditions" (instead of environmental filtering) and "density-dependent biotic interactions" (instead of species interactions) as three axes for depicting and modeling metacommunity dynamics, and established overlap with the conceptual paradigms of Leibold et al. (2004): species sorting, mass effects, patch dynamics, and neutral dynamics. Species sorting fits neatly into the structuring mechanism of environmental filtering or strong species interactions for species with low ability to move between patches (Thompson et al., 2020), and spatial niche separation leads to coexistence. Mass effects is the interaction between environmental filtering or species interactions and dispersal, and has most commonly been empirically investigated as an interaction between environmental effects and dispersal or habitat connectivity (Cottenie, 2005). Consequently, mass effects are similar to species sorting but with a stronger role of dispersal (Thompson et al., 2020). Coexistence through patch dynamics involves trade-offs in species traits such as competitive ability and colonization ability (Holyoak et al., 2005), and hence an interaction of species interactions and dispersal (Thompson et al., 2020). Neutral dynamics require localized dispersal and emphasize stochastic demographic processes or individualistic responses to environmental variation (Leibold et al., 2004; Thompson et al., 2020). These paradigms are neither exhaustive (Brown et al., 2017) nor mutually exclusive (Leibold et al., 2004; Winegardner et al., 2012), and empirical studies frequently discover mixed metacommunity structures (Logue et al., 2011).

We discuss the effects of various forms of temporal dynamics on metacommunities by considering biological mechanisms of community structure and species distribution patterns. Our overarching question is how do temporal and spatiotemporal dynamics affect metacommunity structure and dynamics? We consider how disturbance, seasonality, long-term temporal dynamics, and dormancy affect temporal variation in metacommunity structure. More specifically, we explore the influence of these drivers on the relative importance, strength, and interactions among the biological processes of environmental filtering, dispersal, and species interactions. We identify when and describe how these drivers intersect with the traditional metacommunity paradigms identified by Leibold et al. (2004) to link local-scale community assembly processes to regional dynamics. By doing so, we attempt to unify existing theory surrounding the effects of extrinsic temporal dynamics on traditional metacommunity archetypes with a set of biological processes that can be identified and quantified through empirical study. Finally, we discuss how anthropogenic activity and global climate change impact the drivers of spatiotemporal dynamics of metacommunities, highlight management and conservation implications and suggest directions for future research.

DRIVERS OF TEMPORAL DYNAMICS IN METACOMMUNITIES

Below, we examine the theoretical underpinnings and empirical evidence that demonstrate the temporally dynamic nature of metacommunities. We describe and summarize the central mechanisms by which dispersal, environmental filtering, and species interactions shift over time and space to structure metacommunities subject to disturbance, seasonality, multi-year climate fluctuations, and dormancy (**Table 1**). We also highlight empirical examples of studies that best exemplify how the temporal drivers of disturbance, seasonality, multi-year climate fluctuations, and dormancy influence the biological structuring mechanisms of dispersal, environmental filtering, and species interactions (**Supplementary Table S1**).

Disturbance

Disturbance can be defined as any discrete event that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment (Petraitis et al., 1989). This definition encompasses lethal and sublethal effects of disturbance but does not include predictable and/or seasonal changes. When applied to metacommunity theory, disturbances create both temporal and spatial variability among habitat patches (Altermatt et al., 2011b). While disturbance theories including the intermediate disturbance hypothesis (IDH, Connell, 1978), the successional mosaic hypothesis (Roxburgh et al., 2004; Battisti et al., 2016), the dynamic equilibrium model (Huston, 1979; Svensson et al., 2012; Battisti et al., 2016), and the subsidy-stress model (Odum et al., 1979; Odum, 1985) discuss how disturbance promotes coexistence, increases diversity, increases productivity, and changes community assembly at a local scale, the role of disturbance on regional metacommunity structure has received little attention (Vanschoenwinkel et al., 2013).

Empirical Evidence

Empirical evidence suggests that disturbance can shift the importance of stochastic vs. deterministic processes in structuring metacommunities by influencing the strength of dispersal, environmental filtering, and species interactions (**Table 1**). Recolonization of disturbed patches with species from undisturbed patches is a key tenet of disturbance models, and, consequently, dispersal should increase in importance in disturbed metacommunities. The limited body of existing empirical work so far supports this idea, since metacommunity structure after a disturbance is driven by strong mass effects and dispersal between disturbed and non-disturbed patches (**Supplementary Table S1**; Warren, 1996; Östman et al., 2006; Starzomski and Srivastava, 2007; Altermatt et al., 2011b; Vanschoenwinkel et al., 2013; Ojima and Jiang, 2017; Sarremejane et al., 2018; Cañedo-Argüelles et al., 2020). For example, disturbance in the form of varying rates of pool drying in isolated pools exacerbated existing dispersal limitation (Vanschoenwinkel et al., 2013). Thus, frequently disturbed patches relied on high dispersal rates, which allowed species eliminated by disturbance to recolonize and contribute to maintaining local diversity

TABLE 1 | Summary of ways in which different temporal drivers influence the biological processes that structure metacommunities.

	Structuring mechanism		
	Dispersal	**Environmental filtering**	**Species interactions**
Disturbance	Strong structuring mechanism following disturbance because dispersal is required for recolonization of species driven locally extinct by disturbance.	Inconclusive evidence suggests changes in environmental filtering depend on the severity of the disturbance. Extreme disturbances (e.g., drought or flooding) increase the importance of environmental filtering. Is only important if species vary in their ability to tolerate disturbance.	Limited empirical evidence, but the IDH suggests that disturbance decreases the importance of species interactions. Little support for the competition-colonization tradeoff suggests that competitive interactions are not structuring. Competitive interactions may increase in importance with time post-disturbance.
Seasonality	Seasonal changes in connectivity increase or decrease constraints on dispersal and therefore its influence on structure. Dispersal traits of species mediate the impact of seasonal changes in connectivity on dispersal ability.	When there are drastically different abiotic conditions between seasons, environmental filtering is often stronger in one of the seasons.	Seasonal pulses in resource availability change the strength of competition and/or predation. Seasonal changes in species behavior have community level impacts (e.g., seasonal change in foraging behavior; seasonal migration of species). Seasonal changes in species' physiology increase or decrease competitive interactions.
Multi-year temporal dynamics	Environmental changes associated with ENSO and NAO can modify dispersal vectors or habitat connectivity. Indirect changes in populations can change their source vs. sink status and whether they produce emigrants or receive immigrants.	ENSO and NAO are associated with weather anomalies, which likely act as strong environmental filters.	Through effects of ENSO and NAO on population dynamics and activity patterns of poikilothermic organisms, changes in the importance of species interactions as metacommunity structuring mechanisms are likely, but few have been documented to date.
Dormancy	Dispersal is favored in unpredictable environments, where spatial predictability in the occurrence of suitable habitat is low and/or infrequent, or where populations or habitats are expanding rapidly.	Predictable occurrence of habitat in time and space with unfavorable seasons or years will favor dormancy, which reduces the relevance of environmental filtering unless dormant propagules emerge in environmentally unfavorable conditions.	Whether conditions favoring dormancy reduce the frequency or strength of species interactions depends on the covariation of species in their environmental responses.

(Vanschoenwinkel et al., 2013). However, it is challenging to directly measure dispersal in metacommunities and, accordingly, empirical work lags behind theoretical developments (Jacobson and Peres-Neto, 2010). Previous empirical research has mostly been confined to laboratory experiments (e.g., Warren, 1996; Östman et al., 2006; Altermatt et al., 2011b; Ojima and Jiang, 2017) where both dispersal and disturbance can be manipulated, field experiments with aquatic protists and invertebrates (Vanschoenwinkel et al., 2013), or correlative tests of the effects of connectivity (Tornwall et al., 2017; Cañedo-Argüelles et al., 2020). Theoretical work suggests that disturbance results in directionally-biased dispersal, which in turn can reduce species diversity and patch occupancy (Altermatt et al., 2011b). However, contradictory findings regarding the impacts of biased dispersal on metacommunity persistence suggest that disturbance severity could play a key role in the interaction between dispersal and disturbance in metacommunities. For example, biased dispersal from undisturbed to disturbed patches reduced metapopulation viability when disturbances eliminated local populations (Elkin and Possingham, 2008). However, when disturbances reduced population densities, metapopulation viability was highest when there was biased dispersal toward undisturbed patches (Altermatt et al., 2011b). Future work should examine how different disturbance severities interact with dispersal to change metacommunity structure.

Changes to the physical environment are one consequence of disturbance. Accordingly, it makes intuitive sense that the strength of environmental filtering in determining metacommunity structure might increase with disturbance. Theoretical models support this idea, whereby species that persist in heavily disturbed patches have high intrinsic growth rates, are competitively inferior, and exhibit high interaction strengths (Altermatt et al., 2011b). This provides strong evidence for species sorting in the metacommunity. Empirical work with protists and rotifers (Östman et al., 2006; Altermatt et al., 2011a), macroinvertebrates (Chase, 2007; Campbell et al., 2015; Cañedo-Argüelles et al., 2020), and plants (Laliberté et al., 2013) also support that environmental filtering becomes a predominant structuring mechanism in a metacommunity following disturbance (S1). Species with higher intrinsic growth rates are more likely to disperse, demonstrating that certain species succeed with the temporal and spatial variation created by disturbance (Altermatt et al., 2011a). However, there is contradicting evidence with protists (Warren, 1996; Limberger and Wickham, 2012) and invertebrates (Vanschoenwinkel et al., 2013) indicating that disturbance may not increase the importance of environmental filtering. For example, environmental filtering was not a dominant structuring mechanism in an invertebrate community in temporary rock pools, potentially because no disturbance tolerant specialists were present in the metacommunity (Vanschoenwinkel et al., 2013). Therefore, environmental filtering may only be an important structuring mechanism if species vary in their ability to tolerate disturbance. The discrepancy between the relative importance of environmental filtering as a structuring process among similar microcosm experiments suggests that its influence may depend on the severity and scale of disturbance. This is congruent with predictions of the IDH and the dynamic equilibrium model, where disturbance frequency or intensity modulates diversity. Future research is needed to quantify the relationship between disturbance severity and the relative importance of environmental filtering.

The IDH states that high diversity is found at intermediate disturbance rates because disturbance prevents competitive exclusion through a reduction in competition (Connell, 1978). Notwithstanding that the IDH is a mechanism that can alter community composition but lacks a robust mechanism for coexistence (Roxburgh et al., 2004), if the IDH is supported, disturbance in a metacommunity could reduce the importance of competitive interactions and elevate survival and recolonization as stronger drivers of metacommunity structure following disturbance. While some studies at a local scale have supported the competition-colonization trade-off component of the IDH (Caswell and Cohen, 1991; Barradas et al., 1996), the majority of empirical studies fail to find support (Mackey and Currie, 2001). However, Cadotte (2007) suggests that the IDH may still apply at a metacommunity scale. Local disturbance creates spatial heterogeneity and a successional mosaic at a regional scale, favoring certain species at each successional stage. In late-successional, undisturbed patches, strong competitors are expected to be favored suggesting that competitive interactions would be the most important structuring mechanism in that patch. However, in recently disturbed patches, strong colonizers have a higher probability of colonization, so the patch is expected to be structured more by dispersal and less by competitive interactions (**Supplementary Table S1**; Cadotte, 2007). Thus, in post-disturbance metacommunities, competitive interactions are expected to decrease in importance while dispersal increases. While this theory was supported in a microcosm experiment with protists and rotifers (Cadotte, 2007), there is no additional empirical work that examines species interactions after disturbance in metacommunities.

Overall, current evidence suggests that following a disturbance, dispersal becomes more important in driving metacommunity organization whereas changes in the relative importance of environmental filtering depend on the severity of the disturbance (**Figure 1**). Although theory suggests that competitive interactions are less important structuring mechanisms in recently disturbed metacommunities, empirical evidence is lacking. While disturbance creates temporally distinct changes – before and after the disturbance event – most metacommunity studies, have examined repeated disturbances but only looked at metacommunity structure at the end of the experiment (e.g., Altermatt et al., 2011b). These studies cannot provide important insight into how the importance of different structuring processes change with time since disturbance or with repeated, predictable disturbance.

Anthropogenic Global Change, Disturbance and Metacommunities

Global climate change is expected to increase both the frequency and severity of many types of disturbance including fire, insect outbreaks, and pathogens (Seidl et al., 2017). An increase in disturbance suggests metacommunities will be more frequently structured by dispersal. In systems that are further stressed by habitat fragmentation, which reduces connectivity and can limit dispersal (Tischendorf and Fahrig, 2000; Dixo et al., 2009), metacommunity persistence might be at risk. Anthropogenic global change has also altered disturbance regimes. Policies of fire suppression have lengthened the natural fire cycle resulting in fuel accumulation and infrequent but unusually intense fires, and flood control has caused more extreme but infrequent flooding events (Sousa, 1984). In systems adapted to a certain disturbance regime, changes to that regime could result in different structuring forces becoming more important than under historic conditions. Additionally, increasing size and spatial extent of disturbances with climate change may mitigate any potential rescue effects, reducing the importance of dispersal as a structuring mechanism.

Urban environments also present a system to examine how disturbance influences metacommunity structure. Anthropogenic disturbance in urban environments (e.g., construction, pollution, gardening, recreation) is more common than natural disturbance in addition to being more localized and sometimes more severe (Rebele, 1994). In cities, barriers to dispersal are highly prevalent (Blakely et al., 2006; Peralta et al., 2011), urban landscapes create a distinct environmental filter (Swan et al., 2011), and species interactions are changed through high amounts of invasive/non-native species, mesopredator release, decreased predation, and altered competition (Rebele, 1994; McKinney, 2002; Grimm et al., 2008). However, if urbanization itself is considered a long-term disturbance, these observations on dispersal, environmental filtering, and species interactions might be explained by the relative importance of metacommunity structuring processes post-disturbance. Following this reasoning, in urban ecosystems, dispersal and environmental filtering would be important structuring mechanisms while species interactions would be less important. However, there is currently little empirical evidence that examines how the importance of dispersal and environmental filtering differ in urban ecosystems, and the relative importance of species interactions varies across studies (Rodewald et al., 2011; Rivera-López and MacGregor-Fors, 2016). Nevertheless, there is a key difference between urbanization as a disturbance and the types of disturbances previously discussed in this paper. Urbanization can create novel ecosystems which require significantly different conservation and restoration practices to return to pre-disturbed, historic states (Hobbs et al., 2009). Thus, temporal variation in the importance of structuring processes

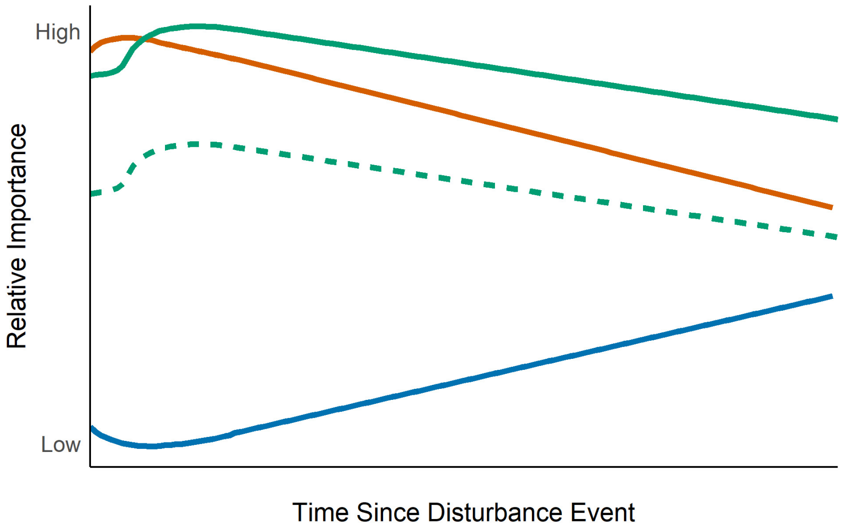

FIGURE 1 | Relative importance of biological processes in structuring metacommunities with increasing time since a disturbance event (at *y*-axis). The orange line indicates dispersal processes, blue line indicates species interactions, and green lines indicate environmental filtering. Current empirical evidence strongly suggests that the importance of environmental filtering is context dependent. Thus, the solid green line indicates severe disturbances (when disturbed patches become uninhabited) while the dashed green line indicates less severe disturbances (some individuals in each patch remain).

in urban ecosystems is likely to be quite different than that of natural systems.

Theories about disturbance in metacommunities can also be applied to anthropogenic stressors such as eutrophication. The impact of eutrophication on freshwater metacommunity organization is poorly understood (Heino, 2013) but by considering eutrophication as a disturbance, one can predict how shifts in the strength of dispersal, environmental filtering, and species interactions associated with eutrophication may impact metacommunity organization. This knowledge may be useful in guiding conservation efforts toward the amelioration of eutrophication's most harmful effects. Similar consideration of metacommunity dynamics can help direct conservation efforts regarding other anthropogenic stressors including pesticides, pollution, and salinization.

Seasonality

Most ecological systems experience seasonal oscillations, defined as consistent and recurring annual changes in environmental conditions, including changes in temperature, precipitation, photoperiod, resource availability, and wind. Cyclical changes in abiotic factors result in seasonal resource pulses, which expand temporal niche availability for many species (Tonkin et al., 2017). However, seasonality can also constrain species, acting as an environmental filter when conditions differ from species' climatic tolerance (Gouveia et al., 2013; Tonkin et al., 2017). Accordingly, seasonality can exert strong controls on biodiversity, and season-diversity relationships are prevalent in many taxa (Mellard et al., 2019).

Empirical Evidence

Despite the recognition that seasonal variation influences community dynamics, seasonality is frequently disregarded in ecological research because it is complex and difficult to investigate (McMeans et al., 2015; White and Hastings, 2018). Similarly, studies of metacommunities have largely ignored seasonality. The shortcomings of excluding seasonality in metacommunity theory are especially salient in highly dynamic systems, where local communities may be affected by intra-annual seasonal changes (Datry et al., 2016; Sarremejane et al., 2017). In such systems, seasonality leads to cyclical fluxes in the drivers of community assembly (e.g., environmental conditions, presence/absence of migrants, resource availability, connectivity) and potentially to subsequent changes in community structure. However, despite the fact that dynamic systems characterized by seasonal change are widespread (e.g., tidal zones, floodplains, intermittent rivers), seasonal variation in metacommunity structure is only recently being explicitly tested (Fernandes et al., 2014; Sarremejane et al., 2017).

Much of the empirical study investigating seasonal changes in metacommunities has focused on intermittent rivers, which provide a strong conceptual basis for understanding the role of seasonality in metacommunity structure because they experience seasonal shifts between aquatic and terrestrial states (Larned et al., 2010). This dynamism is useful for addressing the question of how communities are organized in time and space and which biological processes drive seasonal changes in community structure. For example, in dry phases, flow cessation imposes strong environmental filtering, sorting species such that those adapted to lentic or terrestrial conditions are favored (Datry et al., 2016; Sarremejane et al., 2017). At the start of the wet season, dispersal processes are typically the predominant structuring force since certain species are constrained by dispersal limitation (Datry et al., 2016), ultimately enhancing the effects of patch dynamics in structuring the metacommunity. Later in the wet season, once initial colonization has occurred, species sorting via environmental filtering is expected to again become important with progression toward lentic and terrestrial conditions (**Figure 2**).

Overall, work from intermittent rivers and floodplains indicates that, where there exist significantly different abiotic conditions between seasons, the relative strength of environmental filtering and dispersal as biological processes driving metacommunity structure fluctuate seasonally (**Table 1**; Fernandes et al., 2014; Datry et al., 2016; Sarremejane et al., 2017). Where specific species are located in time and space is additionally mediated by species traits such as dispersal ability (Csercsa et al., 2019) and ability to cope with environmental conditions (Kraft et al., 2015). Though there is evidence that the biological processes of dispersal and environmental filtering seasonally influence metacommunity structure in terrestrial systems (Delciellos et al., 2018), this line of evidence is less robust. Consequently, further research on seasonally driven temporal variation in metacommunity organization should be conducted in dynamic terrestrial systems.

It is widely acknowledged that local interactions among species impact community composition. However, biotic interactions are not static, and the identity and strength of interspecific interactions can change over time (Saavedra et al., 2016) and space (Ruesink, 1998; Leonard, 2000). Accordingly, seasonal changes in species interactions can drive spatiotemporal changes in metacommunity structure (**Table 1**). Seasonality mediates species interactions in various ways. Commonly, seasonal pulses in resource availability can strengthen or weaken competition among species, fundamentally altering metacommunity structure (Cisneros et al., 2015). Seasonal resource pulses can also cause predator-prey dynamics to fluctuate if vulnerability of prey species shift seasonally (Owen-Smith, 2008) and/or predators have higher capture rates (Metz et al., 2012). Predation also fluctuates seasonally if predator activity levels are highly seasonal, as is the case in brumating or hibernating species (e.g., Sperry et al., 2008). Ultimately, seasonal variation in the strength of interspecific competition and predation may drive variation in metacommunity structure.

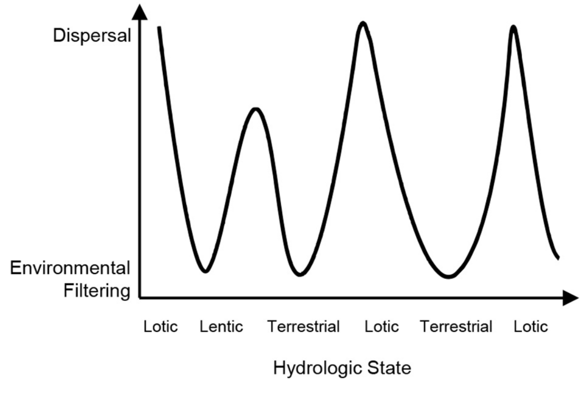

FIGURE 2 | The importance of seasonal shifts in hydrology for environmental filtering and dispersal processes and associated changes in spatial patterns of metacommunity structure (Datry et al., 2016).

The strength of competition and predation can also fluctuate seasonally in metacommunities that experience migration, a special case of dispersal and movement that is both predictable and seasonal (Dingle, 1996). Because migration is a seasonal phenomenon, migratory species can impact communities in spatiotemporally complex ways (Schlägel et al., 2019). Year-long residents may be exposed to seasonal differences in interspecific competition, predation pressure, food resource availability, and disease as a result of the presence or absence of migrating species (Talbot and Talbot, 1963; Sinclair, 1985; Holdo et al., 2011). These pressures that migrating species impose on year-round residents, by definition, only exist for part of the year. Therefore, the metacommunity impact of these features is likely to fluctuate seasonally in systems where seasonal migration occurs. Competition and predation can also be moderated by seasonal increases or decreases in species' physiology. For example, greater resource consumption and demands associated with higher summer temperatures and temperature-dependent metabolic rates may increase the role that competitive interactions play in determining metacommunity organization (Ren et al., 2018).

Anthropogenic Global Change, Seasonality, and Metacommunities

Though the above studies suggest that incorporating seasonality into the metacommunity framework may lead to predictable and cyclic patterns in metacommunity organization, several anthropogenic activities that vary temporally may disrupt such patterns. For example, seasonal release of water from dams may alter flood pulses or remove seasonality completely (Junk et al., 1989). High human water use in urban areas can generate dry-season flows (Solins and Cadenasso, 2020), sometimes converting intermittent streams to perennial ones (White and Greer, 2006). Anthropogenic pollution often varies seasonally, with concentrations of pesticides, salts, and other pollutants fluctuating based on seasonal human use. For example, concentrations of the insecticide fipronil in urban residential runoff reach lethal levels for many arthropod species in the spring and summer but decrease in other seasons (Gan et al., 2012). When pesticide use is coupled with elevated water use in urban environments, natural seasonal processes such as stream-drying may be eliminated, leading to seasonal peaks in pesticide concentration in water bodies and posing potential consequences for community structure (White and Greer, 2006; Ricart et al., 2010). Similarly, road deicing salts applied in winter result in seasonal increases in chloride concentrations, with negative impacts on species, communities, and ecosystems (Kaushal et al., 2005; Hintz and Relyea, 2019).

In recent years, the modified timing and enhanced variability of seasonal events brought about by global climate change may create mismatches within and among species and their environments (Parmesan, 2006; Walther, 2010). For example, as the timing of seasonal events shifts, a species may no longer be suited to its environment, increasing the importance of environmental filtering in metacommunity assembly. This has been observed in the phenology of hibernation, where shifts in emergence dates may negatively impact individual fitness or species persistence (Inouye et al., 2000; Lane et al., 2012).

Mismatches may also occur among interacting species, such as when reproductive timing and prey availability become asynchronous (Visser et al., 2006; Tylianakis et al., 2008) or when shifts in seasonal migratory patterns create novel species combinations that alter species' competitive environments (Gilman et al., 2010; Alexander et al., 2015). How these interactions play out in metacommunities and whether they are generalizable is uncertain (Lurgi et al., 2012).

Multi-Year Temporal Dynamics

A large variety of multi-year temporal climate indices capture information about temporal variation in weather (Stenseth et al., 2003), which have many potential and documented effects on metacommunities. Most ecological studies have investigated the effects of two indices on populations and communities, El Niño Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO) (Glynn, 1988; Post et al., 1997; Lindstrom et al., 2001; Fiedler, 2002; Hurrell et al., 2003; Stenseth et al., 2003). The most obvious biotic events of ENSO and NAO are related to interannual changes in average and extremes of temperature and rainfall, with much local variability in rainfall (Fraedrich and Müller, 1992; Hurrell, 1995; Diaz et al., 2001; Hurrell et al., 2003). ENSO and NAO are marked by their periodicity and occurrence over large spatial scales, and are often more strongly correlated with local population dynamics than are local weather variables (Stenseth et al., 2003; Stenseth and Mysterud, 2005). Of particular relevance to metacommunities, they can also synchronize populations across large spatial scales (Elton, 1924; Lindstrom et al., 2001). Mechanistically, ENSO and NAO can affect population and community dynamics through their influence on local weather, such as temperature, precipitation, and snow (reviewed by Lindstrom et al., 2001). This makes such indices potentially relevant to environmental filtering (e.g., Thompson et al., 2020), and synchrony of local populations, which potentially relates to metacommunity persistence (Gouhier et al., 2010).

Empirical Evidence

Examples of the effects of multi-year climate fluctuations on metacommunities come from rivers, marine and terrestrial systems (**Supplementary Table S1**). ENSO and NAO produced changes in metacommunity structure through dispersal, environmental filtering and species interactions (**Tables 1**, **2**).

In major river systems, El Niño events were associated with flooding, which increased connectivity and reduced spatial heterogeneity (interpatch variation) in biological and limnological conditions (Thomaz et al., 2007). During drying periods that followed river floods, pools became more dissimilar in their conditions (Thomaz et al., 2007), which may increase the potential for environmental filtering and species sorting (Leibold et al., 2004). By contrast, El Niño flood events increased similarity of species composition and environmental conditions among patches (Thomaz et al., 2007). These events may have prevented communities from reaching equilibrium states with local environmental conditions (e.g., Thomaz et al., 2007) and created non-equilibrium metacommunities that do not match any of the four paradigms suggested by Leibold et al. (2004). Likewise, severe flooding in El Niño years made the effects of dispersal stronger than the effects of environmental filtering, and dispersal was the main metacommunity structuring mechanism (Pineda et al., 2019). In marine benthic communities in Chile, El Niño events increased dispersal and mass effects, and also augmented differences in species composition among local communities because many environmental effects of El Niño were localized (Camus, 2008). Overall, ENSO events can increase or decrease dispersal, potentially with opposite events in El Niño and La Niña years. Such effects may extend to other climate indices, since Jeffries (2005) found that interannual variation in dispersal of a *Daphnia* species was associated with year-to-year variation in NAO.

ENSO and NAO events are important factors in global climate anomalies (Fraedrich and Müller, 1992; Diaz et al., 2001; Jeffries, 2005) that have the potential to act as environmental filters. In the one metacommunity study of environmental filtering, Pineda et al. (2019) partitioned diversity of phytoplankton, ciliates and zooplankton in lakes in a subtropical river system and found varied effects for environmental filtering for different taxonomic groups. For phytoplankton and zooplankton, correlations of environmental variables with species richness and diversity indices were indicative of environmental filtering. However, these environmental filtering effects were not statistically significant for ciliates for unclear reasons. Hence, there is a suggestion that El Niño and La Niña events relate to differences in environmental filtering for some, but not all taxa.

A few studies have documented effects of ENSO or NAO that translate directly to the role of species interactions in structuring metacommunities. The intertidal rocky invertebrate study of Camus (2008) targeted prey species of consumers through gut content analyses, showing changes in species interactions through predation in addition to the changes in dispersal and environmental filtering discussed above. In fishes in the Baltic Sea, winter values of NAO and the Baltic Sea Index (another climate index) were correlated with Atlantic cod recruitment, and the system was modeled as a source-sink system with a food web consisting of cod, herring, and sprat (Lindegren et al., 2014). Higher cod numbers led to greater predation on smaller fish species. In productive winters (higher NAO and Baltic Sea Index values) source to sink dispersal was stronger than in less productive winters (Lindegren et al., 2014). Source-sink dynamics are closely related to mass effects and one could expect periodic fluctuations in the strength of mass effects in such a metacommunity, as well as temporal shifts in the roles of species interactions and dispersal. In a terrestrial system ENSO-associated interannual variation in rainfall altered population dynamics, trophic interactions, and activity patterns of organisms in ways that impact species interactions (Meserve et al., 2003). High rainfall associated with ENSO events in a semiarid thorn scrub community in Chile led to strong bottom-up increase in plants and animals with overall greater importance of biotic interactions in these wet years (Meserve et al., 2003). However, how changes to species interactions facilitated by multi-year climate fluctuations influence temporal patterns of metacommunity structure is not well-documented. Beyond such specific examples, warm periods associated with ENSO events or

TABLE 2 | Empirical examples linking temporal drivers of metacommunity structure (disturbance, seasonality, multi-year temporal dynamics, and dormancy) to biological processes of dispersal ("Disp."), environmental filtering ("Env. Filt."), and species interactions ("Sp. Int.") that influence metacommunity structure.

Temporal driver	Total studies	Biological process			Metacommunity context
		Disp.	Env. Filt.	Sp. Int.	
Seasonality	9	7	6	3	9
Disturbance	7	5	6	0	5
Multi-year temporal dynamics	4	3	3	2	3

Metacommunity context is the number of studies placed in a metacommunity context by using the word metacommunity (or metacommunities). Only studies that looked at entire assemblages (or communities) are included in the table, which are listed in more detail in ***Supplementary Table S1****. Studies that looked at multiple, potentially interacting species, or single species and illustrate potential mechanisms of relevance are included in* ***Supplementary Table S1****. The table includes both studies in which authors applied a metacommunity framework of analysis to test for changes in metacommunity structures over time, and studies in which potential temporal metacommunity effects can be inferred. Dormancy is omitted from the table because we found no published studies that were at a species assemblage (community) level.*

correlated with NAO are expected to lead to increased predation through changes in activity of poikilothermic organisms (e.g., Tylianakis et al., 2008).

Anthropogenic Global Change, Multi-Year Temporal Dynamics and Metacommunities

Both empirical observations of climate warming during the last 50 years (Zhang et al., 2008) and simulations of climate models project that anthropogenic climate change could produce systematic increases in ENSO strength over many land regions (Fasullo et al., 2018). These increases are expected to heighten interannual variability in the extremes of regional temperature and increase wildfire frequency (Fasullo et al., 2018). The most obvious effect of increased climate forcing is expected to be greater synchronization of community dynamics across space, which can affect metacommunity persistence in theoretical models (e.g., Gouhier et al., 2010). The extent of environmental forcing and resultant environmental filtering could also affect the occurrence of some species (e.g., Thompson et al., 2020). The effect of shifts in multi-year climate cycles on species interactions is harder to predict. If climatic anomalies result in excess resource availability, one could predict rapid increases in local species diversity and abundance, which could produce large temporary increases in the amount of dispersal because of more individuals being present to disperse (density-independent dispersal) and/or density-dependent emigration (Eveleigh et al., 2007). Beyond this, the effects of climate-change driven alteration of ENSO and NAO on the temporal dynamics of metacommunities are unknown.

Dormancy and Dispersal

Dormancy, by allowing species to survive through periods with environmentally unfavorable or low-resource conditions, creates an alternative mechanism to dispersal by which species diversity can be maintained (McPeek and Kalisz, 1998). Consequently, dormancy may limit the roles of environmental filtering and species interactions in metacommunity dynamics. However, if species emerge from dormancy when conditions differ from those they have evolved to tolerate, environmental filtering could increase. Hence, two important questions about the relevance of temporal dynamics to metacommunities are whether community members have dormant life stages (is dormancy possible?), and whether suitable habitat patches are at fixed locations (is dispersal required for survival? McPeek and Kalisz, 1998). Fixed locations would permit non-dispersive life-stages to survive within a location. This would obviate the need for dispersal as a mechanism to maintain diversity and may permit species to be dormant during periods of environmental stress (reducing filtering) or intense competition or predation (limiting the role of species interactions). The temporal storage effect provides a mechanism for such maintenance of diversity (Chesson, 1994). In contrast, suitable patches that are ephemeral in both time and space would create a need for dispersal among temporary ecosystems. If dispersal is necessary, relevant metacommunity structuring mechanisms include not only dispersal but also environmental filtering and species interactions, which may limit patch colonization following local extinction.

Empirical Evidence

There is some empirical evidence for the importance of dormancy vs. dispersal in species occurrence, but it is limited to a few species. For instance, Alexander et al. (2012) studied the importance of local persistence through dormancy vs. regional dispersal in plants. They found that *Silene latifolia* seed dispersal and landscape connectivity were correlated with local colonization of *S. latifolia*, which lacks seed banks. However, *Helianthus annuus* has dormant seeds and its abundance was predicted by local factors such as previous-year local recruitment and local seed-bank size, but not seed dispersal (Alexander et al., 2012); hence in *H. annuus*, the presence of dormant propagules was the primary determinant of distribution and abundance, above and beyond dispersal and environmental filtering. Scaling up to whole metacommunities, there are expected to be negative correlations between dormancy and dispersal, which therefore trade-off in their importance in adding to species diversity. Dispersal often involves costs and risks, which may select against dispersal. There are costs of developing structures that facilitate dispersal (e.g., winged or fluffy seeds) and risks of mortality or energetic costs during dispersal and of failure to establish in new sites (Bonte et al., 2012). Reality is a bit more complex than this theoretical expectation, and correlations between dormancy and dispersal are often weak or more complex than hypothesized (Buoro and Carlson, 2014).

Wisnoski et al. (2019) explicitly modeled the effects of including dormant propagules into metacommunities. They took a simple model of competitive metacommunities

(Shoemaker and Melbourne, 2016) that could represent each of the common metacommunity types (Leibold et al., 2004) and modified it to include transitions in and out of a seed bank. As expected (Bonte et al., 2012; Buoro and Carlson, 2014), when there was a negative dormancy-dispersal correlation, disturbance increased the importance of dormancy in maintaining species diversity (Wisnoski et al., 2019). Other forms of temporal environmental variation beyond disturbance could act in a similar way, and one would expect different species to be active depending on the prevailing environmental conditions. Some conditions promote the emergence of species from seed banks, while others favor species that persist by dispersal (Bonte et al., 2012; Buoro and Carlson, 2014). Therefore, the contribution of dormancy or dispersal to the maintenance of species diversity is expected to negatively covary through time. Conversely, when there is a positive dispersal-dormancy correlation, such as when habitats change rapidly across space and time (Buoro and Carlson, 2014), both dormancy and dispersal contribute to species diversity over relevant periods of time (Wisnoski et al., 2019). In general, positive dormancy-dispersal correlations homogenize species distributions across space. Under these circumstances there would be a breakdown of environmental filtering and species interactions structuring metacommunities and, similarly, a decrease in species sorting and mass effects. Dormancy and dispersal could then potentially contribute to diversity, though the fate of species emerging from dormancy would depend on environmental conditions (environmental filtering). Further, the effects of species interactions could be enhanced by elevated local species diversity resulting from the confluence of immigration by dispersing species and emergence of species from dormancy. Overall, dormant propagules and the direction of dormancy-dispersal correlations alter the extent to which dormancy and dispersal each contribute to metacommunity diversity (Wisnoski et al., 2019). Much remains to explore about such complex effects of the combination of dormancy and dispersal in metacommunities subject to temporal environmental variation.

Anthropogenic Global Change, Dormancy and Dispersal, and Metacommunities

Whether the storage effect as a coexistence mechanism is maintained under climate change is expected to depend on whether or not climate change affects the entire community equally (Rudolf, 2019; Wisnoski et al., 2019). If competing species respond differently to changing weather conditions, then increased variation in environmental conditions due to climate change could promote local coexistence and enhance metacommunity diversity (Rudolf, 2019). If species respond similarly to changing environmental conditions, there may be a loss of local and regional metacommunity diversity through various mechanisms: increased competition due to more species simultaneously consuming resources (Rudolf, 2019); reduced effects of dispersal because populations are similar across space, and mixing homogeneous populations through dispersal has less effect than mixing heterogeneous populations (Wisnoski et al., 2019); and, enhanced environmental filtering if dormant propagules emerge at times when the environment is adverse due to the environmental variability associated with climate change. These mechanisms of biodiversity loss might involve changes in phenology (e.g., Snyder and Adler, 2011), seasonality, or year-to-year differences in activity such as those related to multi-annual climate cycles. Snyder and Adler (2011) suggest that shifts in the germination time in competing plants are a result of climatic shifts in seasonal temperatures that amplify competition. Likewise, Ooi (2012) suggested that seedbanks may become more important because of increased fire frequency under climate change. However, it is also possible that if multiple species shift in the same ways in response to climate change there could be a loss of the role of dormancy and long-lived individuals in buffering populations. This would either reduce overall metacommunity diversity because of stronger environmental filtering and species interactions and/or increase the reliance of surviving species on dispersal.

DISCUSSION

In their original conception, metacommunities were treated as static where populations colonize and go extinct, but the habitat and environment does not vary (Leibold et al., 2004; Holyoak et al., 2005). However, we have demonstrated that metacommunities experience wide-ranging variation across multiple temporal scales that can have broad effects on metacommunity structure. Temporal drivers such as disturbance, seasonality, multi-year dynamics like ENSO and NAO, and dormancy alter the relative importance, strength, and interactions among the biological processes of dispersal, environmental filtering, and species interactions (**Table 1**). A few patterns are apparent in **Table 2**. Although our literature survey found six studies of species assemblages in metacommunities subject to disturbance, none of them studied or identified the effects of disturbance on species interactions (compared to 3 of 9 studies on seasonality, and 2 of 4 studies on ENSO or NAO). This is surprising given that species interactions are central to one of the most widely cited ideas about the effects of disturbance on species diversity, the intermediate disturbance hypothesis, which proposes that disturbance will prevent dominant competitors from establishing in all habitat patches. The low frequency of metacommunity studies focusing on the effects of disturbance on species interactions likely reflects that species interactions are difficult to quantify, especially in short post-disturbance periods. Conversely, dispersal and environmental filtering were frequently identified in species assemblage (community-level) studies of metacommunities subject to temporal dynamics including disturbance, seasonality and multi-year climate fluctuations (**Table 2**). This finding aligns with the expectation that both dispersal and environmental filtering are central to metacommunity dynamics, as reflected in the metacommunity paradigms of Leibold et al. (2004).

Overall, we located few empirical studies on metacommunities and temporal dynamics that drew explicit connections to dispersal, environmental filtering, and/or species interactions. We identified nine studies of whole assemblages in metacommunities for the temporal dynamics of disturbance, nine for seasonality, nine for multi-annual climate fluctuations, and none for the effects of dormancy vs. dispersal (**Table 2**). Of the studies that focused on assemblages of species in metacommunities subject to the focal types of temporal dynamics, the majority analyzed small-bodied, easily-manipulated, and typically aquatic organisms including algae (1 study), bacteria (1 study), insects (1), macroinvertebrates (9), protists (6), rotifers (4), and zooplankton (1) (**Supplementary Table S1**). This selectivity broadly parallels studies of metacommunities in general that did not look at temporal dynamics (Logue et al., 2011). Beyond this, only two papers addressed small mammals, one addressed fishes, and one addressed plants. Therefore, studies focusing on more long-lived and larger organisms are needed. Fourteen studies were conducted in freshwater systems, three in marine and five in terrestrial systems. Accordingly, freshwater studies were disproportionately represented (**Supplementary Table S1**). Terrestrial systems included grasslands, and tropical, temperate, and boreal forests. The distribution of studies across geographical regions generally followed well-known patterns for ecological studies: 7 studies in N America, 6 studies in Europe, 5 studies in S and Central America, 1 study in Asia, and 2 studies in Oceania. Surprisingly, no studies were conducted in Australia or New Zealand and only one took place in Asia (**Supplementary Table S1**). The only study we located that was relevant to dormancy vs. dispersal focused on the autecology two single plant species in N America and was not specifically conducted in a metacommunity context.

Implications for the Conservation and Management of Metacommunities

Global modification of habitat caused by climate change and anthropogenic disturbance influences species at both local and regional scales. The metacommunity approach can enhance understanding of species persistence under anthropogenic global change by linking community interactions within patches to regional dispersal (Gilbert and O'Connor, 2013). Climate change is expected to intensify the frequency and severity of disturbance regimes (Seidl et al., 2011; Millar and Stephenson, 2015), increase the variability of seasonal events (Von Holle et al., 2010; Feng et al., 2013), and enhance temporal variability in ENSO and NAO (Fasullo et al., 2018). The effects of climate change on coexistence in metacommunities with dormant propagules are expected to vary depending on the extent to which species are correlated in their responses to global environmental change (Rudolf, 2019; Wisnoski et al., 2019). When coupled with anthropogenic modifications to the landscape, these effects of climate change further complicate the ability of researchers to define, predict, and manage patterns of temporal dynamism in metacommunities. Given this uncertainty, the challenge of incorporating metacommunity dynamics into a framework for management in the face of global change is one of the largest faced by ecologists (Urban et al., 2012; Gilbert and O'Connor, 2013).

Understanding of spatial and temporal variation in metacommunities provides insights into strategies for invasive species management. The increased reliance on dispersal after a disturbance combined with the propensity for invasive species to be strong dispersers (Sakai et al., 2001) indicates that lax management of invasive species will be unsuccessful in disturbed ecosystems. However, although efforts to constrain dispersal may help limit invasions, the importance of dispersal for metacommunity persistence in frequently disturbed systems suggests that restricting dispersal may be detrimental to the metacommunity, especially if dispersal among patches (e.g., through corridors) is critical for maintaining metacommunity diversity (Östman et al., 2006). Better understanding of how disturbance theory and metacommunity theory intersect may help guide corridor construction that promotes metacommunity persistence while managing for invasive species. Species invasions may also be influenced by the timing of seasonal activity (Wainwright et al., 2012) and have the potential to alter otherwise predictable temporal patterns in metacommunity structure (Erős et al., 2014). Both insights suggest that phenology, and therefore the temporal dynamics of metacommunities, are important factors to consider for the development of successful restoration strategies and invasive species management. Temporal dynamics also point to the need to consider the presence of dormant or long-lived life stages as traits that are relevant to management strategies. For example, being long-lived or having a seed bank might allow species to become successful invaders, as these individuals may be less vulnerable to stochasticity and better able to cope in novel environments (Sol et al., 2012). Ultimately, where invasive species management is particularly important, better management practices may be developed through the integration of insights learned from the study of metacommunity spatiotemporal dynamics.

Understanding if dispersal or dormancy are required for species coexistence and how they contribute to species diversity is potentially of great importance to conservation (McPeek and Kalisz, 1998). If high temporal predictability is coupled with habitat heterogeneity (low spatial autocorrelation) dispersal is favored over dormancy, whereas high spatial predictability but low temporal predictability favors dormancy over dispersal (Buoro and Carlson, 2014). Such insights are relevant to the construction of permanent (fixed-location) nature reserves, which may favor species exhibiting dormancy traits that can buffer against temporally variable conditions. However, where long-lived individuals have been disproportionately removed, such as the overfishing of older individuals, the buffering effect they provide against temporally variable conditions may be lost (Buoro and Carlson, 2014), and populations may become more vulnerable to large fluctuations and local extinction. In this way, such systems might necessarily switch to become more dependent on dispersal, and trophic interactions (e.g., bycatch) may extend well beyond the target species of fisheries or other harvesting schemes.

Finally, regular seasonal variation in dispersal, environmental filtering, and species interactions underlines the necessity to conduct surveys in all seasons, rather than assuming that the structure observed and management decisions made during one period are applicable to future periods. Recognition that temporal variation in dispersal, environmental filtering, and species interactions exists could improve the accuracy of biomonitoring methods and help guide effective ecosystem management strategies (Cid et al., 2020). Additionally, long-term dynamics such as ENSO and NAO are known to alter metacommunity structure, but the implications of these changes for conservation are unknown because existing studies typically present correlational rather than causational evidence. However, managers should still be aware that conservation strategies may have different impacts along climatic indexes.

Future Research Needs

We have focused on metacommunities at the mesoscale, conceptualizing metacommunities as dynamically fluctuating around some kind of equilibrium set by dispersal, environmental filtering, and species interactions. Indeed, plant metacommunity structure in an English woodland was the same at two points in time, seven decades apart (Keith et al., 2011). However, over longer timescales, metacommunities may not be characterized by such an equilibrial view and may be on a continuous trajectory of change. For example, metacommunities may be undergoing systematic decline (e.g., slow-acting extinction debt that cannot be easily measured in an empirical study) – after all, all species do go extinct eventually. Conversely, metacommunities may be expanding and growing as species continue to spread geographically since the last glacial period, or because of increased primary productivity from anthropogenic fertilization. Just as there are both short-term population studies that investigate demographic processes and long-term studies of population trends, one could envisage short-term studies of metacommunities at the mesoscale and long-term studies as more extensive metacommunity datasets become available. For example, disturbance and seasonality create short-term fluctuations in the structure of metacommunities, but these drivers may operate within multi-year climate cycles and occur in tandem with the removal or emergence of dormant propagules over multi-year periods. This overlap in temporal drivers can shape the trajectory of metacommunities over time in complex ways through synergistic interaction or time-lags (Blanchard et al., 2020). Accordingly, metacommunities are not structurally static at any time scale, but long-term datasets may be required for dynamic patterns to emerge.

There is also a need for models that explicitly include temporal dynamics and evaluate the emergent types of metacommunity dynamics. The framework of dispersal, environmental filtering, and species interactions, or similar axes adopted by Thompson et al. (2020), offers a promising approach for the evaluation of metacommunity structuring mechanisms, with a few caveats. Certainly, the use of the traditional metacommunity paradigms (Leibold et al., 2004) to categorize empirical and model systems can be problematic, as many of these systems do not neatly fit the archetypal types (e.g., Logue et al., 2011; Brown et al., 2017). However, these paradigms do capture both interactions among dispersal and environmental filtering and among dispersal and species interactions in mass effects that could easily be overlooked if we did not use the traditional paradigms. Further, interspecific or individual variation such as competition-colonization trade-offs are essential for patch dynamics, and they could also be passed over by only considering mean or variance of dispersal per species or modeling using dispersal kernels. Studies such as Wisnoski et al. (2019) stand out in reviewing the effect of combining dormancy and dispersal on metacommunity dynamics and structuring mechanisms.

Most work to date investigating the temporal dynamics of metacommunities is theoretical or focuses on invertebrates and protists in highly dynamic aquatic systems (e.g., intermittent rivers, tidal zones). This is especially prevalent in studies that examine the temporal drivers of disturbance and seasonality. Future research that explicitly tests metacommunity organization at different points in time is needed in various taxa, especially large, terrestrial species (**Table 3**). Further, investigation focusing on these taxonomic groups should explore how temporal changes in species' physiology (e.g., metabolic rate; Scantlebury et al., 2005; Chamane and Downs, 2009; Lang et al., 2012; McClune et al., 2015) and behavior (e.g., migration, foraging; Ben-David et al., 1997; Schmidt et al., 2008; Davidson et al., 2013) influence metacommunity organization. Additionally, empirical study in more systems will help address questions regarding the generalizability of the temporal patterns identified in simpler, aquatic systems.

While many studies identifying temporal variation in metacommunity structure highlight the biological processes of environmental filtering and dispersal, far fewer explicitly test and quantify the importance of species interactions (**Supplementary Table S1**). However, metacommunity assembly may be primarily driven by biotic interactions (García-Girón et al., 2020). How disturbance may change the importance of species interactions is unknown. Though seasonality is known to alter competition and predation, few studies extend these ideas to quantify structural changes in metacommunities in different seasons (**Supplementary Table S1**). Further, though facilitation and positive interactions can be important in community assembly (Bruno et al., 2003), they have not typically been included in metacommunity studies (Biswas and Wagner, 2012; but see Hoopes et al., 2005).

Despite mounting evidence that human activity affects both local and regional processes, few studies have attempted to apply metacommunity theory to human-modified landscapes (but see Swan et al., 2011; Johnson et al., 2013), especially in terrestrial systems. Urbanization frequently fragments habitat and impedes connectivity (McKinney, 2002), and, accordingly, theory predicts that dispersal and mass-effects may be especially relevant in human-modified landscapes (Parris, 2006; Johnson et al., 2013). Cities may act as an environmental filter (Swan et al., 2011), eliminating some species (e.g., apex predators) with potential cascading effects on species interactions, but, within a city, successful species may be buffered from environmental extremes (Rodewald and Gehrt, 2014). Accordingly, the environmental conditions associated with seasonal variability may become more subdued and temporal homogenization of metacommunity structure in urban ecosystems may be possible. Alternatively, highly seasonal human behavior exhibited by urban residents (e.g., pesticide use, water use, etc.) may reinstate temporal fluctuations, but these fluctuations would be moderated by anthropogenic activity, therefore linking socioeconomic patterns and processes to ecological theory. Much remains unknown,

TABLE 3 | Suggested future work to advance thinking about the effects of temporal dynamics on metacommunities.

Temporal driver	Direction for future research	Suggested research questions
Disturbance	Explore disturbance and metacommunities in terrestrial, complex systems	• Most work to date has been theoretical or in aquatic protists and invertebrates. Are similar patterns found in other taxa, biomes, and regions? • How does the relative importance of metacommunity structuring processes change with time since disturbance?
	Distinguish between frequency and intensity of disturbance	• How do different severities of disturbance (e.g., loss of some vs. all individuals in a local patch) change metacommunity structure?
	Species interactions	• Does disturbance change the importance of species interactions?
	Human-induced rapid environmental change (Sih et al., 2011)	• How might the importance of dispersal and environmental filtering differ in urban environments?
Seasonality	Explore seasonality and metacommunities in terrestrial, complex systems	• Is seasonal variation in environmental filtering and dispersal widespread outside of intermittent aquatic systems?
	Species interactions	• How do positive interactions and facilitation influence metacommunity organization over time and space?
	Migration	• Does the presence of seasonal migration result in cyclical patterns in metacommunity structure?
	Human-induced rapid environmental change	• How do seasonal patterns in human activity (e.g., pollution, water-use) disrupt seasonal variation in metacommunity structuring mechanisms and dynamics? • How do climate change-induced mismatches among interacting species and their environments affect patterns of temporal variation in metacommunity structure, and are these effects generalizable? • How do disruptions to the predictability or severity of seasons caused by climate change influence the temporal dynamics of metacommunities?
Multi-year temporal dynamics	Human-induced rapid environmental change (Sih et al., 2011)	• How do multi-year climate cycles such as ENSO events influence temporal variation in metacommunity structuring mechanisms and dynamics? • For how long after their occurrence do El Niño and La Niña events effect local and regional metacommunity dynamics? • Beyond increased synchronization of community dynamics across space, what are the effects of climate-change driven alteration of ENSO and NAO on the temporal dynamics of metacommunities and metacommunity structuring mechanisms?
Dormancy	Empirical research on metacommunities	• What are the effects of manipulating the presence of dormant propagules vs. dispersal on local and regional dynamics in metacommunities?
	Management of metacommunities	• How will having fixed location nature reserves increase the frequency of or select for species with dormant propagules at the expense of gene flow?

and further empirical study is needed to bridge metacommunity theory and urbanization research (**Table 3**).

Finally, global climate change requires scientists to consider how climate impacts on both local and regional dynamics synergistically interact to affect metacommunity persistence (**Table 3**). Metacommunity theory has been conceptualized without the explicit consideration of changing climate. Acknowledging how temporal drivers such as disturbance, seasonality, multi-year climate fluctuations, and dormancy influence the spatiotemporal dynamics of metacommunities is an important first step to add ecological realism to simplified theory. However, global climate change presents an immense challenge to our ability to extrapolate findings on the spatiotemporal dynamics of metacommunities in a contemporary context. The insights that metacommunity theory has provided on the consistency and patterns of temporal variation in metacommunity structure may not be relevant in a world defined by global climate change. We have suggested various ways in which a changing global climate has the propensity to disrupt predictions about the temporal dynamics of metacommunities – but what exactly these dynamic changes look like is a critical yet unanswered question for the conservation of metacommunities globally.

AUTHOR CONTRIBUTIONS

All authors contributed equally to literature research and the writing of the manuscript. It was planned, researched, written, and revised together.

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SUPPLEMENTARY MATERIAL

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REFERENCES

Alexander, H. M., Foster, B. L., Ballantyne, F., Collins, C. D., Antonovics, J., and Holt, R. D. (2012). Metapopulations and metacommunities: combining spatial and temporal perspectives in plant ecology. *J. Ecol.* 100, 88–103. doi: 10.1111/j.1365-2745.2011.01917.x

Alexander, J. M., Diez, J. M., and Levine, J. M. (2015). Novel competitors shape species' responses to climate change. *Nature* 525, 515–518. doi: 10.1038/nature14952

Altermatt, F., Bieger, A., Carrara, F., Rinaldo, A., and Holyoak, M. (2011a). Effects of connectivity and recurrent local disturbances on community structure and population density in experimental metacommunities. *PLoS One* 6:e19525. doi: 10.1371/journal.pone.0019525

Altermatt, F., Schreiber, S., and Holyoak, M. (2011b). Interactive effects of disturbance and dispersal directionality on species richness and composition in metacommunities. *Ecology* 92, 859–870. doi: 10.1890/10-1095.1

Andersson, M. (1980). Nomadism and site tenacity as alternative reproductive tactics in birds. *J. Anim. Ecol.* 49, 175–184. doi: 10.2307/4282

Barradas, I., Caswell, H., and Cohen, J. E. (1996). Competition during colonization vs competition after colonization in disturbed environments: a metapopulation approach. *Bull. Math. Biol.* 58, 1187–1207. doi: 10.1007/BF02458389

Battisti, C., Poeta, G., and Fanelli, G. (2016). *An Introduction to Disturbance Ecology: A Road Map for Wildlife Management and Conservation*. Berlin: Springer International Publishing. doi: 10.1007/978-3-319-32476-0

Ben-David, M., Flynn, R. W., and Schell, D. M. (1997). Annual and seasonal changes in diets of martens: evidence from stable isotope analysis. *Oecologia* 111, 280–291. doi: 10.1007/s004420050236

Bieber, C., Lebl, K., Stalder, G., Geiser, F., and Ruf, T. (2014). Body mass dependent use of hibernation: why not prolong the active season, if they can? *Funct. Ecol.* 28, 167–177. doi: 10.1111/1365-2435.12173

Biswas, S. R., and Wagner, H. H. (2012). Landscape contrast: a solution to hidden assumptions in the metacommunity concept? *Landsc. Ecol.* 27, 621–631. doi: 10.1007/s10980-012-9732-5

Blakely, T. J., Harding, J. S., Mcintosh, A. R., and Winterbourn, M. J. (2006). Barriers to the recovery of aquatic insect communities in urban streams. *Freshw. Biol.* 51, 1634–1645. doi: 10.1111/j.1365-2427.2006.01601.x

Blanchard, G., Birnbaum, P., and Munoz, F. (2020). Extinction-immigration dynamics lag behind environmental filtering in shaping the composition of tropical dry forests within a changing landscape. *Ecography* 43, 869–881. doi: 10.1111/ecog.04870

Bonte, D., Van Dyck, H., Bullock, J. M., Coulon, A., Delgado, M., Gibbs, M., et al. (2012). Costs of dispersal. *Biol. Rev.* 87, 290–312. doi: 10.1111/j.1469-185X.2011.00201.x

Boudell, J. A., and Stromberg, J. C. (2008). Flood pulsing and metacommunity dynamics in a desert riparian ecosystem. *J. Veg. Sci.* 19, 373–380. doi: 10.3170/2008-8-18377

Boyce, M. S. (1979). Seasonality and patterns of natural selection for life histories. *Am. Nat.* 114, 569–583. doi: 10.1086/283503

Brown, B. L., Sokol, E. R., Skelton, J., and Tornwall, B. (2017). Making sense of metacommunities: dispelling the mythology of a metacommunity typology. *Oecologia* 183, 643–652. doi: 10.1007/s00442-016-3792-1

Bruno, J. F., Stachowicz, J. J., and Bertness, M. D. (2003). Inclusion of facilitation into ecological theory. *Trends Ecol. Evol.* 18, 119–125. doi: 10.1016/S0169-5347(02)00045-9

Buoro, M., and Carlson, S. M. (2014). Life-history syndromes: integrating dispersal through space and time. *Ecol. Lett.* 17, 756–767. doi: 10.1111/ele.12275

Cadotte, M. W. (2007). Competition-colonization trade-offs and disturbance effects at multiple scales. *Ecology* 88, 823–829. doi: 10.1890/06-1117

Cadotte, M. W., and Tucker, C. M. (2017). Should environmental filtering be abandoned? *Trends Ecol. Evol.* 32, 429–437. doi: 10.1016/j.tree.2017.03.004

Campbell, R. E., Winterbourn, M. J., Cochrane, T. A., and McIntosh, A. R. (2015). Flow-related disturbance creates a gradient of metacommunity types within stream networks. *Landsc. Ecol.* 30, 667–680. doi: 10.1007/s10980-015-0164-x

Camus, P. A. (2008). Understanding biological impacts of ENSO on the eastern Pacific: an evolving scenario. *Int. J. Environ. Health* 2, 5–19. doi: 10.1504/IJEnvH.2008.018668

Cañedo-Argüelles, M., Gutiérrez-Cánovas, C., Acosta, R., Castro-López, D., Cid, N., Fortuño, P., et al. (2020). As time goes by: 20 years of changes in the aquatic macroinvertebrate metacommunity of Mediterranean river networks. *J. Biogeogr.* 47, 1861–1874. doi: 10.1111/jbi.13913

Caswell, H., and Cohen, J. E. (1991). Disturbance, interspecific interaction and diversity in metapopulations. *Biol. J. Linn. Soc.* 42, 193–218. doi: 10.1111/j.1095-8312.1991.tb00560.x

Chamane, S. C., and Downs, C. T. (2009). Seasonal effects on metabolism and thermoregulation abilities of the red-winged starling (*Onychognathus morio*). *J. Therm. Biol.* 34, 337–341. doi: 10.1016/j.jtherbio.2009.06.005

Chase, J. M. (2007). Drought mediates the importance of stochastic community assembly. *Proc. Natl. Acad. Sci. U.S.A.* 104, 17430–17434. doi: 10.1073/pnas.0704350104

Chave, J. (2004). Neutral theory and community ecology. *Ecol. Lett.* 7, 241–253. doi: 10.1111/j.1461-0248.2003.00566.x

Chesson, P. (1994). Multispecies competition in variable environments. *Theor. Popul. Biol.* 45, 227–276. doi: 10.1006/tpbi.1994.1013

Cid, N., Bonada, N., Heino, J., Cañedo-Argüelles, M., Crabot, J., Sarremejane, R., et al. (2020). A metacommunity approach to improve biological assessments in highly dynamic freshwater ecosystems. *Bioscience* 70, 427–438. doi: 10.1093/biosci/biaa033

Cisneros, L. M., Fagan, M. E., and Willig, M. R. (2015). Season-specific and guild-specific effects of anthropogenic landscape modification on metacommunity structure of tropical bats. *J. Anim. Ecol.* 84, 373–385. doi: 10.1111/1365-2656.12299

Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science* 199, 1302–1310. doi: 10.1126/science.199.4335.1302

Cottenie, K. (2005). Integrating environmental and spatial processes in ecological community dynamics. *Ecol. Lett.* 8, 1175–1182. doi: 10.1111/j.1461-0248.2005.00820.x

Csercsa, A., Krasznai, -K. E. Á, Várbíró, G., Szivák, I., and Tóth, M. (2019). Seasonal changes in relative contribution of environmental control and spatial structuring on different dispersal groups of stream macroinvertebrates. *Hydrobiologia* 828, 101–115. doi: 10.1007/s10750-018-3806-6

Datry, T., Bonada, N., and Heino, J. (2016). Towards understanding the organisation of metacommunities in highly dynamic ecological systems. *Oikos* 125, 149–159. doi: 10.1111/oik.02922

Davidson, Z., Valeix, M., Van Kesteren, F., Loveridge, A. J., Hunt, J. E., Murindagomo, F., et al. (2013). Seasonal diet and prey preference of the African lion in a waterhole-driven semi-arid savanna. *PLoS One* 8:e55182. doi: 10.1371/journal.pone.0055182

Delciellos, A. C., Borges-Júnior, V. N. T., Prevedello, J. A., Ribeiro, S. E., Braga, C., Vieira, M. V., et al. (2018). Seasonality in metacommunity structure: an empirical test in the Atlantic Forest. *Landsc. Ecol.* 33, 1769–1783. doi: 10.1007/s10980-018-0701-5

Diaz, H. F., Hoerling, M. P., and Eischeid, J. K. (2001). ENSO variability, teleconnections and climate change. *Int. J. Climatol.* 21, 1845–1862. doi: 10.1002/joc.631

Dingle, H. (1996). *Migration: The Biology of Life on the Move*. Oxford: Oxford University Press.

Dixo, M., Metzger, J. P., Morgante, J. S., and Zamudio, K. R. (2009). Habitat fragmentation reduces genetic diversity and connectivity among toad populations in the Brazilian Atlantic Coastal Forest. *Biol. Conserv.* 142, 1560–1569. doi: 10.1016/j.biocon.2008.11.016

Drake, J. M., and Lodge, D. M. (2004). Effects of environmental variation on extinction and establishment. *Ecol. Lett.* 7, 26–30. doi: 10.1046/j.1461-0248.2003.00546.x

Elkin, C. M., and Possingham, H. (2008). The role of landscape-dependent disturbance and dispersal in metapopulation persistence. *Am. Nat.* 172, 563–575. doi: 10.1086/590962

Ellis, A. M., Lounibos, L. P., and Holyoak, M. (2006). Evaluating the long-term metacommunity dynamics of tree hole mosquitoes. *Ecology* 87, 2582–2590. doi: 10.1890/0012-9658(2006)87[2582:etlmdo]2.0.co;2

Elton, C. S. (1924). Periodic fluctuations in the numbers of animals: their causes and effects. *J. Exp. Biol.* 2, 119–163.

Emerson, B. C., and Gillespie, R. G. (2008). Phylogenetic analysis of community assembly and structure over space and time. *Trends Ecol. Evol.* 23, 619–630. doi: 10.1016/j.tree.2008.07.005

Erős, T., Sály, P., Takács, P., Higgins, C. L., Bíró, P., and Schmera, D. (2014). Quantifying temporal variability in the metacommunity structure of stream fishes: the influence of non-native species and environmental drivers. *Hydrobiologia* 722, 31–43. doi: 10.1007/s10750-013-1673-8

Eveleigh, E. S., McCann, K. S., McCarthy, P. C., Pollock, S. J., Lucarotti, C. J., Morin, B., et al. (2007). Fluctuations in density of an outbreak species drive diversity cascades in food webs. *Proc. Natl. Acad. Sci. U.S.A.* 104, 16976–16981. doi: 10.1073/pnas.0704301104

Fasullo, J. T., Otto-Bliesner, B. L., and Stevenson, S. (2018). ENSO's changing influence on temperature, precipitation, and wildfire in a warming climate. *Geophys. Res. Lett.* 45, 9216–9225. doi: 10.1029/2018GL079022

Feng, X., Porporato, A., and Rodriguez-Iturbe, I. (2013). Changes in rainfall seasonality in the tropics. *Nat. Clim. Chang.* 3, 811–815. doi: 10.1038/nclimate1907

Fernandes, I. M., Henriques-Silva, R., Penha, J., Zuanon, J., and Peres-Neto, P. R. (2014). Spatiotemporal dynamics in a seasonal metacommunity structure is predictable: the case of floodplain-fish communities. *Ecography* 37, 464–475. doi: 10.1111/j.1600-0587.2013.00527.x

Fiedler, P. C. (2002). Environmental change in the eastern tropical Pacific Ocean: review of ENSO and decadal variability. *Mar. Ecol. Prog. Ser.* 244, 265–283. doi: 10.3354/meps244265

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., et al. (2004). Regime shifts, resilience, and biodiversity in ecosystem management. *Annu. Rev. Ecol. Evol. Syst.* 35, 557–581. doi: 10.1146/annurev.ecolsys.35.021103.105711

Foster, D. R., Knight, D. H., and Franklin, J. F. (1998). Landscape patterns and legacies resulting from large, infrequent forest disturbances. *Ecosystems* 1, 497–510. doi: 10.1007/s100219900046

Fraedrich, K., and Müller, K. (1992). Climate anomalies in Europe associated with ENSO extremes. *Int. J. Climatol.* 12, 25–31. doi: 10.1002/joc.3370120104

Gan, J., Bondarenko, S., Oki, L., Haver, D., and Li, J. X. (2012). Occurrence of fipronil and its biologically active derivatives in urban residential runoff. *Environ. Sci. Technol.* 46, 1489–1495. doi: 10.1021/es202904x

García-Girón, J., Heino, J., García-Criado, F., Fernández-Aláez, C., and Alahuhta, J. (2020). Biotic interactions hold the key to understanding metacommunity organisation. *Ecography* 43, 1180–1190. doi: 10.1111/ecog.05032

Gilbert, B., and O'Connor, M. I. (2013). Climate change and species interactions: beyond local communities. *Ann. N. Y. Acad. Sci.* 1297, 98–111. doi: 10.1111/nyas.12149

Gilman, S. E., Urban, M. C., Tewksbury, J., Gilchrist, G. W., and Holt, R. D. (2010). A framework for community interactions under climate change. *Trends Ecol. Evol.* 25, 325–331. doi: 10.1016/j.tree.2010.03.002

Glynn, P. W. (1988). El Nino Southern oscillation 1982-1983: nearshore population, community, and ecosystem responses. *Annu. Rev. Ecol. Syst.* 19, 309–346. doi: 10.1146/annurev.es.19.110188.001521

Gouhier, T. C., Guichard, F., and Gonzalez, A. (2010). Synchrony and stability of food webs in metacommunities. *Am. Nat.* 175, E16–E34. doi: 10.1086/649579

Gouveia, S. F., Hortal, J., Cassemiro, F. A. S., Rangel, T. F., and Diniz-Filho, J. A. F. (2013). Nonstationary effects of productivity, seasonality, and historical climate changes on global amphibian diversity. *Ecography* 36, 104–113. doi: 10.1111/j.1600-0587.2012.07553.x

Grimm, N. B., Faeth, S. H., Golubiewski, N. E., Redman, C. L., Wu, J., Bai, X., et al. (2008). Global change and the ecology of cities. *Science* 319, 756–760. doi: 10.1126/science.1150195

Hart, S. P., Usinowicz, J., and Levine, J. M. (2017). The spatial scales of species coexistence. *Nat. Ecol. Evol.* 1, 1066–1073. doi: 10.1038/s41559-017-0230-7

Hastings, A. (2003). Metapopulation persistence with age-dependent disturbance or succession. *Science* 301, 1525–1526. doi: 10.1126/science.1087570

Hastings, A. (2004). Transients: the key to long-term ecological understanding? *Trends Ecol. Evol.* 19, 39–45. doi: 10.1016/j.tree.2003.09.007

Heino, J. (2013). The importance of metacommunity ecology for environmental assessment research in the freshwater realm. *Biol. Rev.* 88, 166–178. doi: 10.1111/j.1469-185X.2012.00244.x

Hintz, W. D., and Relyea, R. A. (2019). A review of the species, community, and ecosystem impacts of road salt salinisation in fresh waters. *Freshw. Biol.* 64, 1081–1097. doi: 10.1111/fwb.13286

Hobbs, R. J., Higgs, E., and Harris, J. A. (2009). Novel ecosystems: implications for conservation and restoration. *Trends Ecol. Evol.* 24, 599–605. doi: 10.1016/j.tree.2009.05.012

Holdo, R. M., Holt, R. D., Sinclair, A. R. E., Godley, B. J., and Thirgood, S. (2011). "Migration impacts on communities and ecosystems: empirical evidence and theoretical insights," in *Animal Migration*, eds E. J. Milner-Gulland, J. M. Fryxell, and A. R. E. Sinclair (Oxford: Oxford University Press), 130–143. doi: 10.1093/acprof:oso/9780199568994.003.0009

Holt, R. D. (1993). "Ecology at the mesoscale: the influence of regional processes on local communities," in *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*, eds R. E. Ricklefs and D. Schluter (Chicago, IL: University of Chicago Press).

Holyoak, M., Leibold, M. A., Holt, R. D., Moquet, N., Hoopes, M. F., and Amarasekare, P. (2005). "Metacommunities: a framework for large-scale community ecology," in *Metacommunities: Spatial Dynamics and Ecological Communities*, eds M. Holyoak, M. A. Leibold, and R. D. Holt (Chicago, IL: University of Chicago Press).

Hoopes, M. F., Holt, R. D., and Holyoak, M. (2005). "The effects of spatial processes on two species interactions," in *Metacommunities: Spatial Dynamics and Ecological Communities*, eds M. Holyoak, M. A. Leibold, and R. D. Holt (Chicago, IL: The University of Chicago Press), 35–67.

Hurrell, J. W. (1995). Decadal trends in the North Atlantic oscillation: regional temperatures and precipitation. *Science* 269:676. doi: 10.1126/science.269.5224.676

Hurrell, J. W., Kushnir, Y., Ottersen, G., and Visbeck, M. (eds) (2003). *The North Atlantic Oscillation: Climatic Significance and Environmental Impact*. New York, NY: John Wiley and Sons. doi: 10.1029/GM134

Huston, M. (1979). A general hypothesis of species diversity. *Am. Nat.* 113, 81–101. doi: 10.1086/283366

Inouye, D. W., Barr, B., Armitage, K. B., and Inouye, B. D. (2000). Climate change is affecting altitudinal migrants and hibernating species. *Proc. Natl. Acad. Sci. U.S.A.* 97, 1630–1633. doi: 10.1073/pnas.97.4.1630

Jabot, F., Laroche, F., Massol, F., Arthaud, F., Crabot, J., Dubart, M., et al. (2020). Assessing metacommunity processes through signatures in spatiotemporal turnover of community composition. *Ecol. Lett.* 23, 1330–1339. doi: 10.1111/ele.13523

Jacobson, B., and Peres-Neto, P. R. (2010). Quantifying and disentangling dispersal in metacommunities: how close have we come? How far is there to go? *Landsc. Ecol.* 25, 495–507. doi: 10.1007/s10980-009-9442-9

Jeffries, M. (2005). Small ponds and big landscapes: the challenge of invertebrate spatial and temporal dynamics for European pond conservation. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 15, 541–547. doi: 10.1002/aqc.753

Johnson, P. T. J., Hoverman, J. T., McKenzie, V. J., Blaustein, A. R., and Richgels, K. L. D. (2013). Urbanization and wetland communities: applying metacommunity theory to understand the local and landscape effects. *J. Appl. Ecol.* 50, 34–42. doi: 10.1111/1365-2664.12022

Junk, W. J., Bayley, P. B., and Sparks, R. E. (1989). The flood pulse concept in river-floodplain systems. *Can. Spec. Publ. Fish. Aquat. Sci.* 106, 110–127.

Kaushal, S. S., Groffman, P. M., Likens, G. E., Belt, K. T., Stack, W. P., Kelly, V. R., et al. (2005). Increased salinization of fresh water in the northeastern United States. *Proc. Natl. Acad. Sci. U.S.A.* 102, 13517–13520. doi: 10.1073/pnas.0506414102

Keith, S. A., Newton, A. C., Morecroft, M. D., Golicher, D. J., and Bullock, J. M. (2011). Plant metacommunity structure remains unchanged during biodiversity loss in English woodlands. *Oikos* 120, 302–310. doi: 10.1111/j.1600-0706.2010.18775.x

Kneitel, J. M., and Miller, T. E. (2002). Resource and top-predator regulation in the pitcher plant (*Sarracenia purpurea*) inquiline community. *Ecology* 83, 680–688. doi: 10.1890/0012-9658(2002)083[0680:ratpri]2.0.co;2

Kolasa, J., and Romanuk, T. N. (2005). "Assembly of unequals in the unequal world of a rock pool metacommunity," in *Metacommunities: Spatial Dynamics and Ecological Communities*, eds M. Holyoak, M. A. Leibold, and R. D. Holt (Chicago, IL: University of Chicago Press), 212–231.

Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., and Levine, J. M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Funct. Ecol.* 29, 592–599. doi: 10.1111/1365-2435.12345

Laliberté, E., Norton, D. A., and Scott, D. (2013). Contrasting effects of productivity and disturbance on plant functional diversity at local and metacommunity scales. *J. Veg. Sci.* 24, 834–842. doi: 10.1111/jvs.12044

Lane, J. E., Kruuk, L. E. B., Charmantier, A., Murie, J. O., and Dobson, F. S. (2012). Delayed phenology and reduced fitness associated with climate change in a wild hibernator. *Nature* 489, 554–557. doi: 10.1038/nature11335

Lang, B., Rall, B. C., and Brose, U. (2012). Warming effects on consumption and intraspecific interference competition depend on predator metabolism: temperature effects on interference competition. *J. Anim. Ecol.* 81, 516–523. doi: 10.1111/j.1365-2656.2011.01931.x

Larned, S. T., Datry, T., Arscott, D. B., and Tockner, K. (2010). Emerging concepts in temporary-river ecology. *Freshw. Biol.* 55, 717–738. doi: 10.1111/j.1365-2427.2009.02322.x

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., et al. (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.* 7, 601–613. doi: 10.1111/j.1461-0248.2004.00608.x

Leonard, G. H. (2000). Latitudinal variation in species interactions: a test in the New England rocky intertidal zone. *Ecology* 81, 1015–1030. doi: 10.1890/0012-9658(2000)081[1015:lvisia]2.0.co;2

Limberger, R., and Wickham, S. A. (2012). Disturbance and diversity at two spatial scales. *Oecologia* 168, 785–795. doi: 10.1007/s00442-011-2140-8

Lindegren, M., Andersen, K. H., Casini, M., and Neuenfeldt, S. (2014). A metacommunity perspective on source-sink dynamics and management: the Baltic Sea as a case study. *Ecol. Appl.* 24, 1820–1832. doi: 10.1890/13-0566.1

Lindstrom, J., Ranta, E., Kokko, H., Lundberg, P., and Kaitala, V. (2001). From arctic lemmings to adaptive dynamics: charles Elton's legacy in population ecology. *Biol. Rev.* 76, 129–158. doi: 10.1017/S1464793100005637

Logue, J. B., Mouquet, N., Peter, H., and Hillebrand, H. (2011). Empirical approaches to metacommunities: a review and comparison with theory. *Trends Ecol. Evol.* 26, 482–491. doi: 10.1016/j.tree.2011.04.009

Lurgi, M., López, B. C., and Montoya, J. M. (2012). Novel communities from climate change. *Philos. Trans. R. Soc. B Biol. Sci.* 367, 2913–2922. doi: 10.1098/rstb.2012.0238

Mackey, R. L., and Currie, D. J. (2001). The diversity-disturbance relationship: is it generally strong and peaked? *Ecology* 82, 3479–3492. doi: 10.2307/2680166

Marrec, R., Pontbriand-Paré, O., Legault, S., and James, P. M. A. (2018). Spatiotemporal variation in drivers of parasitoid metacommunity structure in continuous forest landscapes. *Ecosphere* 9:e02075. doi: 10.1002/ecs2.2075

McClune, D. W., Kostka, B., Delahay, R. J., Montgomery, W. I., Marks, N. J., and Scantlebury, D. M. (2015). Winter is coming: seasonal variation in resting metabolic rate of the European badger (*Meles meles*). *PLoS One* 10:e0135920. doi: 10.1371/journal.pone.0135920

McKinney, M. L. (2002). Urbanization, biodiversity, and conservation. *Bioscience* 52, 883–890. doi: 10.1641/0006-3568(2002)052[0883:UBAC]2.0.CO;2

McMeans, B. C., McCann, K. S., Humphries, M., Rooney, N., and Fisk, A. T. (2015). Food web structure in temporally-forced ecosystems. *Trends Ecol. Evol.* 30, 662–672. doi: 10.1016/j.tree.2015.09.001

McPeek, M. A., and Kalisz, S. (1998). On the joint evolution of dispersal and dormancy in metapopulations. *Adv. Limnol.* 52, 33–51.

Mellard, J. P., Audoye, P., and Loreau, M. (2019). Seasonal patterns in species diversity across biomes. *Ecology* 100:e02627. doi: 10.1002/ecy.2627

Meserve, P. L., Kelt, D. A., Milstead, W. B., and Gutiérrez, J. R. (2003). Thirteen years of shifting top-down and bottom-up control. *Bioscience* 53, 633–646. doi: 10.1641/0006-3568(2003)053[0633:tyosta]2.0.co;2

Metz, M. C., Smith, D. W., Vucetich, J. A., Stahler, D. R., and Peterson, R. O. (2012). Seasonal patterns of predation for gray wolves in the multi-prey system of Yellowstone National Park. *J. Anim. Ecol.* 81, 553–563. doi: 10.1111/j.1365-2656.2011.01945.x

Millar, C. I., and Stephenson, N. L. (2015). Temperate forest health in an era of emerging megadisturbance. *Science* 349, 823–826. doi: 10.1126/science.aaa9933

Mouquet, N., and Loreau, M. (2002). Coexistence in metacommunities: the regional similarity hypothesis. *Am. Nat.* 159, 420–426. doi: 10.1086/338996

Odum, E. P. (1985). Trends expected in stressed ecosystems. *Bioscience* 35, 419–422. doi: 10.2307/1310021

Odum, E. P., Finn, J. T., and Franz, E. H. (1979). Perturbation theory and the subsidy-stress gradient. *Bioscience* 29, 349–352. doi: 10.2307/1307690

Ojima, M. N., and Jiang, L. (2017). Interactive effects of disturbance and dispersal on community assembly. *Oikos* 126, 682–691. doi: 10.1111/oik.03265

Ooi, M. K. J. (2012). Seed bank persistence and climate change. *Seed Sci. Res.* 22, S53–S60. doi: 10.1017/S0960258511000407

Östman, Ő., Kneitel, J. M., and Chase, J. M. (2006). Disturbance alters habitat isolation's effect on biodiversity in aquatic microcosms. *Oikos* 114, 360–366. doi: 10.1111/j.2006.0030-1299.14521.x

Owen-Smith, N. (2008). Changing vulnerability to predation related to season and sex in an African ungulate assemblage. *Oikos* 117, 602–610. doi: 10.1111/j.0030-1299.2008.16309.x

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* 37, 637–669. doi: 10.1146/annurev.ecolsys.37.091305.110100

Parris, K. M. (2006). Urban amphibian assemblages as metacommunities. *J. Anim. Ecol.* 75, 757–764. doi: 10.1111/j.1365-2656.2006.01096.x

Peralta, G., Fenoglio, M. S., and Salvo, A. (2011). Physical barriers and corridors in urban habitats affect colonisation and parasitism rates of a specialist leaf miner. *Ecol. Entomol.* 36, 673–679. doi: 10.1111/j.1365-2311.2011.01316.x

Petraitis, P. S., Latham, R. E., and Niesenbaum, R. A. (1989). The maintenance of species diversity by disturbance. *Q. Rev. Biol.* 64, 393–418. doi: 10.1086/416457

Pineda, A., Peláez, Ó., Dias, J. D., Segovia, B. T., Bonecker, C. C., Velho, L. F. M., et al. (2019). The El Niño Southern Oscillation (ENSO) is the main source of variation for the gamma diversity of plankton communities in subtropical shallow lakes. *Aquat. Sci.* 81:49. doi: 10.1007/s00027-019-0646-z

Poff, N. L. (1992). Why disturbances can be predictable: a perspective on the definition of disturbance in streams. *J. North Am. Benthol. Soc.* 11, 86–92. doi: 10.2307/1467885

Post, E., Stenseth, N. C., Langvatn, R., and Fromentin, J.-M. (1997). Global climate change and phenotypic variation among red deer cohorts. *Proc. R. Soc. Lond. B Biol. Sci.* 264, 1317–1324. doi: 10.1098/rspb.1997.0182

Rebele, F. (1994). Urban ecology and special features of urban ecosystems. *Glob. Ecol. Biogeogr. Lett.* 4:173. doi: 10.2307/2997649

Ren, L., Song, X., He, D., Wang, J., Tan, M., Xia, X., et al. (2018). Bacterioplankton metacommunity processes across thermal gradients: weaker species sorting but stronger niche segregation in summer than in winter in a subtropical bay. *Appl. Environ. Microbiol.* 85:e02088-18. doi: 10.1128/AEM.02088-2018

Resh, V. H., Brown, A. V., Covich, A. P., Gurtz, M. E., Li, H. W., Minshall, G. W., et al. (1988). The role of disturbance in stream ecology. *J. North Am. Benthol. Soc.* 7, 433–455. doi: 10.2307/1467300

Ricart, M., Guasch, H., Barceló, D., Brix, R., Conceição, M. H., Geiszinger, A., et al. (2010). Primary and complex stressors in polluted Mediterranean rivers: pesticide effects on biological communities. *J. Hydrol.* 383, 52–61. doi: 10.1016/j.jhydrol.2009.08.014

Rivera-López, A., and MacGregor-Fors, I. (2016). Urban predation: a case study assessing artificial nest survival in a neotropical city. *Urban Ecosyst.* 19, 649–655. doi: 10.1007/s11252-015-0523-z

Rodewald, A. D., and Gehrt, S. D. (2014). "Wildlife population dynamics in urban landscapes," in *Urban Wildlife*, eds R. A. McCleery, C. E. Moorman, and M. N. Peterson (Boston, MA: Springer), 117–147. doi: 10.1007/978-1-4899-7500-3_8

Rodewald, A. D., Kearns, L. J., and Shustack, D. P. (2011). Anthropogenic resource subsidies decouple predator-prey relationships. *Ecol. Appl.* 21, 936–943. doi: 10.1890/10-0863.1

Roxburgh, S. H., Shea, K., and Wilson, J. B. (2004). The intermediate disturbance hypothesis: patch dynamics and mechanisms of species coexistence. *Ecology* 85, 359–371. doi: 10.1890/03-0266

Rudolf, V. H. W. (2019). The role of seasonal timing and phenological shifts for species coexistence. *Ecol. Lett.* 22, 1324–1338. doi: 10.1111/ele.13277

Ruesink, J. L. (1998). Variation in per capita interaction strength: thresholds due to nonlinear dynamics and nonequilibrium conditions. *Proc. Natl. Acad. Sci. U.S.A.* 95, 6843–6847. doi: 10.1073/pnas.95.12.6843

Saavedra, S., Rohr, R. P., Fortuna, M., Selva, N., and Bascompte, J. (2016). Seasonal species interactions minimize the impact of species turnover on the likelihood of community persistence. *Ecology* 97, 865–873. doi: 10.1890/15-1013.1

Sakai, A. K., Allendorf, F. W., Holt, J. S., Lodge, D. M., Molofsky, J., With, K. A., et al. (2001). The population biology of invasive species. *Annu. Rev. Ecol. Syst.* 32, 305–332. doi: 10.1146/annurev.ecolsys.32.081501.114037

Sarremejane, R., Cañedo-Argüelles, M., Prat, N., Mykrä, H., Muotka, T., and Bonada, N. (2017). Do metacommunities vary through time? Intermittent rivers as model systems. *J. Biogeogr.* 44, 2752–2763. doi: 10.1111/jbi.13077

Sarremejane, R., Mykrä, H., Huttunen, K.-L., Mustonen, K.-R., Marttila, H., Paavola, R., et al. (2018). Climate-driven hydrological variability determines inter-annual changes in stream invertebrate community assembly. *Oikos* 127, 1586–1595. doi: 10.1111/oik.05329

Scantlebury, M., Oosthuizen, M. K., Speakman, J. R., Jackson, C. R., and Bennett, N. C. (2005). Seasonal energetics of the Hottentot golden mole at 1500 m altitude. *Physiol. Behav.* 84, 739–745. doi: 10.1016/j.physbeh.2005.02.022

Schlägel, U. E., Grimm, V., Blaum, N., Colangeli, P., Dammhahn, M., Eccard, J., et al. (2019). Movement-mediated community assembly and coexistence. *EcoEvoRxiv* [Preprint], doi: 10.32942/osf.io/d8a4m

Schmidt, N. M., Berg, T. B., Forchhammer, M. C., Hendrichsen, D. K., Kyhn, L. A., Meltofte, H., et al. (2008). Vertebrate predator-prey interactions in a seasonal environment. *Adv. Ecol. Res.* 40, 345–370. doi: 10.1016/S0065-2504(07)00015-3

Seidl, R., Schelhaas, M.-J., and Lexer, M. J. (2011). Unraveling the drivers of intensifying forest disturbance regimes in Europe. *Glob. Change Biol.* 17, 2842–2852. doi: 10.1111/j.1365-2486.2011.02452.x

Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., et al. (2017). Forest disturbances under climate change. *Nat. Clim. Chang.* 7, 395–402. doi: 10.1038/nclimate3303

Shoemaker, L. G., and Melbourne, B. A. (2016). Linking metacommunity paradigms to spatial coexistence mechanisms. *Ecology* 97, 2436–2446. doi: 10.1002/ecy.1454

Sih, A., Ferrari, M. C. O., and Harris, D. J. (2011). Evolution and behavioural responses to human-induced rapid environmental change. *Evol. Appl.* 4, 367–387. doi: 10.1111/j.1752-4571.2010.00166.x

Sinclair, A. R. E. (1985). Does interspecific competition or predation shape the African ungulate community? *J. Anim. Ecol.* 54:899. doi: 10.2307/4386

Snyder, R. E., and Adler, P. B. (2011). Coexistence and coevolution in fluctuating environments: can the storage effect evolve? *Am. Nat.* 178, E76–E84. doi: 10.1086/661905

Sol, D., Maspons, J., Vall-llosera, M., Bartomeus, I., García-Peña, G. E., Piñol, J., et al. (2012). Unraveling the life history of successful invaders. *Science* 337, 580–583. doi: 10.1126/science.1221523

Solins, J. P., and Cadenasso, M. L. (2020). Urban channel incision and stream flow subsidies have contrasting effects on the water status of riparian trees. *Urban Ecosyst.* 23, 419–430. doi: 10.1007/s11252-020-00926-2

Sousa, W. P. (1984). The role of disturbance in natural communities. *Annu. Rev. Ecol. Syst.* 15, 353–391. doi: 10.1146/annurev.es.15.110184.002033

Sperry, J. H., Peak, R. G., Cimprich, D. A., and Weatherhead, P. J. (2008). Snake activity affects seasonal variation in nest predation risk for birds. *J. Avian Biol.* 39, 379–383. doi: 10.1111/j.0908-8857.2008.04451.x

Starzomski, B. M., and Srivastava, D. S. (2007). Landscape geometry determines community response to disturbance. *Oikos* 116, 690–699. doi: 10.1111/j.0030-1299.2007.15547.x

Stenseth, N. C., and Mysterud, A. (2005). Weather packages: finding the right scale and composition of climate in ecology. *J. Anim. Ecol.* 74, 1195–1198. doi: 10.1111/j.1365-2656.2005.01005.x

Stenseth, N. C., Ottersen, G., Hurrell, J. W., Mysterud, A., Lima, M., Chan, K., et al. (2003). Review article. Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern oscillation and beyond. *Proc. R. Soc. Lond. B Biol. Sci.* 270, 2087–2096. doi: 10.1098/rspb.2003.2415

Svensson, J. R., Lindegarth, M., Jonsson, P. R., and Pavia, H. (2012). Disturbance-diversity models: what do they really predict and how are they tested? *Proc. R. Soc. B Biol. Sci.* 279, 2163–2170. doi: 10.1098/rspb.2011.2620

Swan, C. M., Pickett, S. T. A., Szlavecz, K., Warren, P., and Willey, K. T. (2011). "Biodiversity and community composition in urban ecosystems: coupled human, spatial, and metacommunity processes," in *Urban Ecology*, eds J. H. Breuste, T. Elmqvist, G. Guntenspergen, P. James, and N. E. McIntyre (Oxford: Oxford University Press), 179–186. doi: 10.1093/acprof:oso/9780199563562.003.0021

Talbot, L. M., and Talbot, M. H. (1963). The Wildebeest in Western Masailand, East Africa. *Wildl. Monogr*. 12, 3–88.

Thomaz, S. M., Bini, L. M., and Bozelli, R. L. (2007). Floods increase similarity among aquatic habitats in river-floodplain systems. *Hydrobiologia* 579, 1–13. doi: 10.1007/s10750-006-0285-y

Thompson, P. L., Guzman, L. M., De Meester, L., Horváth, Z., Ptacnik, R., Vanschoenwinkel, B., et al. (2020). A process-based metacommunity framework linking local and regional scale community ecology. *Ecol. Lett.* 23, 1314–1329. doi: 10.1111/ele.13568

Tischendorf, L., and Fahrig, L. (2000). On the usage and measurement of landscape connectivity. *Oikos* 90, 7–19. doi: 10.1034/j.1600-0706.2000.900102.x

Tonkin, J. D., Bogan, M. T., Bonada, N., Rios-Touma, B., and Lytle, D. A. (2017). Seasonality and predictability shape temporal species diversity. *Ecology* 98, 1201–1216. doi: 10.1002/ecy.1761

Tornwall, B. M., Swan, C. M., and Brown, B. L. (2017). Manipulation of local environment produces different diversity outcomes depending on location within a river network. *Oecologia* 184, 663–674. doi: 10.1007/s00442-017-3891-7

Tylianakis, J. M., Didham, R. K., Bascompte, J., and Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.* 11, 1351–1363. doi: 10.1111/j.1461-0248.2008.01250.x

Urban, M. C., De Meester, L., Vellend, M., Stoks, R., and Vanoverbeke, J. (2012). A crucial step toward realism: responses to climate change from an evolving metacommunity perspective. *Evol. Appl.* 5, 154–167. doi: 10.1111/j.1752-4571.2011.00208.x

Vanschoenwinkel, B., Buschke, F., and Brendonck, L. (2013). Disturbance regime alters the impact of dispersal on alpha and beta diversity in a natural metacommunity. *Ecology* 94, 2547–2557. doi: 10.1890/12-1576.1

Visser, M. E., Holleman, L. J. M., and Gienapp, P. (2006). Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia* 147, 164–172. doi: 10.1007/s00442-005-0299-6

Von Holle, B., Wei, Y., and Nickerson, D. (2010). Climatic variability leads to later seasonal flowering of Floridian plants. *PLoS One* 5:e11500. doi: 10.1371/journal.pone.0011500

Wainwright, C. E., Wolkovich, E. M., and Cleland, E. E. (2012). Seasonal priority effects: implications for invasion and restoration in a semi-arid system. *J. Appl. Ecol.* 49, 234–241. doi: 10.1111/j.1365-2664.2011.02088.x

Walther, G.-R. (2010). Community and ecosystem responses to recent climate change. *Philos. Trans. R. Soc. B Biol. Sci.* 365, 2019–2024. doi: 10.1098/rstb.2010.0021

Warren, P. H. (1996). Dispersal and destruction in a multiple habitat system: an experimental approach using protist communities. *Oikos* 77, 317–325. doi: 10.2307/3546071

West-Eberhard, M. J. (1989). Phenotypic plasticity and the origins of diversity. *Annu. Rev. Ecol. Syst.* 20, 249–278. doi: 10.1146/annurev.es.20.110189.001341

White, E. R., and Hastings, A. (2018). Seasonality in ecology: progress and prospects in theory. *PeerJ* [Preprints], doi: 10.7287/peerj.preprints.27235v1

White, M. D., and Greer, K. A. (2006). The effects of watershed urbanization on the stream hydrology and riparian vegetation of Los Peñasquitos Creek, California. *Landsc. Urban Plan.* 74, 125–138. doi: 10.1016/j.landurbplan.2004.11.015

Winegardner, A. K., Jones, B. K., Ng, I. S. Y., Siqueira, T., and Cottenie, K. (2012). The terminology of metacommunity ecology. *Trends Ecol. Evol.* 27, 253–254. doi: 10.1016/j.tree.2012.01.007

Wisnoski, N. I., Leibold, M. A., and Lennon, J. T. (2019). Dormancy in metacommunities. *Am. Nat.* 194, 135–151. doi: 10.1086/704168

Ydenberg, R. (1987). Nomadic predators and geographical synchrony in microtine population cycles. *Oikos* 50, 270–272. doi: 10.2307/3566014

Zhang, Q., Guan, Y., and Yang, H. (2008). ENSO amplitude change in observation and coupled models. *Adv. Atmos. Sci.* 25, 361–366. doi: 10.1007/s00376-008-0361-5

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Metacommunity Structures of Macroinvertebrates and Diatoms in High Mountain Streams, Yunnan, China

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The metacommunity concept has received increasing interest in the past two decades. However, there has been limited research examining metacommunity structure of communities in high mountain streams. These ecosystems are often physically constrained and can display large environmental gradients within a relatively small spatial extent. Here, we examined metacommunity structures of stream organisms in a high mountain region, which is part of the Hengduan Mountains region in Southwest China. Macroinvertebrates and diatoms were collected from six streams in two opposite aspects of the same mountain with different connectivity between streams. On the west aspect, streams are tributaries of a river (i.e., river-connected) while streams flow into a lake (i.e., lake-connected) on the east aspect. We used Elements of Metacommunity Structure analysis to explore the metacommunity structuring of these two biological models. We also compared the contribution of dispersal and environmental filtering in structuring metacommunities by looking at Euclidean, network, topographic, and environmental distances. Communities of diatoms and macroinvertebrates were structured with clear turnover on both aspects. Further, diatom communities exhibited Clementsian structure on both aspects. Macroinvertebrates exhibited different metacommunity structures on the river-connected aspect (Quasi-Clementsian) and lake-connected aspect (Clementsian). Our results indicated that on the lake-connected aspect, environmental filtering had a stronger association with community dissimilarity than on the river-connected aspect for both macroinvertebrate and diatom communities. Diatom communities were more influenced by environmental filtering on the east aspect with weakened network connectivity compared with those on the west aspect. Our results also emphasized the potential effects of biotic interactions between macroinvertebrates and diatoms on shaping community structures of one other. Our study provides substantial elements to further understand metacommunity structure and highlights the necessity of future research to reveal the underlying mechanisms of community structuring in these remote ecosystems.

Keywords: dispersal, network, connectivity, Hengduan Mountains (Hengduanshan), elevation, distance-decay, biotic interactions

INTRODUCTION

Patterns and variation in biodiversity and their underlying mechanisms are central topics in biogeographical and ecological research (Gaston, 2000; Willig et al., 2003; Sanders and Rahbek, 2012). The metacommunity concept provides a theoretical framework for understanding biodiversity patterns and their variations and has received increasing attention from researchers in the last two decades (Leibold et al., 2004; Logue et al., 2011; Heino, 2013). Four different paradigms have been proposed to explain how spatial and environmental factors influence ecological patterns within the metacommunity, including neutral, patch dynamics, species sorting, and mass effects (Leibold et al., 2004; Logue et al., 2011). All four metacommunity paradigms are defined by dispersal, whether it is high, low, constant, or species-dependent as individual communities do not exist in isolation and are often linked to one another (Leibold et al., 2004; Logue et al., 2011).

The exchange of species between river communities is promoted by overland dispersal, dispersal along the river network, or a combination of both (Thompson and Townsend, 2006). Studies focusing on river ecosystems have emphasized the important role of river networks in influencing the dispersal of organisms (Brown and Swan, 2010; Altermatt, 2013; Maasri et al., 2018; Tonkin et al., 2018). For example, diatoms often disperse passively overland through wind or animal vectors or passively within rivers, following the flow direction, while fishes disperse actively within the river networks and are restricted to the stream corridor (Heino et al., 2015; Dong et al., 2016). Macroinvertebrates disperse through a variety of pathways including actively dispersing overland and instream, dispersing passively overland, and drifting downstream along the river network (Grönroos et al., 2013; Heino et al., 2015).

Network connectivity can therefore influence how communities are linked to one another, in turn influencing the roles that dispersal, the local environment, and local biotic interactions play in structuring them (Schmera et al., 2017; Tonkin et al., 2018), as well as the relative strength of source-sink dynamics between communities (Gundersen et al., 2001). Compared to lowland streams, streams in high mountain regions are more spatially isolated from one another by topographic barriers (Finn and Adler, 2006; Brown and Swan, 2010). Therefore, the dispersal of species in high mountain streams is often dominated by network dispersal, as opposed to overland dispersal (Wang et al., 2012; Altermatt et al., 2013; Dong et al., 2016). In addition to dispersal limitation by mountain ridges and steep valleys, the steep elevational gradient of high mountain streams can be a strong driver of change in local environmental conditions including solar radiation, riparian vegetation, water temperature, or dissolved oxygen levels (Jacobsen, 2008; Presley and Willig, 2010; Altermatt et al., 2013), in turn influencing the interaction between dispersal and environmental filtering. Several studies have demonstrated the effects of elevation-driven environment on stream communities (Wang et al., 2012; Dong et al., 2016; Tonkin et al., 2016; He S. et al., 2020). However, the role of network connectivity in structuring metacommunities of macroinvertebrates and diatoms in high mountain streams is rarely explored.

Here we aim to examine the metacommunity structures of macroinvertebrates and diatoms in high-mountain streams located in the Cangshan Mountain, a part of the Hengduan Mountains, and to understand how they are affected by network connectivity and environmental factors. Previous studies have suggested that communities in streams with large elevational gradients witness significant turnover rates (Shah et al., 2015; Tonkin et al., 2016). Turnover is therefore considered a prominent characteristic of high-mountain stream metacommunities (Presley et al., 2010; e.g., Wang et al., 2012; Shah et al., 2015; Tonkin et al., 2016). Given the large elevational gradient in our study streams, we hypothesize that turnover exists in both macroinvertebrate and diatom communities (H1).

Additionally, on the west aspect of the Cangshan Mountain, streams are connected by the Heihui River while streams on the east aspect are connected by Lake Erhai (**Figure 1**). The distance-decay relationships (DDRs) in stream communities, i.e., associations between community dissimilarity and environmental or physical distances (Nekola and White, 1999), could be different between two aspects due to distinct stream connectivity. We assume that macroinvertebrates flushed into the lake via drift are likely to face mortality because of environmental change (i.e., from lotic to lentic environment) or predation by fish in the lake, limiting the in-stream dispersal between streams (Brittain and Eikeland, 1988). In comparison, local environmental similarities between the Heihui River and its tributary streams, such as similar flow velocities, water depths and substrates, would allow within-river upstream dispersal into other streams for macroinvertebrates. Therefore, we expect the river-connected aspect to provide a better in-stream, network connection for dispersal of macroinvertebrates than the lake-connected aspect. Hence, we hypothesize that the contribution of physical distance, particularly network distance, to dissimilarities among macroinvertebrate communities on the lake-connected aspect to be lower than the contribution of these same distances on the river-connected aspect (H2). Diatoms, like most passively dispersing microbial organisms, do not move actively against the flow within stream and their dispersal is strongly influenced by the flow direction of the stream (Finlay, 2002; Wang et al., 2012; Dong et al., 2016). We therefore expect

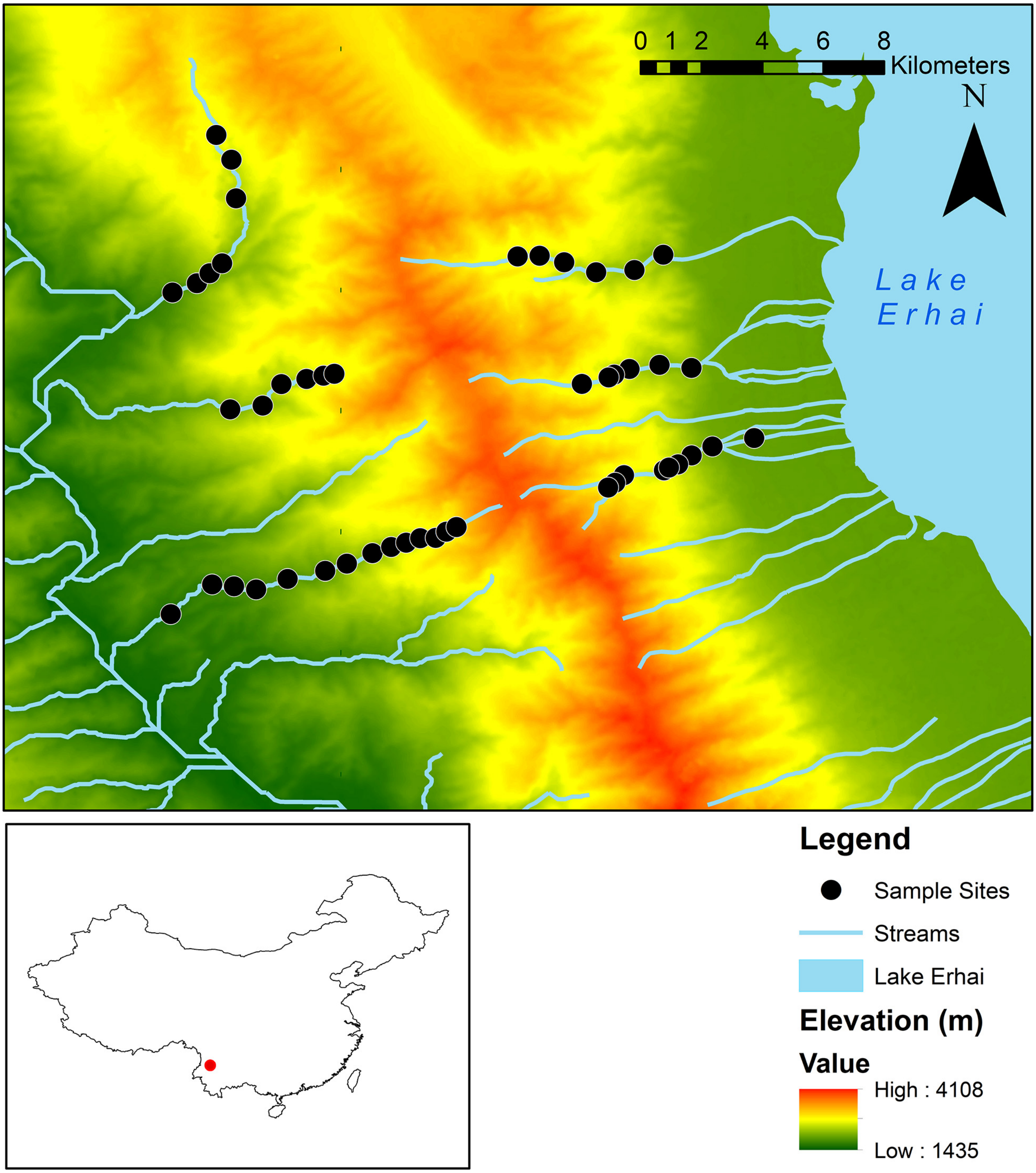

FIGURE 1 | Map of Cangshan Mountain and sampled sites (n = 48). Study sites on the west or river-connected aspect (n = 27) had an elevational range of 1,623–2,905 m a.s.l, while study sites on the east or lake-connected aspect (n = 21) had an elevational range of 2,042–2,825 m a.s.l. The inset map depicts the study area in red, in the context of mainland China.

that their within-stream dispersal is similar between the lake-connected and river-connected aspects (i.e., diatoms are mainly flushed to downstream reaches from upstream reaches by flow). Hence, we further hypothesize that diatom communities will be structured similarly on both aspects, regardless of the weakened connectivity between streams on the lake-connected aspect (H3). Finally, emerging research has emphasized the influence of biotic interactions in structuring communities (Ohlmann et al., 2018; García-Girón et al., 2020). Considering the links between macroinvertebrates and diatoms (dispersal vector, consumer-resource relationship), we hypothesize, biotic interactions between macroinvertebrate and diatom communities have influence on the metacommunity structuring of them (H4).

MATERIALS AND METHODS

Field Sampling and Lab Analysis

The study area is located in the Cangshan-Erhai National Nature Reserve (25.64–25.85°N, 99.95–100.20°E), Northwest Yunnan, China. The Cangshan Mountain, which is part of the Hengduan Mountains, is characterized by a series of 19 mountain ridges with almost parallel streams running between them (**Figure 1**). The highest of these ridges reaches 4,122 m a.s.l. On the east aspect, streams flow into Lake Erhai, while on the west aspect, streams are connected by the Yangbi River. In addition, vegetation exhibits different elevational patterns between the east and the west aspects due to the influence of solar radiation (Sun, 2008). From here on, the east aspect will be referred to as the lake-connected aspect and the west as the river-connected aspect. The region is located in the Mekong River basin and characterized by a monsoon season from May to October and a dry season from November to April.

From November to December 2012, 48 sites were sampled from six streams (i.e., three on each aspects), ranging from 1,623 to 2,905 m a.s.l. (He F. et al., 2020). At each site, conductivity (Cond), dissolved oxygen (DO), pH, salinity (Sal), total dissolved solids (TDS), water temperature (Wtemp), and oxidation reduction potential (ORP) were measured *in situ* with a multiparameter probe (YSI Professional plus, US). Stream width was measured as the average of three cross sections. Depth and velocity were measured along a transect every 50 cm using a water flow probe and averaged (Global Water FP201, US). Geographical coordinates and elevations of sampling sites were determined using a portable GPS device (Magellan 500E, US). Water samples were collected and preserved using sulfuric acid to keep pH under 2. In the lab, total phosphorus (TP), orthophosphate ($PO_4{}^{3-}$), total nitrogen (TN), nitrate ($NO_3{}^{-}$), ammonium ($NH_4{}^{+}$), and dissolved silica (SiO_2) were measured using a segmented flow analyzer (Skalar San ++, Netherlands).

Macroinvertebrate samples were collected using a Surber net (30 × 30 cm, 500 μm). Five sub-samples were taken at each site to cover multiple habitat types. Macroinvertebrates were identified following Morse et al. (1994) and literature in the lab. All macroinvertebrates were identified to genus level, except for Chironomidae, which was classified to the subfamily, and Oligochaeta, Turbellaria, and Nematoda, to the class level.

Benthic diatom samples were collected from pebble or cobble substrates. A cap with a radius of 2.7 cm was placed over the substrate. The periphyton around the cap was removed with a nylon brush and flushed away. Then the periphyton under the cap was collected. In the lab, samples were digested using acid and examined at a magnification of 1,000 using oil immersion (Olympus CX21, Japan). Diatoms were classified to the species level using Krammer and Lange-Bertalot (1986, 1988, 1991a,b) and Qi et al. (1995, 2004a,b, 2009, 2013). More details are described in Dong et al. (2016).

Data Analysis

Sites were grouped by aspect (i.e., a river-connected network on the west aspect and a lake-connected network on the east aspect). Collinearity between variables was tested using a pairwise Spearman correlation. The threshold of $r = |0.7|$ (Dormann et al., 2012) were used to exclude highly correlated variables (e.g., TDS, pH, $PO_4{}^{3-}$, $NO_3{}^{-}$, $NH_4{}^{+}$, and SiO_2) for further analysis. Taxon richness and dominant diatom and macroinvertebrate taxa were calculated for each aspect, as well as each individual stream sampled.

In order to determine the metacommunity structure on different aspects, an Elements of Metacommunity Structure (EMS) analysis was performed using the function *Metacommunity* in the package *metacom* (Dallas, 2018) in R (R Core Team, 2017). The *metacom* function runs through a three-step analysis with species-site data, in which coherence, species turnover, and boundary clumping are tested to determine the idealized metacommunity structure. Coherence is measured by comparing species absences in the data to a null-model checkerboard presence-absence matrix using a *z*-score. A significant negative coherence indicates a checkerboard structure, a non-significant coherence represents random coherence, and a significant positive coherence suggests a structure other than checkerboard or random. Turnover, or species replacement, is tested against a null model without species replacement. A significant positive *z*-score suggests significant species turnover, while a significant negative *z*-score indicates a nested metacommunity structure. Non-significant *z*-scores are treated ambiguously and are considered quasi-structures. Boundary clumping measures whether the metacommunity exhibits individual or grouped turnover and is measured using Morista's Index (MI). A mean MI value significantly greater than one represents clumped or Clementsian metacommunity structure while a mean MI value significantly smaller than one indicates an evenly-spaced metacommunity structure. Metacommunities with a mean MI value not significantly different from one are thought to have Gleasonian structure (Dallas, 2018). The site-scores were extracted from the primary EMS axis and Spearman correlations were run to identify which environmental variables provide the structuring force behind the EMS. Although it has limitations, the use of EMS to fit community data to a theoretical pattern is widespread and of interest due to the small study area we sampled (approximately 100 km^2 on the river-connected aspect, approximately 50 km^2 on the lake-connected aspect).

Four different matrices were calculated to measure distances between sites, including environmental, Euclidean, topographic, and network distances. The environmental distances between sites were determined with log10-transformed environmental variables with the package *vegan* (Oksanen et al., 2019). Euclidean distance between sites was calculated using the *earth.dist* function in the package *fossil* (Vavrek, 2011) while topographic distance was calculated using CIRCUITSCAPE v. 4.0 with a 30 m digital elevation model

(DEM). Detailed methods can be found in Dong et al. (2016). The network distance was calculated in QGIS (version 2.8; QGIS Development Team, 2015). On the lake-connected aspect, streams are connected by a lake and not a river. Because some macroinvertebrates can live in the littoral zones and flying insects can still actively disperse along the lake's edge, some degree of connectivity could still be maintained (Bagge, 1995). Although we realize that stream-lake connection provides a weaker dispersal path for macroinvertebrates than the connection between a stream and river, for the sake of comparison, the edge of the lake was still regarded as a network path for both macroinvertebrates and diatoms. With abundance data, the community dissimilarity between sites was calculated with Bray-Curtis index with the package *vegan*. To determine the correlation between each of the four distances and community dissimilarity, we performed Mantel tests using Spearman's rank-order correlation with 999 permutations.

We further analyzed the association between community dissimilarity and all measured distances using a distance-decay relationships (DDRs). We plotted the site-values of community dissimilarity against the site-values of physical (Euclidean, Topographic, Network) distances and environmental distances, conducting a logarithmic regression to determine which model best described the relationship between community dissimilarities and distances. To disentangle contributions of different distance matrices to community dissimilarity, partial Mantel tests were conducted using Spearman's rank-order correlation also with 999 permutations. Partial Mantel tests allow for the further analysis of Mantel tests and can be used to unmask the effects of different distances matrices that could be auto-correlated (Moritz et al., 2013). The associations between community dissimilarity and the three physical distances were adjusted while controlling environmental distance. The association between community dissimilarity and environmental distance was also adjusted to control for the influence of each physical distance. Partial Mantel tests were conducted in using the package *ecodist* (Goslee and Urban, 2007).

Moreover, we investigated the potential influence of biotic interactions between macroinvertebrates and diatoms on community structuring of these two organisms by conducting partial Mantel tests. We examined the associations between community dissimilarity and physical distance controlling for environmental distance and the other taxa community dissimilarity, as well as a partial Mantel test to analyze the association between community dissimilarity physical distance controlling for environmental distance and the other taxa community dissimilarity. We also included a partial Mantel test to determine the association between macroinvertebrate community dissimilarity and diatom community dissimilarity, controlling for all physical and environmental distances.

The elevational range of sampling sites on the river-connected aspect (1,623–2,905 m a.s.l.) is almost twice that of the lake-connected aspect (2,042–2,825 m a.s.l.). To test whether there was any bias caused by difference in elevational range, the EMS, Mantel tests, and partial Mantel tests were also conducted on sites within the common zone (sites with an elevation between 2,042 and 2,825 m a.s.l. on both aspects).

RESULTS

In total, 70 macroinvertebrates and 74 diatom taxa were identified on the lake-connected aspect. On the river-connected aspect, 79 macroinvertebrate taxa and 119 diatom taxa were identified. Dominant taxa were similar on both aspects. For macroinvertebrates the most abundant taxa were *Baetis* spp., *Baetiella* spp., and Orthocladiinae spp. For diatoms, the most abundant taxa were *Achnanthidium minutissimum* (Kützing) Czarnecki, *Anchnathidium rivulare* Potapova & Ponader, and *Cocconeis placentula* Ehrenberg.

Diatom communities on both aspects, as well as macroinvertebrate communities on the lake-connected aspect exhibited Clementsian metacommunity structure (significant positive coherence, significant turnover, significant boundary clumping; **Table 1**). The macroinvertebrate community on the river-connected aspect had a Quasi-Clementsian metacommunity structure (significant positive coherence, non-significant turnover, significant boundary clumping). In the macroinvertebrate communities on the lake-connected aspect, EMS site scores were significantly correlated with conductivity ($r = -0.66, p < 0.01$), velocity ($r = -0.62, p < 0.01$), DO ($r = 0.55$, $p = 0.01$), and water temperature ($r = -0.51$, $p = 0.02$). All the aforementioned environmental variables are significantly correlated with elevation on the lake-connected aspect. Water temperature ($r = 0.77$, $p < 0.01$), conductivity ($r = 0.55$, $p < 0.01$, TN ($r = 0.55$, $p < 0.01$), TP ($r = 0.46$, $p = 0.02$), and velocity ($r = 0.45$, $p = 0.02$) were all significantly correlated with macroinvertebrate community EMS site scores on the river-connected aspect. Elevation was significantly correlated with conductivity, water temperature, and TN on the river-connected aspect. The EMS site scores of the diatom communities on the lake-connected aspect were not significantly correlated with any environmental variables or elevation. On the

TABLE 1 | Elements of metacommunity structure (EMS) data for macroinvertebrates and diatoms on both aspects.

		Macroinvertebrates		Diatoms	
		Lake-connected	River-connected	Lake-connected	River-connected
Coherence	df	18	24	18	24
	Abs	416	549	580	1446
	z	15.24	16.74	1.10	10.96
	p	<0.01	<0.01	<0.01	<0.01
Turnover	Re	7,387	18,522	11,314	43,388
	z	−3.10	−1.61	−4.26	−3.77
	p	<0.01	0.08	<0.01	<0.01
Clumping	MI	3.06	1.45	1.67	1.78
	p	<0.01	<0.01	<0.01	<0.01
Structure		Clementsian	Quasi-clementsian	Clementsian	Clementsian

river-connected aspect, diatom community EMS site scores were significantly correlated with conductivity ($r = -0.50$, $p < 0.01$). In the common zone analysis, EMS results were similar with the whole range sites, with diatom and macroinvertebrate communities exhibited Clementsian metacommunity structure on both aspects (**Supplementary Table S1**).

For both diatom and macroinvertebrate communities, there was were significant positive Distance Decay Relationships (DDRs) between Bray-Curtis dissimilarity and all distances based on Mantel tests (**Figure 2** and **Table 2**), except for topographic distance on the lake-connected aspect. The DDRs in common zone showed the same patterns as in the whole range for both the diatom and macroinvertebrate communities (**Supplementary Figure S1** and **Supplementary Table S2**).

In the whole range analysis, Euclidean DDR and network DDRs had higher R^2 values that topographic DDRs for diatoms and macroinvertebrates on both aspects. When only analyzing sites in the common zone, the R^2 values of topographic DDRs,

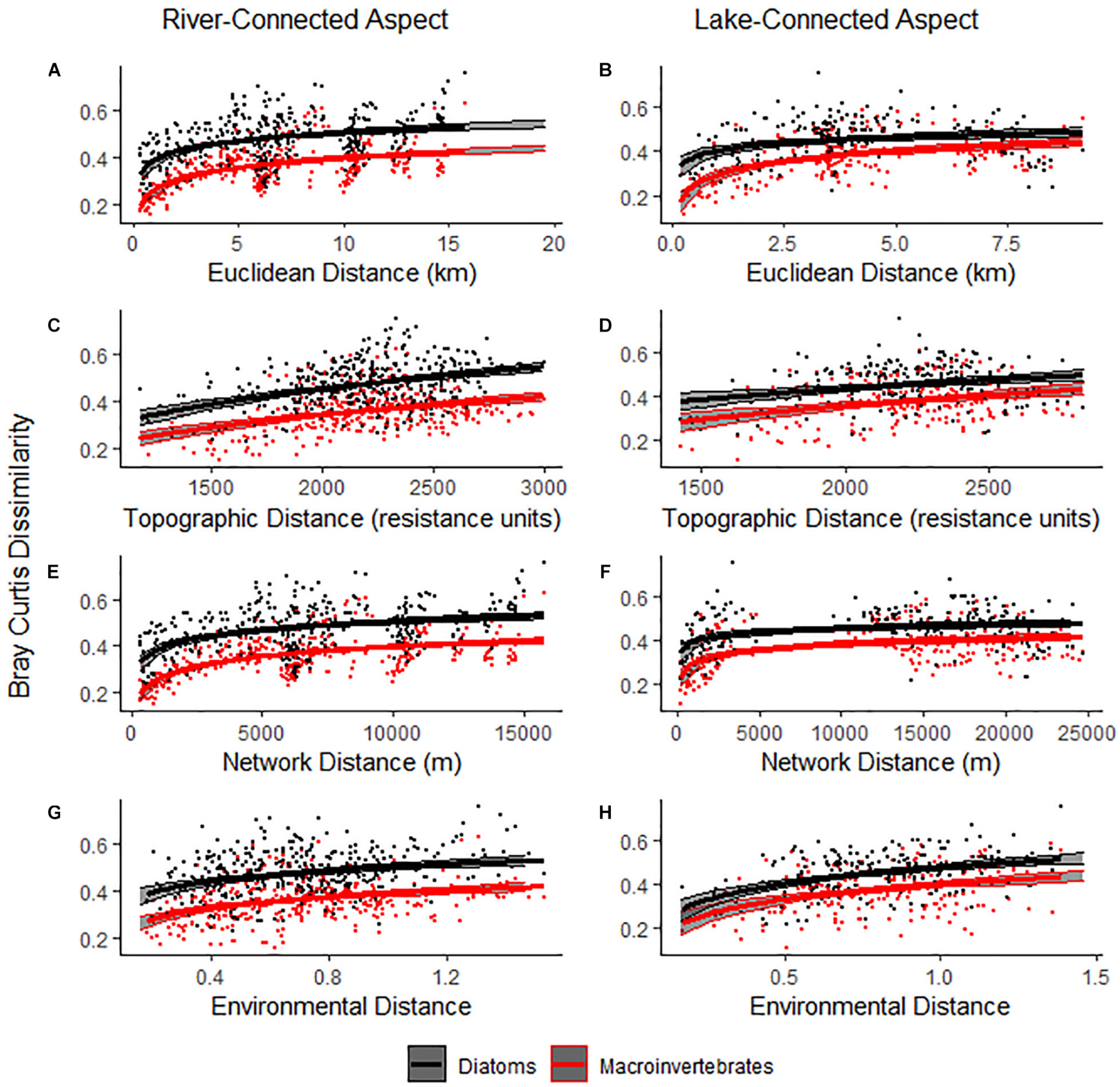

FIGURE 2 | Distance Decay Relationships (DDR) of macroinvertebrates and diatoms. Points represent individual distances between two given sites, while lines represent the logarithmic regression for each group of points. Macroinvertebrates are represented by red points and lines, while diatoms are represented by black points and lines. The lines shown in the figures are based on logarithmic models. Solid lines represent significant Mantel tests, while dashed lines represent insignificant Mantel tests. The gray area surrounding the logarithmic regressions represents a 95% CI. Formulas and R^2 values for each regression can be found in **Supplementary Table S3**.

TABLE 2 | Mantel test between community dissimilarity (Bray-Curtis dissimilarity) and physical and environmental distances for macroinvertebrates and diatoms.

	Macroinvertebrates				Diatoms			
	Lake-connected		River-connected		Lake-connected		River-connected	
	r	***p***	***r***	***p***	***r***	***p***	***r***	***p***
Euclidean	0.40	<0.01	0.51	<0.01	0.15	0.04	0.40	<0.01
Topographic	0.18	0.06	0.30	<0.01	0.14	0.07	0.32	<0.01
Network	0.25	0.01	0.53	<0.01	0.16	0.04	0.40	<0.01
Environment	0.37	<0.01	0.31	<0.01	0.42	<0.01	0.24	0.01

Euclidean DDRs and network DDRs on the river-connected aspect were similar (**Supplementary Table S4**).

Partial Mantel tests showed that macroinvertebrate community dissimilarity on the lake-connected aspect had a significant association with Euclidean distance when adjusted for environmental distance ($r = 0.40$, $p < 0.01$, **Table 3**), as well as significant associations with environmental distance when adjusted for all three physical distances (Euclidean distance, $r = 0.37$, $p < 0.01$; topographic distance, $r = 0.35$, $p < 0.01$; network distance, $r = 0.36$, $p < 0.01$). On the river-connected aspect, macroinvertebrate communities had significant associations with all three physical distances when adjusted for environmental distance, with Euclidean distance ($r = 0.44$, $p < 0.01$) having the greatest correlation coefficient, followed by the network distance ($r = 0.43$, $p < 0.01$) and topographic distance ($r = 0.21$, $p = 0.01$). Additionally, there was a significant association between macroinvertebrate community dissimilarity on the river-connected aspect and environmental distance adjusted for topographic distance ($r = 0.22$, $p = 0.02$, **Table 3**). On the river-connected aspect of the common zone analysis, macroinvertebrate communities were significantly associated with all adjusted distances except for environmental distance adjusted for Euclidean distance and environmental distance adjusted for network distance (**Supplementary Table S5**).

Compared to macroinvertebrates, major differences in the results of the partial Mantel test for diatoms were observed between the lake- and river-connected aspects. Diatom community dissimilarity on the lake-connected aspect was significantly associated with environmental distances adjusted for all physical distances (adjusted for Euclidean distance, $r = 0.42$, $p < 0.01$; topographic distance, $r = 0.41$, $p < 0.01$, network distance, $r = 0.42$, $p < 0.01$, **Table 3**). On the river-connected aspect, diatom community dissimilarity was significantly associated with all physical distances when adjusted for environmental distance (Euclidean distance, $r = 0.17$, $p < 0.01$; topographic distance, $r = 0.17$, $p < 0.01$; network distance, $r = 0.18$, $p < 0.01$). The common zone analysis of diatom communities on the lake-connected aspect was similar to that of the whole range analysis (**Supplementary Table S1**). On the river-connected aspect of the common zone analysis, diatom community dissimilarity was significantly associated with Euclidean distance adjusted for environmental distance ($r = 0.35$, $p < 0.01$), topographic distance adjusted for environmental distance ($r = 0.42$, $p < 0.01$) and network distance adjusted for environmental distance ($r = 0.34$, $p < 0.01$).

We found a significant association between macroinvertebrate and diatom community dissimilarity on both the lake-connected ($r = 0.31$, $p < 0.01$) and river-connected aspect ($r = 0.33$, $p < 0.01$, **Tables 4**, **5**), when corrected for all other physical distances and environmental distance. In the common zone analysis, macroinvertebrate and diatom dissimilarities were significant on the lake-connected aspect ($r = 0.31$, $p < 0.01$) but not on the river-connected aspect ($r = 0.2$, $p = 0.08$, **Supplementary Tables S6, S7**).

We found significant associations between Euclidean distance and network distance and macroinvertebrate community dissimilarity on both river- and lake-connected aspects, when controlled for environmental distance and diatom dissimilarity (**Table 4**). However, no significant association between macroinvertebrate community dissimilarity and environmental distances was observed when effects of physical distance and diatom dissimilarity were considered (**Table 4**). On the river-connected aspect, diatom community dissimilarity was significantly associated with all physical distances controlled for environmental distance and macroinvertebrate community dissimilarity (**Table 5**). On the lake-connected aspect, diatom community dissimilarity was only significantly

TABLE 3 | Partial mantel tests of Bray-Curtis dissimilarity using Spearman's rank correlation for macroinvertebrate communities on the lake-connected and river-connected aspects and diatom communities on the east and west aspects.

	Macroinvertebrates				Diatoms			
	Lake-connected		River-connected		Lake-connected		River-connected	
	r	***p***	***r***	***p***	***r***	***p***	***r***	***p***
Euclidean | Environmental	0.40	<0.01	0.44	<0.01	0.12	0.08	0.17	<0.01
Topographic | Environmental	0.12	0.15	0.21	0.01	0.07	0.25	0.17	0.044
Network | Environmental	0.24	0.01	0.43	<0.01	0.13	0.08	0.18	<0.01
Environmental | Euclidean	0.37	<0.01	0.12	0.11	0.42	<0.01	0.07	0.24
Environmental | Topographic	0.35	<0.01	0.22	0.02	0.41	<0.01	0.08	0.23
Environmental | Network	0.36	<0.01	0.12	0.1	0.42	<0.01	0.07	0.25

"|" stands for "adjusted for."

TABLE 4 | Partial mantel tests of Bray-Curtis dissimilarity using Spearman's rank correlation for macroinvertebrate communities on the lake-connected and river-connected aspects of the whole range.

	Macroinvertebrates			
	Lake-connected		**River-connected**	
	r	***p***	***r***	***p***
Euclidean | Environmental and Diatom	0.38	<0.01	0.34	<0.01
Topographic | Environmental and Diatom	0.11	0.19	0.11	0.14
Network | Environmental and Diatom	0.21	0.03	0.34	<0.01
Environmental | Euclidean and Diatom	0.19	0.7	0.09	0.17
Environmental | Topographic and Diatom	0.17	0.1	0.18	0.06
Environmental | Network and Diatom	0.18	0.09	0.09	0.19
Diatom | Environmental and all physical distances	0.31	<0.01	0.33	<0.01

"|" stands for "adjusted for."

TABLE 5 | Partial mantel tests of Bray-Curtis dissimilarity using Spearman's rank correlation for diatoms communities on the lake-connected and river-connected aspects on the whole range.

	Diatoms			
	Lake-connected		**River-connected**	
	r	***p***	***r***	***p***
Euclidean | Environmental and Macroinvertebrates	0.0	0.46	0.19	<0.01
Topographic | Environmental and Macroinvertebrates	0.03	0.36	0.21	<0.01
Network | Environmental and Macroinvertebrates	0.06	0.25	0.19	<0.01
Environmental | Euclidean and Macroinvertebrates	0.29	<0.01	0.07	0.23
Environmental | Topographic and Macroinvertebrates	0.29	<0.01	0.06	0.27
Environmental | Network and Macroinvertebrates	0.29	<0.01	0.07	0.27
Macroinvertebrates| Environmental and all physical distances	0.31	<0.01	0.33	<0.01

"|" stands for "adjusted for."

associated with environmental distance adjusted for physical distance and macroinvertebrate community dissimilarity (**Table 5**). These observed associations suggested the influence of biotic interactions on community structuring of both macroinvertebrate and diatom communities.

DISCUSSION

Metacommunity Turnover

Turnover was observed in both stream macroinvertebrates and diatoms communities in the Cangshan Mountain, supporting our first hypothesis (H1). This finding stands in line with previous studies focusing on communities of high-mountain stream systems with large elevational gradients (Shah et al., 2015; Tonkin et al., 2016). A large elevational gradient is often coupled with changes in local environmental variables, like DO, water temperature, conductivity, riparian vegetation, wind exposure, solar radiation, and precipitation (Townsend et al., 2003; Körner, 2007; Jacobsen, 2008; Sundqvist et al., 2013; Willig and Presley, 2015; Kim and Lee, 2017). Local environmental conditions play a critical role in determining which organisms can be found at a given site through species sorting or environmental filtering. For example, macroinvertebrate species richness showed a negative association with elevation in Andes because of the sub-lethal effects of low DO levels in high-elevational areas, like lowered metabolism (Jacobsen, 2008). Kim and Lee (2017) described a change in diatom communities due to decreases in water temperature, pH, and total phosphorus associated with increases in elevation and He F. et al., 2020 also found that elevation is important in structuring diatoms species in China.

Moreover, the observed Clementsian and Quasi-Clementsian metacommunity structuring suggests that there is a grouped community response to changes in the local environmental variables (Leibold and Mikkelson, 2002). That is, species pools are thought to replace each other, suggesting either trait-related grouping based on dispersal related processes or environmental filtering or groupings related to biotic interactions between species, or some combination of forces (Presley et al., 2010; Heino et al., 2015). Other studies focused on freshwater organisms have found significant Clementsian structuring at larger scales, where Clementsian structuring is likely caused by multiple different ecotones and species pools within the study area (Tonkin et al., 2015, low mountain stream macroinvertebrates, 20–1,000 km^2; Tonkin et al., 2016, high mountain macroinvertebrates, 400–650 km^2; Heino et al., 2017, aquatic insects and diatoms, 63,609 km^2).

The Clementsian structuring in a smaller study area like ours is likely caused by the large elevational gradient and the associated heterogeneous environmental gradients, where multiple taxon-pools can occur within a small area. Clementsian metacommunity structures indicate significant turnover and niche-based, grouped, species sorting (Leibold and Mikkelson, 2002). Instead of constant turnover, like in Clementsian structure, Quasi-Clementsian structures is thought to exhibit turnover at the ends of the environmental gradient, resulting in insignificant turnover, but still have significant grouped, niche-based sorting occurring (Presley et al., 2010). This aligns with our results, which show that for the macroinvertebrate community on the river-connected aspect, the whole range metacommunity has a Quasi-Clementsian structure while the common-zone has a Clementsian structure. The switch between Quasi-Clementsian and Clementsian could be caused by the removal of low-elevation communities, which may be more homogenous due to human impacts and have less turnover than communities in higher elevations.

Influence of Connectivity on Dispersal and Metacommunities

The significant relationships between community dissimilarity and physical distances confirm the role of dispersal in structuring metacommunities in high-mountain streams, where source-sink dynamics are limited (Göthe et al., 2013; Heino et al., 2015). Additionally, significant relationships between environmental distance and community dissimilarity often signal species sorting dynamics (Leibold et al., 2004), which was also observed in our study. Hence, it is likely that dispersal limitation and species sorting jointly shape metacommunities of stream macroinvertebrates and diatoms in the Cangshan Mountain. The metacommunity paradigms described by Leibold et al. (2004) are not mutually exclusive and combinations of more than one paradigm are common (Thompson and Townsend, 2006; Brown and Swan, 2010; Grönroos et al., 2013; Brown et al., 2017).

In stream ecosystems, connectivity of dendritic networks and dispersal ability through that network play an important role in structuring metacommunities (Altermatt and Fronhofer, 2017; Hayes and Anderson, 2017; Tonkin et al., 2018). When the connectivity between communities is weakened, dispersal pathways are disrupted and the communities become more isolated (Cañedo-Argüelles et al., 2015). Consequently, the influence of environmental filtering increases as more isolated communities are more strongly structured by local environmental factors (Brown and Swan, 2010; Cañedo-Argüelles et al., 2015). Studies focused on European high mountain lakes, which are more isolated than high mountain streams and rivers, have found that local environmental factors are more important in structuring macroinvertebrate communities than spatial factors (Kernan et al., 2009; de Mendoza and Catalan, 2010; de Mendoza et al., 2015). On the lake-connected aspect of the Cangshan Mountain, the interaction between dispersal and environmental filtering on river metacommunities has been altered compared to the river-connected aspect. The Mantel tests showed that environmental distance exhibited stronger correlation with community dissimilarity on the lake-connected aspect than on the river-connected aspect for macroinvertebrates, and the partial Mantel tests further supported this result. This verified our second hypothesis (H2) that environmental factors contribute more to the community dissimilarity of macroinvertebrates when connectivity between streams is weakened.

Our results contradicted our third hypothesis (H3) that diatom communities would be more similarly structured on the differently connected aspects than macroinvertebrates. This hypothesis was based on the differences in dispersal capabilities of macroinvertebrates and diatoms. Apart from in-stream passive dispersal via flow, many macroinvertebrates can move actively along the network corridor and fly overland as well. Flying adult insects can disperse along the lake shore from confluence to confluence, as well as along the littoral zone of the lake (Bagge, 1995), contributing, therefore, to the dispersal between streams on the lake-connected aspect. Thus, there is weakened network connectivity between the macroinvertebrate communities in streams on the lake-connected aspect compared to the river-connected aspect.

Compared to macro-organisms such as macroinvertebrates, diatoms are efficient and ubiquitous passive dispersers like other micro-organisms (Finlay, 2002). The Baas-Becking hypothesis, i.e., diatoms are ubiquitous dispersers and their biodiversity patterns are structured by local environmental conditions (Baas Becking, 1934; Finlay, 2002), has been challenged in recent research. Both lowland and high mountain stream diatom biodiversity is thought to be shaped not only by local environmental factors, but by dispersal-related spatial processes as well (Potapova and Charles, 2002; Soininen, 2004; Martiny et al., 2006; Bottin et al., 2014; Dong et al., 2016). In addition, Vilmi et al. (2020) observed more stochastic patterns in stream micro-organism (i.e., bacteria) than in macro-organism (i.e., macroinvertebrates) in the Hengduan Mountains. Our results suggest that diatom communities in high mountain streams are influenced by both spatial and environmental factors (Wang et al., 2012; Dong et al., 2016). Similar results from high mountain lakes in Europe and in the Andes have also shown that diatom assemblages are structured by both local environmental and spatial factors, although local environmental factors are more important in structuring lentic diatoms than geographical factors in Europe (Kernan et al., 2009; Benito et al., 2018). Diatoms are fundamentally limited to passive dispersal, either depending on wind or biotic vectors for overland dispersal or dispersing along the network in the direction of flow (Heino et al., 2015; Dong et al., 2016). Barriers, like the presence of a lake, may affect diatom dispersal. For example, diatoms flushed into lakes via in-stream drift may be unable to tolerate lentic conditions, as lake and stream diatom communities are known to be different from one another (Soininen and Weckström, 2009). This may limit in-stream dispersal to adjacent lotic habitats, although some dispersal may be possible via wind or other animal vectors (Kristiansen, 1996). However, topographical barriers can affect the dispersal of vectors themselves in high mountain ecosystems. For example, macroinvertebrates are important vectors for diatom dispersal (Kristiansen, 1996). If macroinvertebrate dispersal is weakened in high mountain streams, this could weaken the dispersal ability of diatoms. In the Hengduan Mountains, small-mammal communities had high turnover and were found to be dispersal limited by topographical and environmental barriers (Wen et al., 2016). Additionally, Adams et al. (2000) found that Brook Trout with a small body size in the western USA had limited upstream dispersal ability in headwater streams with steep slopes. Thus, the dispersal limitation of important vectors like macroinvertebrates, aquatic mammals, and fish could affect the dispersal of diatoms, in turn, posing impact on metacommunity structuring of diatoms.

Our results showing significant associations between macroinvertebrate and diatoms community dissimilarity when adjusted for all other distances support our hypothesis that biotic interactions significantly affect the community structure of aquatic organisms in the Cangshan Mountain (H4). Macroinvertebrate and diatom communities can interact with one another through producer-consumer relationships, as grazer macroinvertebrates consume diatoms in the periphyton, which could lead to the significant association between macroinvertebrate and diatom dissimilarity (Thompson et al., 2020). Additionally, as mentioned above, macroinvertebrates are a dispersal vector for diatoms, which could lead to co-occurrence. However, co-variation between two groups of taxa, as in our results, could also be caused by responses to abiotic filtering (Zhao et al., 2019; García-Girón et al., 2020) not examined in this study. Previous studies have found that in addition to abiotic factors, like landscape structure and local environmental conditions, biotic interactions can significantly shape metacommunities. For example, macrophyte communities were found to structure filter-feeding zooplankton and predacious macroinvertebrate communities in pond ecosystems (García-Girón et al., 2020). However, we found that when comparing the whole range to the common zone, the association between macroinvertebrate and diatom community dissimilarity is no longer significant. There could be an underlying environmental gradient to which diatoms and macroinvertebrates respond, for example, a shortened gradient of water temperature or DO gradient (Jacobsen, 2008; Kim and Lee, 2017). If part of the underlying gradient is not included, it is possible that community structure responses or biotic interactions will no longer be significant. In addition to underlying abiotic and biotic gradients, the potential spatial autocorrelation between distance matrices could also have impacts on our results. For example, the presence of spatial autocorrelation between distance matrices may cause Mantel test results to have an inflated Type I error, that is, rejecting the null hypothesis even though it is true (Guillot and Rousset, 2013). Partial Mantel tests are often used to control for an underlying spatial matrix, but research has suggested that partial Mantel tests may not be adequate for controlling for spatial autocorrelation (Guillot and Rousset, 2013; Crabot et al., 2019). Future research focused on how abiotic (physical distance, local environment) and biotic (competition, predation, symbiosis) factors interact will provide more insight to the different roles that each factor plays in shaping metacommunities (Chiu et al., 2020).

Summary and Outlook

We explored metacommunity structures of macroinvertebrate and diatom communities in the Cangshan Mountain and found that like many other high mountain stream communities, both macroinvertebrate and diatom communities exhibit a clear turnover. Furthermore, we found that weakened network connectivity resulted in environmental variables being stronger structuring forces than spatial factors. Macroinvertebrate metacommunities were jointly shaped by dispersal limitation and environmental filtering in networks with weakened connectivity while environmental filtering showed a stronger influence on diatom metacommunities than dispersal limitation. We found significant associations between diatom and macroinvertebrate community dissimilarity, however, the concrete cause of this association is speculative. Disentangling the local metacommunity structure and the influence of spatial and environmental factors on local areas provides valuable insight into the structuring forces of this high biodiversity region and its vulnerability to human impacts (Chase et al., 2020) and can help improve biological assessments and conservation in these dynamic ecosystems (Cid et al., 2020). Future research should expand metacommunity analysis to include other high mountain areas and use replicated metacommunities at multiple spatial scales to disentangle drivers of this variability for different organismal groups.

DATA AVAILABILITY STATEMENT

Publicly available datasets were analyzed in this study. This data can be found at: https://doi.org/10.1016/j.scitotenv.2020.140548; https://doi.org/10.1038/srep24711.

AUTHOR CONTRIBUTIONS

FH, AM, QC, and SJ conceived the research idea. FH and XD collected the data. AK conducted the data analysis, with assistance from FH and AM. AK, FH, and AM drafted the manuscript. All authors contributed to the manuscript revision.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.571887/full#supplementary-material

REFERENCES

Adams, S. B., Frissell, C. A., and Rieman, B. E. (2000). Movements of nonnative brook trout in relation to stream channel slope. *Trans. Am. Fish. Soc.* 129, 623–638. doi: 10.1577/1548-8659(2000)129<0623:monbti>2.3.co;2

Altermatt, F. (2013). Diversity in riverine metacommunities: a network perspective. *Aquat. Ecol.* 47, 365–377. doi: 10.1007/s10452-013-9450-3

Altermatt, F., and Fronhofer, E. (2017). Dispersal in dendritic networks: ecological consequences on the spatial distribution of population densities. *Freshw. Biol.* 63, 22–32. doi: 10.1111/fwb.12951

Altermatt, F., Seymour, M., and Martinez, N. (2013). River network properties shape α-diversity and community similarity patterns of aquatic insect communities across major drainage Basins. *J. Biogeogr.* 40, 2249–2260. doi: 10.1111/jbi.12178

Baas Becking, L. G. M. (1934). *Geobiologie of Inleiding Tot De Milieukunde (in Dutch)*. The Hague: Van Stockum and Zoon.

Bagge, P. (1995). Emergence and upstream flight of lotic mayflies and caddisflies. *Entomol. Fenn.* 6, 91–97. doi: 10.33338/ef.83844

Benito, X., Fritz, S. C., Steinitz-Kannan, M., Vélez, M. I., and McGlue, M. M. (2018). Lake regionalization and diatom metacommunity structuring in tropical South America. *Ecol. Evol.* 8, 7865–7878. doi: 10.1002/ece3.4305

Bottin, M., Soininen, J., Ferrol, M., and Tison-Rosebery, J. (2014). Do spatial patterns of benthic diatom assemblages vary across regions and years?. *Freshw. Sci.* 33, 402–416. doi: 10.1086/675726

Brittain, J. E., and Eikeland, T. J. (1988). Invertebrate drift - a review. *Hydrobiologia* 166, 77–93. doi: 10.1007/BF00017485

Brown, B. L., Sokol, E. R., Skelton, J., and Tornwall, B. (2017). Making sense of metacommunities: dispelling the mythology of a metacommunity typology. *Oecologia* 183, 643–652. doi: 10.1007/s00442-016-3792-1

Brown, B. L., and Swan, C. M. (2010). Dendritic network structure constrains metacommunity properties in riverine ecosystems. *J. Anim. Ecol.* 79, 571–580. doi: 10.1111/j.1365-2656.2010.01668.x

Cañedo-Argüelles, M., Boersma, K. S., Bogan, M. T., Olden, J. D., Phillipsen, I., Schriever, T. A., et al. (2015). Dispersal strength determines meta-community structure in a dendritic riverine network. *J. Biogeogr.* 42, 778–790. doi: 10.1111/jbi.12457

Chase, J. M., Jeliazkov, A., Ladouceur, E., and Duarte, V. S. (2020). Biodiversity conservation through the lens of metacommunity ecology. *Ann. N. Y. Acad. Sci.* 1469, 86–104. doi: 10.1111/nyas.14378

Chiu, M. C., Ao, S., He, F., Resh, V. H., and Cai, Q. (2020). Elevation shapes biodiversity patterns through metacommunity-structuring processes. *Sci. Total. Environ.* 743:140548. doi: 10.1016/j.scitotenv.2020.140548

Cid, N., Bonada, N., Heino, J., Cañedo-Argüelles, M., Crabot, J., Sarremejane, R., et al. (2020). A metacommunity approach to improve biological assessments in highly dynamic freshwater ecosystems. *Bioscience* 70, 427–438. doi: 10.1093/biosci/biaa033

Crabot, J., Clappe, S., Dray, S., and Datry, T. (2019). Testing the mantel statistic with a spatially-constrained permutation procedure. *Methods Ecol. Evol.* 10, 532–540. doi: 10.1111/2041-210X.13141

Dallas, T. (2018). *Metacom: Analysis of the 'Elements of Metacommunity Structure*. Available online at: https://CRAN.R-project.org/package=metacom (accessed November 1, 2018).

de Mendoza, G., and Catalan, J. (2010). Lake macroinvertebrates and the altitudinal environmental gradient in the pyrenees. *Hydrobiologia* 648, 51–72. doi: 10.1007/s10750-010-0261-264

de Mendoza, G., Ventura, M., and Catalan, J. (2015). Environmental factors prevail over dispersal constraints in determining the distribution and assembly of *Trichoptera* Species in Mountain Lakes. *Ecol. Evol.* 5, 2518–2532. doi: 10.1002/ece3.1522

Dong, X., Li, B., He, F., Gu, Y., Sun, M., Zhang, H., et al. (2016). Flow directionality, mountain barriers and functional traits determine diatom metacommunity structuring of high mountain streams. *Sci. Rep.* 6:24711. doi: 10.1038/srep24711

Dormann, C., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., et al. (2012). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36, 27–46. doi: 10.1111/j.1600-0587.2012.07348.x

Finlay, B. (2002). Hypothesis: the rate and scale of dispersal of freshwater diatom species is a function of their global abundance. *Protist* 153, 261–273. doi: 10.1078/1434-4610-4103

Finn, D. S., and Adler, P. H. (2006). Population genetic structure of a rare high-elevation black fly, Metacnephia Coloradensis, occupying Colorado lake outlet streams. *Freshw. Biol.* 51, 2240–2251. doi: 10.1111/j.1365-2427.2006.01647.x

García-Girón, J., Heino, J., García-Criado, F., Fernández-Aláez, C., and Alahuhta, J. (2020). Biotic interactions hold the key to understanding metacommunity organisation. *Ecography* 43, 1–11. doi: 10.1111/ecog.05032

Gaston, K. (2000). Global patterns in biodiversity. *Nature* 504, 220–227.

Goslee, S. C., and Urban, D. L. (2007). The ecodist package for dissimilarity-based analysis of ecological data. *J. Statis. Softw.* 22, 1–19.

Göthe, E., Angeler, D. G., and Sandin, L. (2013). Metacommunity structure in a small boreal stream network. *J. Anim. Ecol.* 82, 449–458. doi: 10.1111/1365-2656.12004

Grönroos, M., Heino, J., Siqueira, T., Landeiro, V. L., Kotanen, J., and Bini, L. M. (2013). Metacommunity structuring in stream networks: roles of dispersal mode, distance type, and regional environmental context. *Ecol. Evol.* 3, 4473–4487. doi: 10.1002/ece3.834

Guillot, G., and Rousset, F. (2013). Dismanteling the mantel tests. *Methods Ecol. Evol.* 4, 336–344. doi: 10.1111/2041-210x.12018

Gundersen, G., Johannensen, E., Andreassen, H. P., and Ims, R. A. (2001). Source–sink dynamics: how sinks affect demography of sources. *Ecol. Lett.* 4, 14–21. doi: 10.1046/j.1461-0248.2001.00182.x

Hayes, S. M., and Anderson, K. E. (2017). Beyond connectivity: how the structure of dispersal influences metacommunity dynamics. *Theor. Ecol.* 11, 151–159. doi: 10.1007/s12080-017-0355-y

He, S., Chen, K., Soininen, J., Heino, J., Ding, N., and Wang, B. (2020). Elements of metacommunity structure of diatoms and Macroinvertebrates within stream networks differing in environmental heterogeneity. *J. Biogeogr.* 47, 1–10. doi: 10.1111/jbi.13859

He, F., Wu, N., Dong, X., Tang, T., Domisch, S., Cai, Q., et al. (2020). Elevation, aspect, and local environment jointly determine diatom and Macroinvertebrate diversity in the Cangshan Mountain, Southwest China. *Ecol. Indic.* 108:105618. doi: 10.1016/j.ecolind.2019.105618

Heino, J. (2013). The importance of metacommunity ecology for environmental assessment research in the freshwater realm. *Biol. Rev.* 88, 166–178. doi: 10.1111/j.1469-185X.2012.00244.x

Heino, J., Nokela, T., Soininen, J., Tolkkinen, M., Virtanen, L., and Virtanen, R. (2015). Elements of metacommunity structure and community-environment relationships in stream organisms. *Freshw. Biol.* 60, 973–988. doi: 10.1111/fwb.12556

Heino, J., Soininen, J., Alahuhta, J., Lappalainen, J., and Virtanan, R. (2017). Metacommunity ecology meets biogeography: effects of geographical region, spatial dynamics and environmental filtering on community structure in aquatic organisms. *Oecologica* 183, 121–137. doi: 10.1007/s00442-016-3750-y

Jacobsen, D. (2008). Low oxygen pressure as a driving factor for the altitudinal decline in taxon richness of stream macroinvertebrates. *Oecologia* 154, 795–807. doi: 10.1007/s00442-007-0877-x

Kernan, M., Ventura, M., Bitušík, P., Brancelj, A., Clarke, G., Velle, G., et al. (2009). Regionalisation of remote european mountain lake ecosystems according to their biotia: environmental versus geographical patterns. *Freshw. Biol.* 54, 2470–2493. doi: 10.1111/j.1365-2427.2009.02284.x

Kim, Y. J., and Lee, O. M. (2017). A study of low-temperature and mountain epilithic diatom community in mountain stream at the Han River System, Korea. *J. Ecol. Environ.* 41, 1–10. doi: 10.1186/s41610-017-0048-x

Körner, C. (2007). The use of 'altitude' in ecological research. *Trends Ecol. Evol.* 22, 569–574. doi: 10.1016/j.tree.2007.09.006

Krammer, K., and Lange-Bertalot, H. (1986). "Bacillariophyceae 1. Teil: naviculaceae," in *Süsswasser Von Mitteleuropa. Bacillariophyceae*, eds G. Gärtner, H. Ettl, J. Gerloff, H. Heynig, and D. Mollenhauser (Stuttgart: Gustav Fischer Verlag).

Krammer, K., and Lange-Bertalot, H. (1988). "Bacillariophyceae 2. Teil: bacillariaceae, Epithemiaceae, Surirellaceae," in *Süsswasserflore Von Mitteleuropa. Bacillariophyceae*, eds G. Gärtner, H. Ettl, J. Gerloff, H. Heynig, and D. Mollenhauser (Stuttgart: Gustav Fischer Verlag).

Krammer, K., and Lange-Bertalot, H. (1991a). "Bacillariophyceae 3. Teil: centrales, fragilariaceae, eunotiaceae," in *Süsswasserflora Von Mitteleuropa. Bacillariophyceae*, eds G. Gärtner, H. Ettl, J. Gerloff, H. Heynig, and D. Mollenhauser (Stuttgart: Gustav Fischer Verlag).

Krammer, K., and Lange-Bertalot, H. (1991b). "Bacillariophyceae 4. Teil: achnanthaceae," in *Süsswasserflora Von Mitteleuropa. Bacillariophyceae*, eds G. Gärtner, H. Ettl, J. Gerloff, H. Heynig, and D. Mollenhauser (Stuttgart: Gustav Fischer Verlag).

Kristiansen, J. (1996). 16. Dispersal of freshwater algae - a review. *Hydrobiologia* 336, 151–157. doi: 10.1007/BF00010829

Leibold, M., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J., Hoopes, M., et al. (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.* 7, 601–613. doi: 10.1111/j.1461-0248.2004.00608.x

Leibold, M. A., and Mikkelson, G. M. (2002). Coherence, species turnover, and boundary clumping: elements of meta-community structure. *Oikos* 97, 237–250. doi: 10.1034/j.1600-0706.2002.970210.x

Logue, J. B., Mouquet, N., Peter, H., and Hillebrand, H. (2011). Empirical approaches to metacommunities: a review and comparison with theory. *Trends Ecol. Evol.* 26, 482–491. doi: 10.1016/j.tree.2011.04.009

Maasri, A., Hayford, B., Erdenee, B., and Gelhaus, J. (2018). Macroscale drivers influencing the structural and functional organization of stream macroinvertebrate metacommunities: potential role of hydrological connectivity. *Freshw. Sci.* 37, 159–168. doi: 10.1086/695945

Martiny, J. B. H., Bohannan, B. J. M., Brown, J. H., Colwell, R. K., Fuhrman, J. A., Green, J. L., et al. (2006). Microbial biogeography: putting microorganisms on the map. *Nat. Rev. Microbiol.* 4, 101–112. doi: 10.1038/nrmicro1341

Moritz, C., Meynard, C., Devictor, V., Guizien, K., Labrune, C., Guarini, J., et al. (2013). Disentangling the role of connectivity, environmental filtering, and spatial structure on metacommunity dynamics. *Oikos* 122, 1401–1410. doi: 10.1111/j.1600-0706.2013.00377.x

Morse, J. C., Yang, L., and Tian, L. (1994). *Aquatic Insects of China Useful for Monitoring Water Quality*. Nanjing: Hohai University Press.

Nekola, J. C., and White, P. S. (1999). The distance decay of similarity in biogeography and ecology. *J. Biogeogr.* 26, 867–878. doi: 10.1046/j.1365-2699.1999.00305.x

Ohlmann, M., Maxel, F., Chalmandrier, L., Bec, S., Coissac, E., Gielly, L., et al. (2018). Mapping the imprint of biotic interactions on B-diversity. *Ecol. Lett.* 21, 1660–1669. doi: 10.1111/ele.13143

Oksanen, J., Guillaume Blanchet, F., Friendly, M., Kindt, R., Legendre, P., and McGlinn, D. (2019). *Vegan: Community Ecology Package. : R Package Version 2.5.4.* Available online at: https://CRAN.R-project.org/package=vegan (accessed May 15, 2019).

Potapova, M., and Charles, D. (2002). Benthic diatoms in USA rivers: distributions along spatial and environmental gradients. *J. Biogeogr.* 29, 167–187. doi: 10.1046/j.1365-2699.2002.00668.x

Presley, S., and Willig, M. (2010). Bat metacommunity structure on caribbean islands and the role of endemics. *Glob. Ecol. Biogeogr.* 19, 185–199. doi: 10.1111/j.1466-8238.2009.00505.x

Presley, S. J., Higgins, C. L., and Willig, M. R. (2010). A comprehensive framework for the evaluation of metacommunity structure. *Oikos* 199, 908–917. doi: 10.1111/j.1600-0706.2010.18544.x

QGIS Development Team (2015). *QGIS Geographic Information System*. Available online at: http://qgis.org (accessed November 1, 2018).

Qi, Y., Li, J., and Shi, Z. (1995). *Flora Algarum Sinicarum Aquae Dulcis*, Vol. Tomus IV, X, XII, XIV, XVI. Beijing: Science Press.

Qi, Y., Li, J., and Shi, Z. (2004a). *Flora Algarum Sinicarum Aquae Dulcis*, Vol. Tomus X. Beijing: Science Press.

Qi, Y., Li, J. and Shi, Z. (2004b). *Flora Algarum Sinicarum Aquae Dulcis*, Vol. Tomus XII. Beijing: Science Press.

Qi, Y., Li, J. and Shi, Z. (2009). *Flora Algarum Sinicarum Aquae Dulcis*, Vol. Tomus XIV. Beijing: Science Press.

Qi, Y., Li, J., and Shi, Z. (2013). *Flora Algarum Sinicarum Aquae Dulcis*, Vol. Tomus XVI. Beijing: Science Press.

R Core Team (2017). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Sanders, N., and Rahbek, C. (2012). The patterns and causes of elevational diversity gradients. *Ecography* 35, 1–3. doi: 10.1111/j.1600-0587.2011.07338.x

Schmera, D., Árva, D., Boda, P., Bódis, E., Bolgovics, Á, Borics, G., et al. (2017). Does isolation influence the relative role of environmental and dispersal-related processes in stream networks? an empirical test of the network position hypothesis using Multiple Taxa. *Freshw. Biol.* 63, 74–85. doi: 10.1111/fwb.12973

Shah, R. D. T., Sharma, S., Haase, P., Jähnig, S. C., and Pauls, S. U. (2015). The climate sensitive zone along an altitudinal gradient in central himalayan rivers: a useful concept to monitor climate change impacts in mountain regions. *Clim. Chang.* 132, 265–278. doi: 10.1007/s10584-015-1417-z

Soininen, J. (2004). Determinants of benthic diatom community structurein boreal streams: the role of environmental and spatial factors at different scales. *Intern. Rev. Hydrobiol.* 89, 139–150. doi: 10.1002/iroh.200310714

Soininen, J., and Weckström, J. (2009). Diatom community structure along environmental and spatial gradients in lakes and streams. *Fundament. Appl. Limnol.* 174, 205–213. doi: 10.1127/1863-9135/2009/0174-0205

Sun, M. (2008). *Monograph of Cangshan Mountains*. Kunming: Yunnan Ethnic Press.

Sundqvist, M. K., Sanders, N. J., and Wardle, D. A. (2013). Community and ecosystem responses to elevational gradients: processes, mechanisms and insights for global change. *Annu. Rev. Ecol. Evol. Syst.* 44, 261–280. doi: 10.1146/annurev-ecolsys-110512-135750

Thompson, P. L., Guzman, L. M., de Meester, L., Horvath, Z., Ptacnik, R., Vanschoenwinkel, B., et al. (2020). A process-based metacommunity framework linking local and regional scale community ecology. *Ecol. Lett.* 23, 1314–1329. doi: 10.1111/ele.13568

Thompson, R., and Townsend, C. (2006). A truce with neutral theory: local deterministic factors, species traits and dispersal limitation together determine patterns of diversity in stream invertebrates. *J. Anim. Ecol.* 75, 476–484. doi: 10.1111/j.1365-2656.2006.01068.x

Tonkin, J. D., Heino, J., and Altermatt, F. (2018). Metacommunities in river networks: the importance of network structure and connectivity on patterns and processes. *Freshw. Biol.* 63, 1–5. doi: 10.1111/fwb.13045

Tonkin, J. D., Sundermann, A., Jähnig, S. C., and Haase, P. (2015). Environmental controls on river assemblages at the regional scale: an application of the elements of Metacommunity structure framework. *PLoS One* 10:e0135450. doi: 10.1371/journal.pone.0135450

Tonkin, J. D., Tachamo Shah, R. D., Shah, D. N., Hoppeler, F., Jähnig, S. C., and Pauls, S. U. (2016). Metacommunity structuring in himalayan streams over large elevational gradients: the role of dispersal routes and niche characteristics. *J. Biogeogr.* 44, 62–74. doi: 10.1111/jbi.12895

Townsend, C. R., Dolédec, S., Norris, R., Peacock, K., and Arbuckle, C. (2003). The influence of scale and geography on relationships between stream community composition and landscape variables: description and prediction. *Freshw. Biol.* 48, 768–785. doi: 10.1046/j.1365-2427.2003.01043.x

Vavrek, M. J. (2011). Fossil: palaeoecological and palaeogeographical analysis tools. *Palaeontol. Electron.* 14:16.

Vilmi, A., Zhao, W., Picazo, F., Li, M., Heino, J., Soininen, J., et al. (2020). Ecological processes underlyfing community assembly of aquatic bacteria and Macroinvertebrates under contrasting climates on the Tibetan Plateau. *Sci. Total Environ.* 702:134974. doi: 10.1016/j.scitotenv.2019.134974

Wang, J., Soininen, J., Zhang, Y., Wang, B., Yang, X., and Shen, J. (2012). Patterns of elevational beta diversity in micro- and macroorganisms. *Glob. Ecol. Biogeogr.* 21, 743–750. doi: 10.1111/j.1466-8238.2011.00718.x

Wen, Z., Quan, Q., Du, Y., Xia, L., Ge, D., and Yang, Q. (2016). Dispersal, niche, and isolation processes jointly explain species turnover patterns of Nonvolant small mammals in a large mountainous region of China. *Ecol. Evol.* 6, 946–960. doi: 10.1002/ece3.1962

Willig, M., Kaufman, D., and Stevens, R. (2003). Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annu. Rev. Ecol. Evol. Syst.* 34, 273–309. doi: 10.1146/annurev.ecolsys.34.012103.144032

Willig, M., and Presley, S. (2015). Biodiversity and metacommunity structure of animals along altitudinal gradients in tropical Montane forests. *J. Trop. Ecol.* 32, 421–436. doi: 10.1017/S0266467415000589

Zhao, W., Hu, A., Ni, Z., Wang, Q., Zhang, E., Yang, X., et al. (2019). Biodiversity patterns across taxonomic groups along a lake water-depth gradient: effects of abiotic and biotic drivers. *Sci. Total Environ.* 686, 1261–1271. doi: 10.1016/j.scitotenv.2019.05.381

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Environment and Space Rule, but Time Also Matters for the Organization of Tropical Pond Metacommunities

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Metacommunities are dynamic systems, but the influence of time independently of environmental change in their configuration has been rarely considered. In temporary ponds, strong temporal effects are expected to influence their metacommunity structure, even in relatively constant environments such as tropical habitats. We therefore expect that time as an independent factor could modulate tropical pond metacommunities, which would be also less affected by niche-related processes than by dispersal-related processes. In addition, good dispersers should be more environmentally structured than bad dispersers, which should be more spatially structured. Finally, the relevance of temporal effects should vary among organisms with different generation times. To test these hypotheses, we surveyed 30 temporary ponds along the dry tropical region of western Costa Rica and Nicaragua at three different moments of their hydroperiod: shortly after the infilling of the water bodies, at the middle of the hydroperiod and just before desiccation. We obtained data on 56 environmental variables and used geographic coordinates to build spatial variables (Moran Eigenvector Maps). We collected biological samples and estimated the specific abundance of phytoplankton, zooplankton and benthic invertebrates. To evaluate the relative role of environmental, spatial and temporal (sequential sampling season) effects for metacommunity organization, we used variation partitioning with distance-based redundancy analyses for each group of organisms. The inclusion of time in the analysis highlighted that pure temporal effects explained part of metacommunity variance in almost every group, being as important as spatial or even environmental effects for some groups of organisms. In contrast to the assumed low environmental constraints in tropical areas (i.e., high and stable temperatures), we found strong environmental effects. Passive dispersers were more influenced by environmental factors than active ones. We also found a positive relationship between the body size of the different groups of organisms and the magnitude of the temporal effects, interpreted as related to generation time. Finally, when analyzing each sampling period separately, we found differences in the relative role of environment and space at different sampling periods, showing that snapshot surveys may not be representative of highly dynamic metacommunities.

Keywords: multi-taxon study, dbRDA, MEM analysis, dispersal limitation, species sorting, temporal effects, tropical limnology

INTRODUCTION

The establishment of the metacommunity concept as referring to a group of communities linked by dispersal of their interacting species (Hanski and Gilpin, 1991; Wilson, 1992) prompted a turning point in understanding species distributions and abundances. Not only environmental filtering (the species sorting paradigm; Leibold et al., 2004), but other mechanisms related to spatial effects and dispersal rates, play a key role structuring metacommunities. Patch-dynamics (Levins and Culver, 1971), sink-source dynamics (or mass-effects; Holt, 1993) and neutral (Hubbell, 2001) paradigms are complementary to the species sorting approach when studying metacommunity assembly. In this framework, there is however a temporal component that has seldom been considered when testing theoretical expectations with empirical data. The common snapshot-survey studies neglect not only temporal changes in environmental conditions and in the influence of the spatial context, but also direct temporal effects on metacommunity structure due to processes such as life cycles, population growth or priority effects (Brendonck and De Meester, 2003; Fukami, 2015; Leibold and Chase, 2018).

Under the metacommunity framework, freshwater ecosystems are particularly interesting due to their isolation in relation to the terrestrial landscape. Rivers, lakes and ponds have largely been studied in order to understand the role of dispersal limitation and species sorting in such isolated communities (e.g., Soininen et al., 2007; Escrivà et al., 2015; López-Delgado et al., 2019). Pond metacommunities show a high degree of randomness (Chase, 2007), although strong environmental effects are also frequently observed (Leibold and Chase, 2018). Mass and priority effects at small scales (Heino et al., 2015; Castillo-Escrivà et al., 2017b) and dispersal limitation at large (Soininen et al., 2011; Heino et al., 2015) or even small spatial scales (Castillo-Escrivà et al., 2017a) seem also to be important processes affecting pond metacommunity structure. Temporary ponds, as intermittent ecosystems, strongly depend on seasonal dynamics related to their hydroperiod, egg-bank hatching and colonization processes (Williams, 2005; Chase, 2007; Castillo-Escrivà et al., 2017c). Desiccation is a major evolutionary pressure in temporary water bodies, where habitat availability changes cyclically, sometimes unpredictably, and organisms are adapted to this desiccation by means of different life-cycle strategies: while some organisms resist drought in the sediment (resting eggs, anhydrobiosis, seeds, etc.), some others need to abandon the habitat and recolonize from neighboring waterbodies (Brendonck and De Meester, 2003; Richter-Boix et al., 2011; Olmo et al., 2012; Brendonck et al., 2017; Wisnoski et al., 2019). As a consequence, some traits such as generation time, type of dispersal or survival strategy toward desiccation may influence temporal dynamics, which in turn may strongly regulate metacommunity composition (Boix et al., 2004; Holt et al., 2005; Fernandes et al., 2014; Castillo-Escrivà et al., 2017c).

Freshwater metacommunity studies are biased toward temperate regions with strong temperature seasonality, this possibly driving major changes in metacommunity structure. In contrast, tropical regions show a reduced thermal variability, while precipitations, especially in areas with a dry tropical climate, have large annual fluctuations. These fluctuations, consequence of the alternation of rainy and dry seasons, may lead to a high connectivity between ponds through extensive floods, producing a regional environmental homogenization (Thomaz et al., 2007) that locally diverges when the waterbodies become isolated during the dry season (Rojo et al., 2016). Thus, results on spatial and environmental effects on pond metacommunities sampled in temperate regions are expected to notably differ from those of tropical areas, not only because of differences in temperature regimes but also because of heavy rain effects on connectivity.

Previous studies on freshwater metacommunities point toward dispersal mode as an important trait driving metacommunity structure. It is expected that better dispersers will show weaker spatial patterns than those with lower dispersal ability. As a consequence, flying active dispersers and small-size passive dispersers will be more affected by species sorting than non-flying active dispersers or large-bodied passive dispersers (De Bie et al., 2012; Padial et al., 2014). However, this pattern has not been supported by all metacommunity studies (Heino et al., 2012; Schulz et al., 2012; Grönroos et al., 2013; Leibold and Chase, 2018). Perhaps, differences among studies in spatial scales, connectivity or groups of organisms being analyzed may hinder the observation of consistent patterns or, alternatively, dispersal abilities might be more idiosyncratic that one may expect from body size and moving capabilities. For these reasons, a multi-taxon approach in metacommunity research, including groups of different body sizes and dispersal strategies could help to disentangle how metacommunities are actually structured.

In this study, we test the influence of environmental, spatial and temporal factors on metacommunity structure of a wide range of organisms inhabiting tropical temporary ponds, including algae, rotifers, microcrustaceans, and macroinvertebrates (mainly mollusks and insects). Thus, we encompass multiple life-cycle strategies against desiccation (including resting eggs or spores in algae, rotifers and crustaceans, anhydrobiosis in some rotifers and copepods, terrestrial adult stages in insects, etc.) and distinct reproductive strategies (binary fission in cyanobacteria, strict parthenogenesis in some rotifers, cyclic parthenogenesis in rotifers or cladocerans, sexual reproduction in insects, etc.) which are strongly related with dispersal ability (active and passive dispersal) and colonization. In addition, the wide variability of taxa also includes a wide variability in body size, from a few microns in cyanobacteria to several centimeters in adult insects, which is correlated with generation time (Sammarco and Strychar, 2009; Brown et al., 2018). Empirical metacommunity analyses have seldom been carried out surveying multiple taxonomic groups from the same waterbodies, on repeated occasions, and over a wide spatial extent (e.g., Beisner et al., 2006), and even fewer of these at low latitudes (Domis et al., 2013; Padial et al., 2014; Rojo et al., 2016). This work aims at filling these gaps. Considering the standing issues on temporary pond metacommunity dynamics and the differences between groups of organisms and climatic settings we hypothesize that (i) not only spatial and environmental components drive metacommunity structure but also independent temporal factors; (ii) niche-related processes should be relatively less important than dispersal-related processes in structuring tropical pond metacommunities, as compared to published data on more seasonally variable temperate pond metacommunities; (iii) metacommunities of small passive dispersers should be strongly environmentally structured thanks to a high connectivity in tropical ponds through flooding, while metacommunities of larger-bodied organisms with reduced dispersal abilities might still show strong patterns of spatial structure; (iv) the influence of the temporal component should vary between organisms with different generation times, showing a positive relationship between these two variables, and (v) metacommunity patterns observed in snapshot surveys may provide a biased view of the major ecological processes structuring metacommunities because of considerable variation through time.

MATERIALS AND METHODS

Study Area and Environmental Characterization

We surveyed 30 temporary stagnant freshwater bodies from a dry tropical region on the Pacific watersheds of Costa Rica and Nicaragua. These 30 ponds were selected in order to include a wide range of environmental conditions regarding salt content, nutrient concentration or land use, covering a large spatial extent. Selected waterbodies were grouped in four main clusters over a maximum distance among them of 370 km: Palo Verde National Park (Tempisque River lower basin) and the slopes of Miravalles and Tenorio volcanoes (Tempisque River middle basin), both in Costa Rica, and the delta of Estero Real and the Western region of Nicaragua, both in Nicaragua (**Figure 1**). Sasa et al. (2015) provide further details on the location, geographical setting and environmental characterization of sampling sites. Due to the temporality of these water bodies, we surveyed them thrice during their hydroperiod: 2 weeks after infilling (June 2010); once again in the middle of the hydroperiod, during the flooding peak (September 2010) and the last time immediately after the end of the rainy season, before the desiccation of the ponds (January 2011).

We assessed a set of 56 environmental variables for each pond, including limnological, hydrogeomorphological, biotic, climatic, landscape, and conservation status. In every survey, we measured *in situ* water temperature, total dissolved solids (TDS), electric conductivity (EC) and pH using a Hanna pH/EC meter HI 98130; oxygen concentration was measured with the Winkler method and transparency with a Snell tube. In addition, we took water samples in order to analyze nutrient and ion concentrations in the lab: 250 ml of unfiltered water for anion analyses (bicarbonate and carbonate alkalinity (Alk), chloride and sulfate), 100 ml of unfiltered water, fixed with nitric acid, for cation analysis (Na^{+}, K^{+}, Mg^{+2}, Ca^{+2}), and 100 ml of filtered water (through GF/F Whatman filters) for nutrient (PO_4^{3-}, NO_3^{-}, NO_2^{-}, NH_4^{+}) concentration analysis (Rice et al., 1992). The used GF/F filters were analyzed for chlorophyll-a concentration following Jeffrey and Humphrey (1975). Further details on sampling and analytical methods and limnological results are described in Sasa et al. (2015). We calculated some ratios between nutrient or ionic concentrations to be used as possible explanatory variables (Alk/Ca^{+2}, $Alk/(Cl^{-} + SO_4^{2-})$, $(Ca^{+2} + Mg^{+2})/(Na^{-} + K^{-})$, Ca^{+2}/Mg^{+2}, NO_3^{-}/NO_2^{-}, NO_3^{-}/NH_4^{+}). As for hydrogeomorphological variables, we measured the maximum and average depth of each water body, using a graduated stick, and gathered information from field data on the origin of the water (rain, streams, phreatic) and hydroperiod length (seasonal or semipermanent). Furthermore, we measured the area, perimeter, morphology {shoreline development: $DL = L/[2\sqrt{(\pi A)}]$; Aronow, 1982} and altitude. Regarding biotic variables (besides chlorophyll-a concentration), we visually estimated the percentage of water surface and shoreline covered by macrophytes and helophytes, respectively, and recorded the presence of livestock. We downloaded climatic variables, including maximum annual temperature, minimum annual temperature, average annual temperature, temperature range, annual average precipitation, and precipitation seasonality from the online server worldclim.org (using historical climate data from 1970 to 2000; Fick and Hijmans, 2017) and extracted these data by means of ArcGis 10.0 (ESRI, 2006). As for the landscape and land use of the watershed surrounding each pond, we estimated the percentage of land surface occupied by agriculture, buildings, forest, scrub, low grass and high grass, and landscape heterogeneity. For this purpose, we manually measured the percentage cover of these categories in a buffer area of 100 m of diameter around the sampling point using Google Earth (Google Inc.) satellite images. The landscape heterogeneity was calculated with a Shannon index of the proportions of the above-mentioned landscape categories. Finally, we determined the conservation status of each wetland through the ECELS (ECELS1-5 and total ECELS) index (Boix et al., 2010; Sasa et al., 2015). Instead of using latitude and longitude as spatial variables, we calculated Moran's Eigenvector Maps (MEMs) (Dray et al., 2006), consisting of a matrix of positively autocorrelated orthogonal variables of different spatial

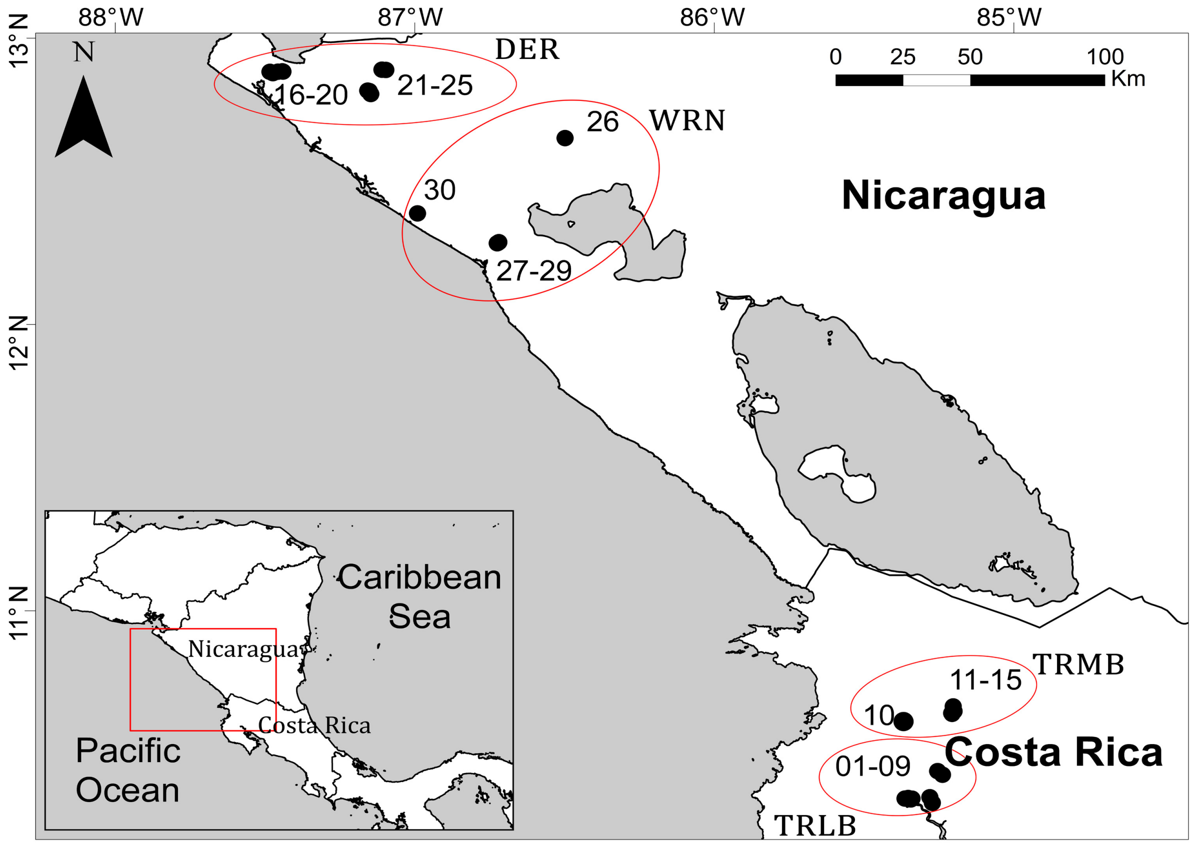

FIGURE 1 | Map of the study area with the location of the studied ponds, grouped in four main clusters: DER (Delta of Estero Real), WRN (Western Region of Nicaragua), TRMB (Tempisque River Medium Basin), and TRLB (Tempisque River Low Basin). Based on Figure 1 in Sasa et al. (2015).

scales. The environmental characterization is summarized in **Supplementary Table S1**.

We built three different matrices with the data gathered: (i) a spatial matrix, including MEMs, presence or absence of connectivity with other neighboring waterbodies and a categorical factor corresponding to the region (Costa Rica or Nicaragua), (ii) a temporal matrix, with the sampling period, as a dummy variable, and (iii) an environmental matrix, with all the variables explained above. These matrices were further used in statistical analyses together with the biological communities data (see below).

Biological Communities

We collected biological samples of phytoplankton, zooplankton, and benthic invertebrates at each site and sampling period. Phytoplankton samples were collected in 100-ml amber-colored glass bottles, directly from the water column, and fixed with Lugol's iodine solution. Zooplankton quantitative samples were taken by filtering a volume of water (2–20 L measured with a graded jar, until filter got plugged) through a 35-μm mesh filter in order to ensure the capture of the smallest rotifers and microcrustaceans, and fixed with 4% formaldehyde. These samples were collected from the different microhabitats observed, including different depths, substrate or vegetation types and coverages. Benthic invertebrates were collected using a 250 μm pore-size hand net, taking samples from every distinct microhabitat. These samples where fixed with ethanol 96%. In the lab, all the collected groups of organisms were identified and counted using a Leica Leitz Biomed microscope, a Leica DMIL Led inverted microscope and a Leica M205C stereomicroscope, up to the maximum taxonomic resolution possible using a variety of taxonomic works, mostly the following: Huber-Pestalozzi (1976–1982) and Wołowski and Hindák (2005) for phytoplankton; Koste (1978) and Segers (1995) for rotifers in the zooplankton samples; Elías-Gutiérrez et al. (2008) and references therein for cladocerans and copepods (Cyclopoida and Calanoida); Meisch (2000) and Karanovic (2012) and references therein for ostracods; and Domínguez and Fernández (2009), Springer et al. (2010), and Thorp and Covich (2010), and references therein, for benthic invertebrates other than ostracods.

With these data, we built species abundance matrices of all three sampling periods for a series of (nested) groups of organisms: the whole phytoplankton dataset, and separately for Cyanobacteria, Chlorophyceae, mixotrophic phytoplankton (Chrysophyceae, Cryptophyceae, Euglenophyta, and Dinoflagellata) and Diatomea; Rotifera; non-Decapoda nor Isopoda crustaceans (from now on, Crustacea), and separately for Branchiopoda, Copepoda, and Ostracoda; all benthic macroinvertebrates (excluding Ostracoda) and separately for Mollusca, Insecta, Paleoptera (Ephemeroptera and Odonata), Heteroptera, Coleoptera, and Diptera.

Statistical Analysis

In order to determine the role of environmental, temporal and spatial factors over the structure of the metacommunity, we carried out variation partitioning analyses (Peres-Neto et al., 2006). The relative abundance matrices were Hellinger-transformed in order to reduce the influence of rare and ubiquitous species (Legendre and Gallagher, 2001). Environmental variables were transformed depending on their initial frequency distribution, using either logarithms, the arcsine of the square root, or the square-root, in order to reduce the leverage effect of outliers and to approach them to a normal distribution.

We implemented 17 partial distance-based redundancy analyses (dbRDA) with the purpose of explaining the variation of each species matrix in relation to the environmental [E], spatial [S], and temporal [T] matrices. Variation partitioning allows quantifying the percentage of variation explained purely by the environmental component $[E| (S + T)]$, purely by the spatial component $[S| (E + T)]$ and purely by the temporal component $[T| (E + S)]$. Furthermore, part of the metacommunity variation can also be explained by an overlap between two or more components: environmental and spatial overlap $[(E \cap S)| T]$, environmental and temporal overlap $[(E \cap T)| S]$, spatial and temporal overlap $[(S \cap T)| E]$ and environmental, spatial and temporal overlap $[E \cap S \cap T]$. Variables from environmental, spatial and temporal data matrices went through a forward selection process prior to each variation partitioning analysis, with a double stopping criterion (Blanchet et al., 2008). To further study the relative effects of the temporal component on metacommunity organization across organisms, we compared three groups of taxa with varying generation times, which are highly correlated with body size (Sammarco and Strychar, 2009; Brown et al., 2018): phytoplankton, microinvertebrates (rotifers, branchiopods, copepods and ostracods) and macroinvertebrates (remaining groups of analyzed benthic invertebrates).

In order to check if snapshot survey results are representative of the whole metacommunity dynamics through time, we performed a variation partitioning analysis for selected groups, following the same method as explained above but now performing a test separately for each sampling period and group of organisms, and therefore excluding temporal variables from analyses.

To test for significant differences in the pure temporal component between groups with different generation times (phytoplankton, micro-, and macroinvertebrates), and in pure components between groups of organisms with different dispersal strategies (passive/active), we performed Kruskal-Wallis tests (Kruskal and Wallis, 1952). All analyses were performed with R (v3.6.0; R Core Team, 2019) and R packages vegan (Oksanen et al., 2019), ade4 (Bougeard and Dray, 2018) and adespatial (Dray et al., 2019).

RESULTS

Altogether, we found 295 phytoplankton taxa, most of them identified to species level (Cyanobacteria: 44 taxa; Chlorophyceae: 114 taxa; mixotrophic phytoplankton: 56 taxa; Diatomea: 77 taxa), 102 rotifer taxa, most of them identified to species level, so as the 80 crustacean taxa (Branchiopoda: 34 taxa, Copepoda: 15 taxa, including 13 Cyclopoida and 2 Calanoida, Ostracoda: 31 taxa) and 169 macroinvertebrate taxa, including 19 mollusks, 34 paleopterans, 19 heteropterans, 28 coleopterans, and 32 dipterans (121 insect taxa). The list of identified species can be found in **Supplementary Table S2**.

Selected variables in dbRDA are shown in the **Supplementary Table S3**. The proportion of metacommunity variation explained by the selected significant variables, considering all three components $(E + S + T)$ together, varied between 0.09 in Insecta and 0.33 in Ostracoda (average 0.20 ± 0.06). The results of the variance partitioning analyses show a significant effect of environmental, spatial and temporal components for most taxonomic groups (**Figure 2** and **Table 1**), with a predominance of pure environmental over pure spatial and temporal effects. Especially remarkable are the mixotrophic phytoplankton, with a stronger pure temporal component than any other phytoplankton group; Heteroptera, with a large pure spatial component; and Diptera, with the highest pure temporal component. We did not find significant pure environmental effects only in Heteroptera and Insecta (probably influenced by Heteroptera). Part of the variation of all phytoplankton groups was significantly explained by pure spatial factors, but none in the case of Rotifera, Branchiopoda and Paleoptera. Finally, we found non-significant pure temporal effects only in small body size taxa (Chlorophyceae, Diatomea, Branchiopoda and Ostracoda), but these effects were always significant in macroinvertebrates.

When comparing passive and active dispersers, the pure environmental component was significantly higher in the former group (**Figure 3**, Kruskal-Wallis: $P = 0.037$). On the other hand, there were no differences neither in pure spatial nor temporal effects between these groups. Therefore, although the spatial structure and temporal dynamics seem to have the same influence for both types of dispersal strategies, passive dispersers seem to be more environmentally structured than active dispersers.

In **Table 2**, we show the number and type of significant environmental variables explaining the variance of each group. In organisms with small body size and passive dispersal (from Phytoplankton to Crustacea), species sorting is dominated by limnological variables. In Mollusca and active dispersers, limnological, climatic, and landscape variables seem to play a similar role, but no hydrogeomorphological variables were selected for insects.

The influence of the temporal component seems to follow an increasing trend that might be related to increasing length of the life-cycle, from phytoplankton groups to microscopic metazoans to macroinvertebrate groups (**Figure 4**). However, we did not find significant differences among these three groups (K-W test, $P = 0.354$).

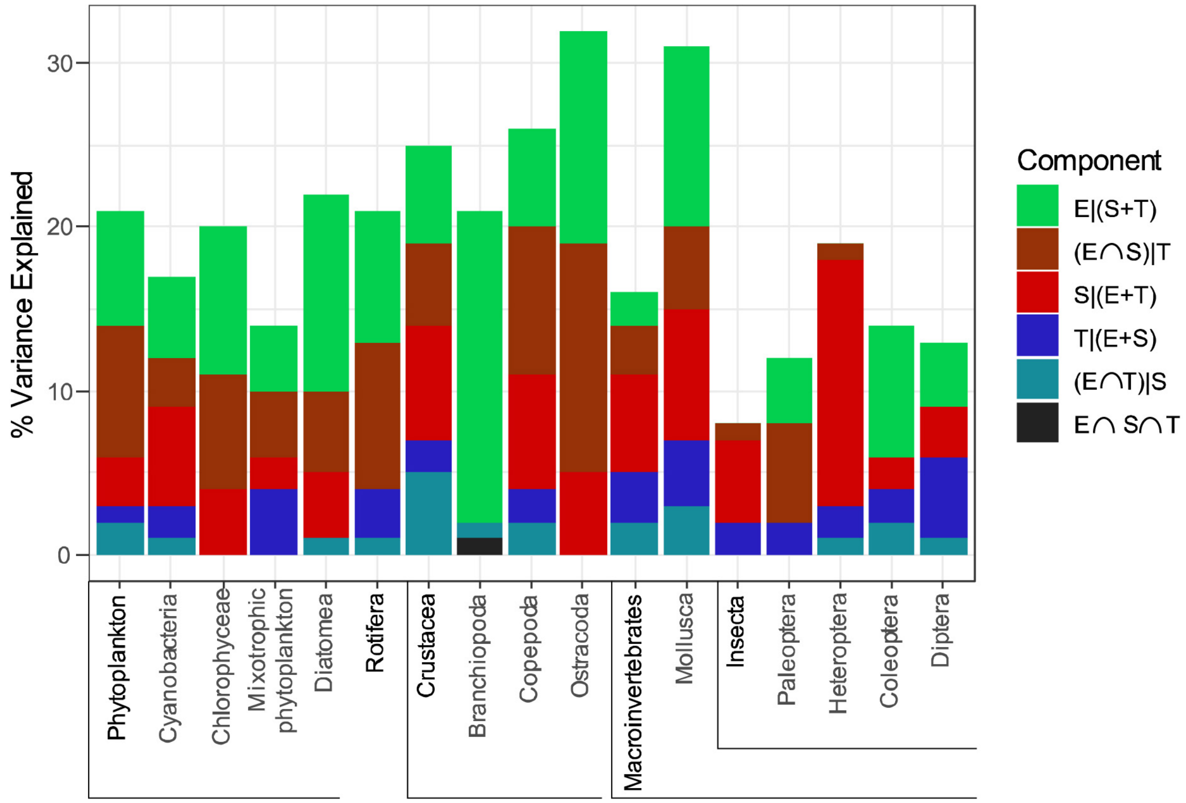

FIGURE 2 | Results of variation partitioning analysis for each group of organisms. The percentage of variation explained by each component is represented with a different color (green: pure environment; brown: environment-space overlap; red: pure space; dark blue: pure time; cyan: environment-time overlap; black: environment-space-time overlap). Only significant components ($P < 0.05$) are shown. Taxa in bold type include species from the following underlined groups.

TABLE 1 | Results of variation partitioning analysis for each group, where E, environmental component; S, spatial component; T, temporal component.

Taxonomic group	E| (S + T)	S| (E + T)	T| (E + S)	(E ∩ S)| T	(E ∩ T)| S	(S ∩ T)| E	E ∩ S ∩ T	E + S + T
Phytoplankton	0.07^{**}	0.03^{**}	0.01^{**}	0.08	0.02	0	0	0.21^{**}
Cyanobacteria	0.05^{**}	0.06^{**}	0.02^{**}	0.03	0.01	0	0	0.17^{**}
Chlorophyceae	0.09^{**}	0.04^{**}	$0^{n.s.}$	0.07	0	0	0	0.20^{**}
Mixotrophic phytoplankton	0.04^{**}	0.02^{*}	0.04^{**}	0.04	0	0	0	0.14^{**}
Diatomea	0.12^{**}	0.04^{**}	$0.01^{n.s.}$	0.05	0.01	0	0	0.23^{**}
Rotifera	0.08^{**}	$0.01^{n.s.}$	0.03^{**}	0.09	0.01	0	0	0.22^{**}
Crustacea	0.06^{**}	0.07^{**}	0.02^{**}	0.05	0.05	0	0	0.25^{**}
Branchiopoda	0.19^{**}	$0^{n.s.}$	$0.02^{n.s.}$	0	0.01	0	0.01	0.23^{**}
Copepoda	0.06^{**}	0.07^{**}	0.02^{*}	0.09	0.02	0	0	0.26^{**}
Ostracoda	0.13^{**}	0.05^{*}	$0.01^{n.s.}$	0.14	0	0	0	0.33^{**}
Macroinvertebrates	0.02^{*}	0.06^{**}	0.03^{**}	0.03	0.02	0	0	0.16^{**}
Mollusca	0.11^{**}	0.08^{**}	0.04^{**}	0.05	0.03	0	0	0.31^{**}
Insecta	$0.01^{n.s.}$	0.05^{**}	0.02^{**}	0.01	0	0	0	0.09^{**}
Paleoptera	0.04^{*}	$0.02^{n.s.}$	0.02^{*}	0.06	0	0	0	0.14^{**}
Heteroptera	$0.02^{n.s.}$	0.15^{**}	0.02^{*}	0.01	0.01	0	0	0.21^{**}
Coleoptera	0.08^{**}	0.02^{*}	0.02^{*}	0	0.02	0	0	0.14^{**}
Diptera	0.04^{**}	0.03^{**}	0.05^{**}	0	0.01	0	0	0.13^{**}

*The table shows the proportion of variation (R^2_{adj}) explained by each pure component and the overlaps between components. Significance codes: **($P < 0.001$), *($P < 0.05$), n.s. (non-significant).*

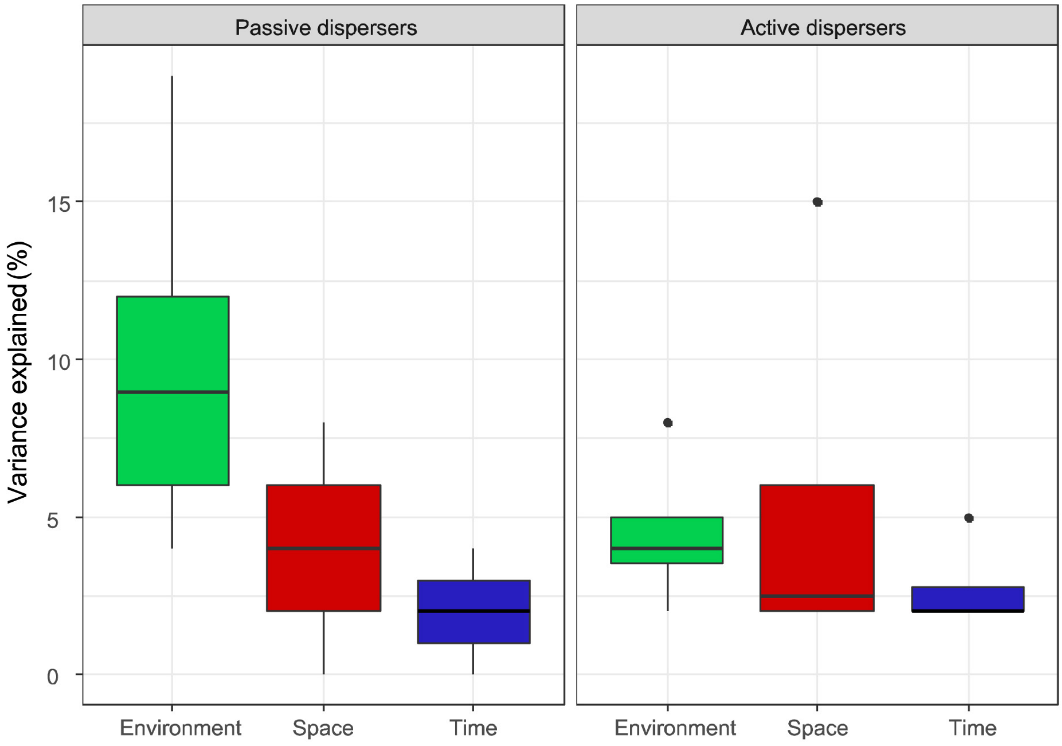

FIGURE 3 | Percentage of metacommunity variance explained by pure environmental, spatial and temporal components, according to the type of dispersal of the studied groups of organisms.

Finally, separated variation partitioning analyses for each of the three sampling seasons were carried out for five different groups of organisms (Phytoplankton, Rotifera, Crustacea, Mollusca, and Insecta) (**Figure 5** and **Table 3**) to check for variability of spatial and environmental effects through time. Selected variables are shown in the **Supplementary Table S4**. We observed a temporal variation in the percentage of variance explained by the pure environmental component,

TABLE 2 | Number and type of environmental variables selected in the variation partitioning analyses for each group of organisms.

Taxonomic group	Limnological variables	Climatic variables	Landscape variables	Hydrogeomorphological variables	Biotic variables	Conservation variables
Phytoplankton	7	2	1	2	2	0
Cyanobacteria	3	1	0	1	0	0
Chlorophyceae	5	1	0	3	0	2
Mixotrophic phytoplankton	2	1	1	1	0	2
Diatomea	4	1	1	3	1	1
Rotifera	5	2	1	1	1	2
Crustacea	6	1	2	2	2	1
Branchiopoda	7	0	0	2	0	0
Copepoda	2	1	1	1	1	0
Ostracoda	3	4	2	2	0	0
Macroinvertebrates	0	2	0	1	2	1
Mollusca	2	1	1	1	1	0
Insecta	0	1	1	0	0	1
Paleoptera	1	1	2	0	0	1
Heteroptera	1	1	0	0	0	0
Coleoptera	1	1	1	0	1	0
Diptera	1	0	1	0	1	0

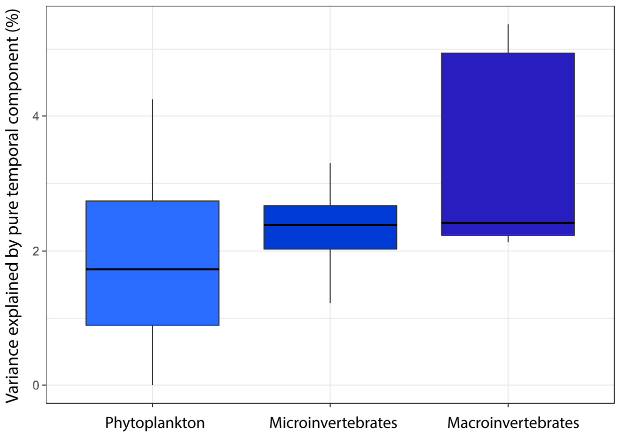

FIGURE 4 | Percentage of variance explained by pure temporal effects for three groups with different generation times: Phytoplankton (Cyanobacteria, Chlorophyceae, mixotrophic phytoplankton, and Diatomea), Microinvertebrates (Rotifera, Branchiopoda, Copepoda, and Ostracoda) and Macroinvertebrates (Mollusca, Paleoptera, Heteroptera, Coleoptera, and Diptera).

even though this component appears to be significant in every group through time. The pure spatial component decreases with time in every group except for Mollusca, which do not present a significant pure spatial component in any sampling period, and for Insecta, whose pure spatial component remains almost constant.

DISCUSSION

Our results show that species distributions of most of the studied taxa are environmentally, spatially and temporally structured, notwithstanding the relatively low percentage of variances explained by the set of selected variables. Such low values are not uncommon, according to previous studies of freshwater metacommunities (Soininen et al., 2007; De Bie et al., 2012; Padial et al., 2014; Rojo et al., 2016) and, because we made an intensive effort of environmental and spatial characterization, the unexplained variation might be largely attributable to other unmeasured processes. For example, biotic interactions such as predation, competition, facilitation, etc. seem to play an important role structuring metacommunities, increasing the influence of environment (both abiotic and biotic) on metacommunity assembly (Leibold and Chase, 2018; García-Girón et al., 2020). Furthermore, ecological drift, or random variation of species abundances, generating differences between sites, is also a strong process influencing metacommunity structure and dynamics (Jeffries, 1988; Chase, 2007).

Temporal effects were found to be relevant in our analysis of metacommunity dynamics. On the one hand, there is an overlap between temporal and environmental components that suggests that part of the significant environmental variables undergo temporal changes throughout the hydroperiod (Bellier et al., 2013). In this sense, species sorting snapshot studies are not fully representative of the whole metacommunity (Rojo et al., 2016). Actually, in highly dynamic ecosystems such as ponds, temporal changes drive fast variations in community structure through

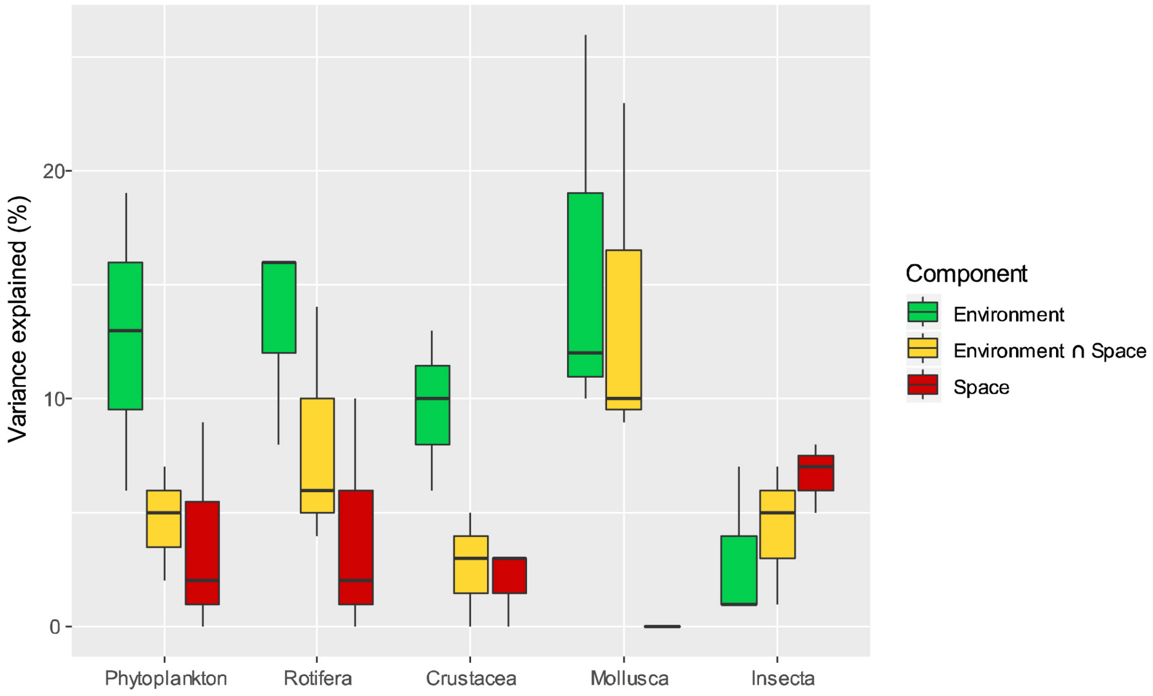

FIGURE 5 | Results of variation partitioning analyses of Phytoplankton, Rotifera, Crustacea, Mollusca, and Insecta studied for each sampling season separately. The variability among seasons is represented in a boxplot graph. The percentage of explained variation for each component is represented with a different color.

TABLE 3 | Results of variation partitioning analysis for Phytoplankton, Rotifera, Crustacea, Mollusca and Insecta, each sampling campaign analyzed separately, where E, environmental component; S, spatial component.

Taxonomic group	E| S	S| E	E ∩ S	E + S
Phytoplankton				
Season 1	0.13**	0.09**	0.07	0.29**
Season 2	0.19**	0.02$^{\text{n.s.}}$	0.02	0.23**
Season 3	0.06**	0$^{\text{n.s.}}$	0.05	0.11**
Rotifera				
Season 1	0.08**	0.02$^{\text{n.s.}}$	0.06	0.16**
Season 2	0.16**	0.1**	0.04	0.30**
Season 3	0.16**	0$^{\text{n.s.}}$	0.14	0.30**
Crustacea				
Season 1	0.06*	0.03$^{\text{n.s.}}$	0.05	0.14**
Season 2	0.13**	0.03$^{\text{n.s.}}$	0	0.16**
Season 3	0.1**	0$^{\text{n.s.}}$	0.03	0.13**
Mollusca				
Season 1	0.12*	0$^{\text{n.s.}}$	0.1	0.22**
Season 2	0.26**	0$^{\text{n.s.}}$	0.09	0.35**
Season 3	0.1$^{\text{n.s.}}$	0$^{\text{n.s.}}$	0.23	0.33*
Insecta				
Season 1	0.01$^{\text{n.s.}}$	0.07**	0.05	0.13**
Season 2	0.01$^{\text{n.s.}}$	0.05**	0.01	0.07**
Season 3	0.07**	0.08**	0.07	0.22**

The table shows the proportion of variation explained (R^2_{adj}) *by each pure component and the overlap between components. Significance codes:* **(P < 0.001), *(P < 0.05), n.s. (non-significant).

turnover processes. On the other hand, we found significant pure temporal effects on most organisms, which even had a stronger influence than pure spatial or pure environmental components in some cases: the temporal component was higher or equal than environmental or spatial effects in 9 out of 17 taxa, being the most important component in Diptera (5% of variance explained, maybe influenced by seasonal dynamics in some families such as Chironomidae or Culicidae; Yunjun and Xiaoyu, 2007). Most previous studies focused on the temporal change of species sorting and neutral effects by comparing between sampling periods (e.g., Fernandes et al., 2014; Rojo et al., 2016), not checking the proportion of variation explained by time itself and, when they did, they usually found a very weak or non-significant influence of temporal effects on the metacommunity (Anderson and Gribble, 1998; Padial et al., 2014). However, our results show that time *per se*, can indeed be an important element in metacommunity structure, even more important than space and environment in some cases, as also found by Bortolini et al. (2019) in a study of subtropical phytoplankton.

Species sorting appears to be an important process for most groups, evidenced by the significant percentage of variance explained by the pure environmental component in all the groups except Heteroptera and Insecta. In addition, this component showed the highest explanatory power in 9 out of 17 metacommunity groups being analyzed. These results highlight the idea that pond communities, even in tropical regions with high species richness and relatively low environmental variability, can be structured by the environment. As a consequence of the relatively small overall niche space in relation to the high number of coexisting species responding to this reduced environmental variability, we might expect narrow realized niches due to niche packing (Lamanna et al., 2014). In addition, we found high percentages of overlap between the environmental and spatial components, perhaps attributable to spatially structured environmental gradients (Clappe et al., 2018), such as climate or landscape variables.

The observed niche-related processes seem to be modulated by dispersal capability. According to the selected environmental variables, passive dispersers were strongly influenced primarily by limnological variables. Many phytoplankton and zooplankton species have wide distributions (Vyverman, 1996; Finlay, 2002; Forró et al., 2008; Segers, 2008) (but see Fontaneto, 2011), and their resting forms are highly resistant to environmental stress (Alekseev et al., 2007; Holzinger and Karsten, 2013; Radzikowski, 2013). The distribution of these organisms is therefore unlikely to be controlled by regional environmental variables, such as climate or landscape, so that local environment might play a stronger influence in their colonization success and population dynamics. On the other hand, we found that active dispersers were influenced at a similar intensity by both local (limnological) and regional (landscape, geographic) variables, being sensitive to aquatic and terrestrial environmental conditions, as also found by other authors (Nnoli et al., 2019). Passive dispersers showed higher pure environmental effects compared to active dispersers, in agreement with previous works that found that the distribution of organisms with high dispersal ability, such as phytoplankton, was more influenced by local environmental conditions (Padial et al., 2014), although other authors consider that actively moving organisms should show a stronger relationship with environmental factors than passively dispersing ones (De Bie et al., 2012; Soininen, 2014). Maybe insects, despite being able to fly, are not so easily dispersed at long distances as are passive dispersers such as algae, rotifers or microcrustaceans. These differences may even be stronger in tropical areas due to the expected increase in dispersal limitations (mountains are "higher" in the tropics; Janzen, 1967). The relative influence of space and environment on metacommunity organization depends on the extent of spatial and environmental gradients and on connectivity, not only on organisms' dispersal traits (Heino et al., 2015; Castillo-Escrivà et al., 2020). One may expect that if we would include semi-permanent ponds and seasonally connected ponds, or other types of water bodies, in the study, the observed influence of species sorting on the structure of aquatic metacommunities would probably increase (Wellborn et al., 1996; Cottenie et al., 2003). We need not to forget that other factors may influence the relative influence of these components, such as the number of measured environmental variables, the way that space is considered in the analyses, the sampling resolution, habitat heterogeneity or species pool size (Leibold and Chase, 2018). In any case, our expectation that small body sized, passively dispersing organisms are proportionally less affected by spatial factors than environmental ones, seem to be supported, although perhaps not so much because of the influence of flood connectivity but rather by regionally related aspects of reduced dispersal in larger bodied organisms such as the abovementioned Janzen's effect.

Neutral processes seem to have high importance in these isolated systems, as suggested by the residuals and the significant pure spatial component in most of the analyzed groups, in agreement with previous studies (De Bie et al., 2012; Baguette et al., 2013). This component was especially strong for the flying Heteroptera, with about 70% of their total variation explained by pure spatial effects. This was unexpected, given the high dispersal ability and colonization efficiency of many heteropterans (Williams, 2005), so this perhaps reflects high small-scale dispersal among nearby ponds, together with larger-scale dispersal limitation. In this sense, the distribution of some groups with low dispersal ability, such as Mollusca, is expected to be more affected by dispersal limitation than by mass effects dynamics, although this depends on sampling extent and connectivity. On the other hand, groups with high dispersal ability, sometimes with cosmopolitan distributions, also showed a significant pure spatial component, which cannot be directly attributable to dispersal limitation but perhaps to mass effects instead (Leibold et al., 2004; Ng et al., 2009; Winegardner et al., 2012). Due to the similar percentage of variance explained by the pure spatial component in groups with very different dispersal strategies and abilities (e.g., Chlorophyceae: 4%; Cyanobacteria: 6%; Copepoda: 7%; Mollusca: 8%; Diptera: 3%) we interpret that both dispersal limitation and mass effects may contribute to spatially structuring the studied metacommunity (Declerck et al., 2011). However, the relative importance of spatial factors compared to species sorting was not as high as we initially expected from the reduced environmental fluctuations in tropical environments, so we must reject our hypothesis that environmental processes should have a lower influence than spatial processes in tropical metacommunity organization.

Even though the temporal effects were found to widely vary among taxonomic groups with similar generation times, the influence of the temporal component related positively (although this relationship was not significant) to organism generation time (or its surrogate of body size). Many biological processes that strongly affect individuals and populations of (aquatic) organisms, such as maturation, reproduction, senescence, or population growth depend on time spanned (Lahr et al., 1999; Cayrou and Céréghino, 2005; Williams, 2005). In addition, egg-bank hatching and immigrant colonization are also time-dependent (Frisch and Green, 2007; Vanschoenwinkel et al., 2010). We found no significant differences in the temporal component between active and dispersal colonizers, so we cannot state that any of these groups is more strongly structured by time-related processes. We could not provide a strong support for our expectation of higher temporal effects in longer-lived organisms, but the observed (non-significant) trend calls for further research on this possibility, maybe increasing the time extent to be able to detect temporal effects (Castillo-Escrivà et al., 2020). The taxonomic groups with non-significant temporal effects were all passive dispersers, which usually leave diapausing propagules in the sediment and have fast life-cycles. These temporal effects or their lack thereof might therefore be related to colonization processes (faster from the sediment, with certain lag from other ponds), increased turbidity and dilution of planktonic populations during the rainy season, overlapping generations, biotic interactions or metamorphosis and flee from the waterbody by juvenile insects when molting to flying adult instars (Anderson et al., 1999; Williams, 2005; Nursuhayati et al., 2013).

Snapshot surveys are common in metacommunity studies, and high variability of results are observed between them regarding the most influential factors, with even contradictory conclusions (e.g., De Bie et al., 2012; Farjalla et al., 2012). When analyzing our temporal series as three separate snapshots, we found clear differences not only between periods but also compared to our overall results when analyzing the three sampling campaigns altogether. These inconsistencies evidence that single-survey metacommunity studies may drive to misleading or uncomplete conclusions. Our results show an unexpectedly high neutral-based structuring during the seasons corresponding to infilling and maximum flooding, that eventually decreases during the dry season (the desiccation phase), in relation to the relative importance of environmental filtering for all groups (except Mollusca). The observation of relatively high neutral structure at the onset of the hydroperiod was previously observed by Castillo-Escrivà et al. (2017c) in ostracods from temporary lakes, suggesting an initial hatching bloom of opportunistic species from the egg bank (Olmo et al., 2012) provoking more random associations that would later become structured by species filtering, i.e., niche-related processes. As previous studies suggest, seasonal floods produce spatial deconstruction, increasing connectivity and dispersal of many organisms, so as dilution effects and environmental homogenization (Thomaz et al., 2007; Rojo et al., 2016). Thus, in early phases of the hydroperiod, community structure might highly depend on egg-bank hatching and, soon after, also on spatial processes, such as hydrochory via flooding or colonization by immigrants. Conversely, pond isolation and consequent environmental heterogenization as the pond succession proceeds toward the end of the rainy season produce an increment of species sorting effects (Fernandes et al., 2014). However, in organisms without an egg bank, such as most aquatic insects, we observe a constant strong influence of pure spatial components. Insects must leave ponds before desiccation and recolonize other water bodies after infilling, so that colonization events can happen repeatedly all along the hydroperiod (Tronstad et al., 2007), but constrained by life-cycles and distance between sites. Anyway, when comparing snapshot and periodic sampling analyses considering time as a set of variables to partial out different structuring effects, remarkable differences can arise; for instance, in the whole hydroperiod analyses of the mollusk metacommunity, the pure spatial component explained an important percentage of variance, while it appeared to be non-significant in single-period analyses, where there is a higher overlap between spatial and environmental effects. This overlap could then be disentangled when considering three sampling periods together.

We may conclude that time is a relevant factor organizing metacommunities of tropical temporary ponds, becoming almost as important as environment and space (Langenheder et al., 2012), as expected from ecological theories of community assembly and succession (Pickett et al., 2011; Fukami, 2015). Many temporal processes are difficult to study, especially long-term ones, but short-term temporal dynamics seems to modulate tropical (pond) metacommunities on a par with niche and dispersal related processes. In addition, species with larger body sizes (and longer generation times) seem to be more influenced by environment-independent temporal effects than smaller, faster developing, organisms. However, despite the importance of spatio-temporal factors influencing metacommunity structure, environment seems to be the main process in metacommunity assembly, supporting the relevance of the species sorting paradigm. Moreover, this environmental component is higher in passive dispersers, mainly influenced by local environment, than in active dispersers, influenced by local and regional environment. Finally, our results show that in many organisms, environmental and spatial components are highly variable between periods, so snapshot surveys provide only partial information about metacommunity organization.

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article/**Supplementary Material**.

AUTHOR CONTRIBUTIONS

FM-J, JM, RR, CR, and MS equally contributed to project design and logistics. FB, JM, RR, MS, FM-J, and CR carried out field work. Phytoplankton identification was supervised by CR. ÁG, CO, and XA identified Rotifera, Branchiopoda, and Calanoida. SI identified Cyclopoida. FM-J and JA-A identified Ostracoda. JR identified macroinvertebrates. ÁG did data analysis and manuscript writing. FM-J supervised and reviewed the manuscript with comments from XA, JR, SI, CR, and CO. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.558833/full#supplementary-material

REFERENCES

Alekseev, V. R., de Stasio, B. T., and Gilbert, J. J. (2007). *Diapause in Aquatic Invertebrates: Theory and Human Use*. Dordretch: Springer.

Anderson, C. R., Peckarsky, B. L., and Wissinger, S. A. (1999). "Tinajas of southeastern Utah: invertebrate reproductive strategies and the habitat templet," in *Invertebrates in Freshwater Wetlands of North America: Ecology and Management*, eds D. P. Batzer, R. B. Rader, and S. A. Wissinger (New York, NY: John Wiley and Sons, Inc), 791–810.

Anderson, M. J., and Gribble, N. A. (1998). Partitioning the variation among spatial, temporal and environmental components in a multivariate data set. *Austr. J. Ecol.* 23, 158–167. doi: 10.1111/j.1442-9993.1998.tb00713.x

Aronow, S. (1982). "Shoreline development ratio," in *Beaches and Coastal Geology*, ed. M. Schwartz (Boston: Springer), 754–755. doi: 10.1007/0-387-30843-1_417

Baguette, M., Blanchet, S., Legrand, D., Stevens, V. M., and Turlure, C. (2013). Individual dispersal, landscape connectivity and ecological networks. *Biol. Rev.* 88, 310–326. doi: 10.1111/brv.12000

Beisner, B. E., Peres-Neto, P. R., Lindström, E. S., Barnett, A., and Longhi, M. L. (2006). The role of environmental and spatial processes in structuring lake communities from bacteria to fish. *Ecology* 87, 2985–2991. doi: 10.1890/0012-9658(2006)87[2985:troeas]2.0.co;2

Bellier, E., Grøtan, V., Engen, S., Schartau, A. K., Herfindal, I., and Finstad, A. G. (2013). Distance decay of similarity, effects of environmental noise and ecological heterogeneity among species in the spatio-temporal dynamics of a dispersal-limited community. *Ecography* 37, 172–182. doi: 10.1111/j.1600-0587.2013.00175.x

Blanchet, F. G., Legendre, P., and Borcard, D. (2008). Forward selection of explanatory variables. *Ecology* 89, 2623–2632. doi: 10.1890/07-0986.1

Boix, D., Caiola, N., Cañedo-Argüelles, M., Gascón, S., Ibàñez, C., Nebra, A., et al. (2010). *Avaluació de l'estat Ecològic de les Zones Humides i Ajust Dels Indicadors de Qualitat. Índexs QAELSe 2010, ECELS i EQAT*. Barcelona: Agència Catalana de l'Aigua, Departament de Medi Ambient i Habitatge, Generalitat de Catalunya.

Boix, D., Sala, J., Quintana, X. D., and Moreno-Amich, R. (2004). Succession of the animal community in a Mediterranean temporary pond. *J. N. Am. Benthol. Soc.* 23, 29–49. doi: 10.1899/0887-3593(2004)023<0029:sotaci>2.0.co;2

Bortolini, J. C., da Silva, P. R. L., Baumgartner, G., and Bueno, N. C. (2019). Response to environmental, spatial, and temporal mechanisms of the phytoplankton metacommunity: comparing ecological approaches in subtropical reservoirs. *Hydrobiologia* 830, 45–61. doi: 10.1007/s10750-018-3849-8

Bougeard, S., and Dray, S. (2018). Supervised multiblock analysis in R with the ade4 package. *J. Statist. Softw.* 86, 1–17. doi: 10.18637/jss.v086.i01

Brendonck, L., and De Meester, L. (2003). Egg banks in freshwater zooplankton: evolutionary and ecological archives in the sediment. *Hydrobiologia* 491, 65–84. doi: 10.1023/A:1024454905119

Brendonck, L., Pinceel, T., and Ortells, R. (2017). Dormancy and dispersal as mediators of zooplankton population and community dynamics along a hydrological disturbance gradient in inland temporary pools. *Hydrobiologia* 796, 201–222. doi: 10.1007/s10750-016-3006-1

Brown, J. H., Hall, C. A. S., and Sibly, R. M. (2018). Equal fitness paradigm explained by a trade-off between generation time and energy production rate. *Nat. Ecol. Evol.* 2, 262–268. doi: 10.1038/s41559-017-0430-1

Castillo-Escrivà, A., Mesquita-Joanes, F., and Rueda, J. (2020). Effects of the temporal scale of observation on the analysis of aquatic invertebrate metacommunities. *Front. Ecol. Evol.* 8:561838. doi: 10.3389/fevo.2020.561838

Castillo-Escrivà, A., Aguilar-Alberola, J. A., and Mesquita-Joanes, F. (2017a). Spatial and environmental effects on a rock pool metacommunity depend on landscape setting and dispersal mode. *Freshw. Biol.* 62, 1004–1011. doi: 10.1111/fwb.12920

Castillo-Escrivà, A., Valls, L., Rochera, C., Camacho, C., and Mesquita-Joanes, F. (2017b). Disentangling environmental, spatial and historical effects on ostracod communities in shallow lakes. *Hydrobiologia* 787, 61–72. doi: 10.1007/s10750-016-2945-x

Castillo-Escrivà, A., Valls, L., Rochera, C., Camacho, A., and Mesquita-Joanes, F. (2017c). Metacommunity dynamics of *Ostracoda* in temporary lakes: overall strong niche effects except at the onset of the flooding period. *Limnologica* 62, 104–110. doi: 10.1016/j.limno.2016.11.005

Cayrou, J., and Céréghino, R. (2005). Life-cycle phenology of some aquatic insects: implications for pond conservation. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 15, 559–571. doi: 10.1002/aqc.739

Chase, J. M. (2007). Drought mediates the importance of stochastic community assembly. *Proc. Natl. Acad. Sci. U.S.A.* 104, 17430–17434. doi: 10.1073/pnas.0704350104

Clappe, S., Dray, S., and Peres-Neto, P. R. (2018). Beyond neutrality: disentangling the effects of species sorting and spurious correlations in community analysis. *Ecology* 99, 1737–1747. doi: 10.1002/ecy.2376

Cottenie, K., Michels, E., Nuytten, N., and de Meester, L. (2003). Zooplankton metacommunity structure: regional vs local processes in highly interconnected ponds. *Ecology* 84, 991–1000. doi: 10.1890/0012-9658(2003)084[0991:zmsrvl]2.0.co;2

De Bie, T., De Meester, L., Brendonck, L., Martens, K., Goddeeris, B., Ercken, D., et al. (2012). Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. *Ecol. Lett.* 15, 740–747. doi: 10.1111/j.1461-0248.2012.01794.x

Declerck, S. A. J., Coronel, J. S., Legendre, P., and Brendonck, L. (2011). Scale dependency of processes structuring metacommunities of cladocerans in temporary pools of High-Andes wetlands. *Ecography* 34, 296–305. doi: 10.1111/j.1600-0587.2010.06462.x

Domínguez, E., and Fernández, H. R. (2009). *Macroinvertebrados Bentónicos Sudamericanos: Sistemática y Biología*. Tucumán: Fundación Miguel Lillo.

Domis, L. N. D. S., Elser, J. J., Gsell, A. S., Huszar, V. M., Ibelings, B. W., Jeppesen, E., et al. (2013). Plankton dynamics under different climatic conditions in space and time. *Freshw. Biol.* 58, 463–482. doi: 10.1111/fwb.12053

Dray, S., Bauman, D., Blanchet, G., Borcard, D., Clappe, S., Guenard, G., et al. (2019). *Adespatial: Multivariate Multiscale Spatial Analysis. R Package Version 0.3-7*. Available online at: https://CRAN.R-project.org/package=adespatial (accessed November 12, 2019).

Dray, S., Legendre, P., and Peres-Neto, P. R. (2006). Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecol. Model.* 196, 483–493. doi: 10.1016/j.ecolmodel.2006.02.015

Elías-Gutiérrez, M., Suárez-Morales, E., Gutiérrez-Aguirre, M., Silva-Briano, M., Granados-Ramírez, J., and Garfias-Espejo, T. (2008). *Cladocera y Copepoda de las Aguas Continentales de México: Guía Ilustrada*. Mexico City: Universidad Nacional Autonoma de México.

Escrivà, A., Poquet, J. M., and Mesquita-Joanes, F. (2015). Effects of environmental and spatial variables on lotic ostracod metacommunity structure in the Iberian Peninsula. *Inland Waters* 5, 283–294. doi: 10.5268/IW-5.3.771

ESRI (2006). *ArcGIS 10*. Redlands, CA: Environmental Systems Research Institute Inc.

Farjalla, V. F., Srivastava, D. S., Marino, N. A. C., Azevedo, F. D., Dib, V., Lopes, P. M., et al. (2012). Ecological determinism increases with organism size. *Ecology* 93, 1752–1759. doi: 10.1890/11-1144.1

Fernandes, I. M., Henriquez-Silva, R., Penha, J., Zuanon, J., and Peres-Neto, P. R. (2014). Spatiotemporal dynamics in a seasonal metacommunity structure is predictable: the case of floodplain-fish communities. *Ecography* 37, 464–475. doi: 10.1111/j.1600-0587.2013.00527.x

Fick, S. E., and Hijmans, R. J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Intern. J. Climatol.* 37, 4302–4315. doi: 10.1002/joc.5086

Finlay, B. J. (2002). Global dispersal of free-living microbial eukaryote species. *Science* 296, 1061–1063. doi: 10.1126/science.1070710

Fontaneto, D. (2011). *Biogeography of Microscopic Organisms, Is Everything Small Everywhere?*. Cambridge: Cambridge University Press.

Forró, L., Korovchinsky, N. M., Kotov, A. A., and Petrusek, A. (2008). Global diversity of cladocerans (Cladocera; Crustacea) in freshwater. *Hydrobiologia* 595, 177–184. doi: 10.1007/978-1-4020-8259-7_19

Frisch, D., and Green, A. J. (2007). Copepods come in first: rapid colonization of new temporary ponds. *Fundamen. Appl. Limnol. Archiv. Hydrobiol.* 168, 289–297. doi: 10.1127/1863-9135/2007/0168-0289

Fukami, T. (2015). Historical contingency in community assembly: integrating niches, species pools, and priority effects. *Annu. Rev. Ecol Evol. Syst.* 46, 1–23. doi: 10.1146/annurev-ecolsys-110411-160340

García-Girón, J., Heino, J., García-Criado, F., Fernández-Aláez, C., and Alahuhta, J. (2020). Biotic interactions hold the key to understanding metacommunity organisation. *Ecography* 43, 1180–1190. doi: 10.1111/ecog.05032

Grönroos, M., Heino, J., Siqueira, T., Landeiro, V. L., Kotanen, J., and Bini, L. M. (2013). Metacommunity structuring in stream networks: roles of dispersal mode, distance type and regional environmental context. *Ecol. Evol.* 3, 4473–4487. doi: 10.1002/ece3.834

Hanski, I., and Gilpin, M. (1991). Metapopulation dynamics: brief history and conceptual domain. *Biol. J. Linnea. Soc.* 42, 3–16. doi: 10.1111/j.1095-8312.1991.tb00548.x

Heino, J., Grönroos, M., Soininen, J., Virtanen, R., and Muotka, T. (2012). Context dependency and metacommunity structuring in boreal headwater streams. *Oikos* 121, 537–544. doi: 10.1111/j.1600-0706.2011.19715.x

Heino, J., Melo, A. S., Siqueira, T., Soininen, J., Valanko, S., and Bini, L. M. (2015). Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. *Freshw. Biol.* 60, 845–869. doi: 10.1111/fwb.12533

Holt, R. D. (1993). "Ecology at the mesoscale: the influence of regional processes on local communities," in *Species Diversity: Historical and Geographical Perspectives*, eds R. Ricklefs and D. Schluter (Chicago: University of Chicago Press), 77–88.

Holt, R. D., Holyoak, M., and Leibold, M. A. (2005). "Future directions in metacommunity ecology," in *Metacommunities: Spatial Dynamics and Ecological Communities*, eds M. A. Holyoak, A. Leibold, and R. D. Holt (Chicago: University of Chicago Press), 465–489.

Holzinger, A., and Karsten, U. (2013). Desiccation stress and tolerance in green algae: consequences for ultrastructure, physiological and molecular mechanisms. *Front. Plant Sci.* 4:327. doi: 10.3389/fpls.2013.00327

Hubbell, S. P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography (MPB-32)*. Princeton: Princeton University Press.

Huber-Pestalozzi, G. (1976–1982). *Das Phytoplankton Des SüSswassers: Systematik und Biologie*. Stuttgart: Schweizerbart.

Janzen, D. H. (1967). Why mountain passes are higher in the tropics. *Am. Nat.* 101, 233–249. doi: 10.1086/282487

Jeffrey, S. W., and Humphrey, G. F. (1975). New spectrophotometric equations for determining chlorophylls a, b, c1 and c2 in higher plants, algae and natural phytoplankton. *Biochem. Physiol. Pflanzen* 167, 191–194. doi: 10.1016/S0015-3796(17)30778-3

Jeffries, M. (1988). Measuring Talling's "elements of chance" in pond populations. *Freshw. Biol.* 20, 383–393. doi: 10.1111/j.1365-2427.1988.tb00464.x

Karanovic, I. (2012). *Recent Freshwater Ostracods of the World: Crustacea, Ostracoda, Podocopida*. Berlin: Springer Science & Business Media.

Koste, W. (1978). *Rotatoria. Die Radertiere Mitteleuropas*. Berlin: Gebruder Borntraeger.

Kruskal, W. H., and Wallis, W. A. (1952). Use of ranks in one-criterion variance analysis. *J. Am. Statist. Assoc.* 47, 583–621. doi: 10.2307/2280779

Lahr, J., Diallo, A. O., Ndour, K. B., Badji, A., and Diouf, P. S. (1999). Phenology of invertebrates living in a temporary pond. *Hydrobiologia* 405, 189–205. doi: 10.1023/A:1003879611584

Lamanna, C., Blonder, B., Violle, C., Kraft, N. J. B., Sandel, B., Šímová, I., et al. (2014). Functional trait space and the latitudinal diversity gradient. *Proc. Natl. Acad. Sci. U.S.A.* 111, 13745–13750. doi: 10.1073/pnas.1317722111

Langenheder, S., Berga, M., Östman, Ö, and Székely, A. J. (2012). Temporal variation of β-diversity and assembly mechanisms in a bacterial metacommunity. *ISME J.* 6, 1107–1114. doi: 10.1038/ismej.2011.177

Legendre, P., and Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia* 129, 271–280. doi: 10.1007/s004420100716

Leibold, M. A., and Chase, J. M. (2018). *Metacommunity Ecology, V.59*. Princeton: Princeton University Press.

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., et al. (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.* 7, 601–613. doi: 10.1111/j.1461-0248.2004.00608.x

Levins, R., and Culver, D. (1971). Regional coexistence of species and competition between rare species. *Proc. Natl. Acad. Sci. U.S.A.* 68, 1246–1248. doi: 10.1073/pnas.68.6.1246

López-Delgado, E. O., Winemiller, K. O., and Villa-Navarro, F. A. (2019). Do metacommunity theories explain spatial variation in fish assemblage structure in a pristine tropical river? *Freshw. Biol.* 64, 367–379. doi: 10.1111/fwb.13229

Meisch, C. (2000). *Freshwater Ostracoda of Western and Central Europe*. Heidelberg: Spektrum Akademischer Verlag.

Ng, I. S. Y., Carr, C. M., and Cottenie, K. (2009). Hierarchical zooplankton metacommunities: distinguishing between high and limiting dispersal mechanisms. *Hydrobiologia* 619, 133–143. doi: 10.1007/s10750-008-9605-8

Nnoli, H., Kyerematen, R., Adu-Acheampong, S., and Hynes, J. (2019). Change in aquatic insect abundance: evidence of climate and land-use change within the Pawmpawm River in Southern Ghana. *Cogent Environ. Sci.* 5, 1–14. doi: 10.1080/23311843.2019.1594511

Nursuhayati, A. S., Yusoff, F. M., and Shariff, M. (2013). Spatial and temporal distribution of phytoplankton in Perak Estuary, Malaysia, during monsoon season. *J. Fish. Aquat. Sci.* 8, 480–493. doi: 10.3923/jfas.2013.480.493

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., et al. (2019). *Vegan: Community Ecology Package. R Package Version 2.5-4*. Available online at: https://Cran.R-project.org/package=vegan (accessed November 12, 2019).

Olmo, C., Armengol, X., and Ortells, R. (2012). Re-establishment of zooplankton communities in temporary ponds after autumn flooding: does restoration age matter? *Limnologica* 42, 310–319. doi: 10.1016/j.limno.2012.08.005

Padial, A. A., Ceschin, F., Declerck, S. A. J., De Meester, L., Bonecker, C. C., Lansac-Tôha, F. A., et al. (2014). Dispersal ability determines the role of environmental, spatial and temporal drivers of metacommunity structure. *PLoS One* 9:e111227. doi: 10.1371/journal.pone.0111227

Peres-Neto, P. R., Legendre, P., Dray, S., and Borcard, D. (2006). Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* 87, 2614–2625. doi: 10.1890/0012-9658(2006)87[2614:vposdm]2.0.co;2

Pickett, S. T. A., Meiners, S. J., and Cadenasso, M. L. (2011). "Domain and propositions of succession theory," in *The Theory of Ecology*, eds S. M. Scheiner and M. R. Willig (Chicago: University of Chicago Press), 185–216.

R Core Team (2019). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Radzikowski, J. (2013). Resistance of dormant stages of planktonic invertebrates to adverse environmental conditions. *J. Plankton Res.* 35, 707–723. doi: 10.1093/plankt/fbt032

Rice, E. W., Baird, R. B., and Eaton, A. D. (1992). *Standard Methods for the Examination of Water and Wastewater*. Washington, DC: American Public Health Association.

Richter-Boix, A., Tejedo, M., and Rezende, E. L. (2011). Evolution and plasticity of anuran larval development in response to desiccation. A comparative analysis. *Ecol. Evol.* 1, 15–25. doi: 10.1002/ece3.2

Rojo, C., Mesquita-Joanes, F., Monrós, J. S., Armengol, J., Sasa, M., Bonilla, F., et al. (2016). Hydrology affects environmental and spatial structuring of microalgal metacommunities in tropical Pacific coast wetlands. *PLoS One* 11:e0149505. doi: 10.1371/journal.pone.0149505

Sammarco, P. W., and Strychar, K. B. (2009). Effects of climate change/global warming on coral reefs: adaptation/exaptation in corals, evolution in zooxanthellae, and biogeographic shifts. *Environ. Bioindic.* 4, 9–45. doi: 10.1080/15555270902905377

Sasa, M., Armengol, X., Bonilla, F., Mesquita-Joanes, F., Piculo, R., Rojo, C., et al. (2015). Seasonal wetlands in the Pacific coast of Costa Rica and Nicaragua: environmental characterization and conservation state. *Limnetica* 34, 1–16. doi: 10.23818/limn.34.01

Schulz, G., Siqueira, T., Stefan, G., and Roque, F. O. (2012). Passive and active dispersers respond similarly to environmental and spatial processes: an example from metacommunity dynamics of tree hole invertebrates. *Fundament. Appl. Limnol.* 181, 315–326. doi: 10.1127/1863-9135/2012/0365

Segers, H. (1995). *Rotifera: vol. 2: The Lecanidae (Monogononta). Guides to the Identification of the Microinvertebrates of the Continental Waters of the World*. North Duncan: Balogh Scientific Books.

Segers, H. (2008). Global diversity of rotifers (Rotifera) in freshwater. *Hydrobiologia* 595, 49–59. doi: 10.1007/s10750-007-9003-7

Soininen, J. (2014). A quantitative analysis of species sorting across organisms and ecosystems. *Ecology* 95, 3284–3292. doi: 10.1890/13-2228.1

Soininen, J., Kokocinski, M., Estlander, S., Kotanen, J., and Heino, J. (2007). Neutrality, niches, and determinants of plankton metacommunity structure across boreal wetland ponds. *Écoscience* 14, 146–154. doi: 10.2980/1195-6860(2007)14[146:nnadop]2.0.co;2

Soininen, J., Korhonen, J. J., Karhu, J., and Vetterli, A. (2011). Disentangling the spatial patterns in community composition of prokaryotic and eukaryotic lake plankton. *Limnol. Oceanogr.* 56, 508–520. doi: 10.4319/lo.2011.56.2.0508

Springer, M., Ramírez, A., and Hanson, P. (2010). Macroinvertebrados de agua dulce de Costa Rica I. *Rev. Biol. Trop.* 58:rbt.v58i4. doi: 10.15517/rbt.v58i4

Thomaz, S. M., Bini, L. M., and Bozelli, R. L. (2007). Floods increase similarity among aquatic habitats in river-floodplain systems. *Hydrobiologia* 579, 1–13. doi: 10.1007/s10750-006-0285-y

Thorp, J. H., and Covich, A. P. (2010). *Ecology and Classification of North American Freshwater Invertebrates*. London: Academic Press.

Tronstad, L. M., Tronstad, B. P., and Benke, A. C. (2007). Aerial colonization and growth: rapid invertebrate responses to temporary aquatic habitats in a river floodplain. *J. N. Am. Benthol. Soc.* 26, 460–471. doi: 10.1899/06-057.1

Vanschoenwinkel, B., Seaman, M., and Brendock, L. (2010). Hatching phenology, life history and egg bank size of fairy shrimp *Branchipodopsis* spp. (Branchiopoda, Crustacea) in relation to the ephemerality of their rock pool habitat. *Ecology* 44, 771–780. doi: 10.1007/s10452-010-9315-y

Vyverman, W. (1996). "The Indo-Malaysian North-Australian phycogeographical region revised," in *Biogeography of Freshwater Algae Developments in Hydrobiology*, ed. J. Kristiansen (Dordrecht: Springer), 107–120. doi: 10.1007/978-94-017-0908-8_10

Wellborn, G. A., Skelly, D. K., and Werner, E. E. (1996). Mechanisms creating community structure across a freshwater habitat gradient. *Annu. Rev. Ecol. Syst.* 27, 337–363. doi: 10.1146/annrev.ecolsys.27.1.337

Williams, D. D. (2005). *The Biology of Temporary Waters*. Oxford: Oxford University Press.

Wilson, D. S. (1992). Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. *Ecology* 73, 1984–2000. doi: 10.2307/1941449

Winegardner, A. K., Jones, B. K., Ng, I. S. Y., Siqueira, T., and Cottenie, K. (2012). The terminology of metacommunity ecology. *Trends Ecol. Evol.* 27, 253–254. doi: 10.1016/j.tree.2012.01.007

Wisnoski, N. I., Leibold, M. A., and Lennon, J. T. (2019). Dormancy in metacommunities. *Am. Nat.* 194, 135–151. doi: 10.1086/704168

Wołowski, K., and Hindák, F. (2005). *Atlas of Euglenophytes*. Bratislava: VEDA.

Yunjun, Y., and Xiaoyu, L. (2007). Production dynamics and life cycle of dominant chironomids (Diptera, Chironomidae) in a subtropical stream in China: adaptation to variable flow conditions in summer and autumn. *Chin. J. Oceanol. Limnol.* 25, 330–342. doi: 10.1007/s00343-007-0330-3

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Effects of the Temporal Scale of Observation on the Analysis of Aquatic Invertebrate Metacommunities

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The development of metacommunity theory has boosted the implementation of numerous empirical tests with field data, mostly focused on the role of spatial and environmental gradients on metacommunity organization. These studies showed an important dependence of the results on the observational scale considered, i.e., spatial grain, sampling spacing, and extent. However, few works deal with time *per se* as a component explaining metacommunity structure, even when data from periodic sampling are available. We suggest adding time explicitly to metacommunity analysis, but taking into account that the temporal scale of observation could affect the estimation of the relative influence of environment, space, and time, as previously recorded for spatial scale variation. Here, we analyze temporal scale dependence using simulated and empirical metacommunities of aquatic invertebrates. The effects of the study duration (i.e., temporal extent) were stronger when most metacommunity variation occurred along the temporal axis, so that local communities were spatially homogenized under high dispersal rates. Contrarily, dispersal limitation and niche differentiation (depending on the spatio-temporal structure of the environment) kept constant the spatial heterogeneity of the metacommunity, reducing the temporal variation and the importance of the temporal scale of observation. Our results highlight the importance of the temporal scale chosen for the analysis of metacommunity dynamics and emphasizes the temporal perspective of metacommunities, suggesting novel and interesting avenues in this research program.

Keywords: temporal scale, selection, dispersal, ecological drift, metacommunity dynamics

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1. INTRODUCTION

Ecological communities are assembled by a complex interaction of processes, such as niche-related selection, dispersal, and ecological drift (Vellend, 2010; Leibold and Chase, 2017). Our perception of these processes strongly depends on the observational scale considered (Soininen et al., 2011; Heino et al., 2015; Viana and Chase, 2019), but most studies have treated this issue from a spatial point of view, suggesting a similar behavior for temporal scales. Nevertheless, the effects of variable temporal scales remain largely unknown (Korhonen et al., 2010; Tomašových and Kidwell, 2010; Dornelas et al., 2014).

The relative importance of selection, dispersal and drift vary with the spatial extent of the study following a generalized conceptual model (Leibold et al., 2004; Leibold and Chase, 2017). At a small spatial extent, environmental conditions can be mostly homogeneous. Then, all the species in the metacommunity may have similar environmental niches and only stochastic dynamics (i.e., ecological drift) foster metacommunity variation (Neutral Theory archetype, NT; Hubbell, 2001). However, despite the small spatial extent, localities could be environmentally heterogeneous, sorting species with different niches. Then, high dispersal (facilitated by short distances among sites) could maintain populations at suboptimal environmental conditions, hindering the deterministic responses of the species to the environment (Mass Effects archetype, ME; Mouquet and Loreau, 2003). At an intermediate spatial scale, environmental heterogeneity can increase, and niche filtering then originates spatial differences in community composition, while dispersal rates still allow the movement of species to reach (without surplus) their potentially suitable localities (Species Sorting archetype, SS; Chase and Leibold, 2003). At a larger spatial extent, dispersal limitation may spatially restrict the distribution of species, creating spatial dissimilarities independently of the environmental conditions and species' niches (Patch Dynamics archetype, PD; Leibold et al., 2004), and biogeographic effects.

Under a temporal focus, local temporal turnover can increase with the study duration (i.e., temporal extent; Wu and Li, 2006) just because of stochastic fluctuations, as NT and PD (even ME) assume (Leibold and Chase, 2017). However, environmental changes can also determine the temporal turnover due to species sorting, potentially reaching rates higher than those predicted by stochastic dynamics (Dornelas et al., 2014). At the metacommunity level, long-term studies have shown either stable (e.g., Azeria and Kolasa, 2008; Huttunen et al., 2018; Lindholm et al., 2020) or changing metacommunities through time, due to environmental fluctuations or disturbances observed (e.g., Datry et al., 2016; Sarremejane et al., 2017; Cañedo-Argüelles et al., 2020). Nevertheless, the spatio-temporal scale of observation in each study could explain these differences, depending on whether or not the study duration covered those relevant environmental fluctuations (Korhonen et al., 2010).

Previous studies estimated the relative relevance of different ecological processes by means of partitioning the metacommunity variation in species composition between the effects of environmental and spatial variables (e.g., Cottenie, 2005). With this approach, we assume that the fraction of the species variation explained by environmental variables is associated with selection (SS) and the rest of the variation (included pure space and unexplained fractions) is due to neutral dispersal and drift (NT and PD, even ME). Spatial variables can capture any spatial variation in the metacommunity, although we usually choose those spatial variables that are associated with broad-scale patterns (Dray et al., 2006). These spatial patterns may be generated by dispersal limitation (i.e., poor connected localities follow different stochastic dynamics; pure spatial fraction) and/or be associated with spatial patterns of the environment (the shared fraction between environment and space). Some studies have also considered introducing temporal variables in variation partitioning analyses (e.g., Anderson and Cribble, 1998; Muylaert et al., 2000; Padial et al., 2014). As with spatial variables, the temporal variables can explain either community changes related to (stochastic) fluctuations and biological cycles or those affected by a temporally-structured environment (the shared fraction between environment and time). Considering the relevance of spatio-temporal variables in these analytical methods is crucial, since metacommunities are to be considered as dynamic structures, with both spatial and temporal variation.

Here, we used simulated metacommunities to analyze the effects of study duration on the relative importance of environmental, spatial, and temporal variables. We expected that (1) the effects of the variation in study duration should be relevant when the metacommunity varies along the temporal axis (high temporal variation; **Figures 1A,B**). This could be a consequence of high dispersal rates, diluting the spatial variation through time. In this context, local communities may experience a process of mixing by the high number of colonizers, temporally synchronizing the metacommunity (Loreau et al., 2003). On the other hand, we envisage that (2) the study duration should be less relevant when the spatial structure of the metacommunity is maintained through time (low temporal variation; **Figures 1C,D**). Dispersal limitation can create permanent differences among localities and therefore spatial patterns would acquire more relevance (with high spatial variation; **Figure 1D**). Similarly, environmental conditions could also create spatial or temporal patterns in those metacommunities depending on the environmental variation, increasing the importance of the temporal scale when the environmental conditions vary through time. These two predictions can be considered two extremes of a continuum between unique temporal or spatial variation. Additionally, we analyze empirical data sets of aquatic invertebrates from a temperate setting to compare our expectations as resulting from the simulations with the field data.

2. MATERIALS AND METHODS

2.1. Model for Simulated Metacommunities

The objective of our simulations was to emulate the temporal dynamics of metacommunities constrained by different conditions of selection and dispersal (**Figure 2A**). To this aim, we obtained species matrices (i.e., locality × species) at several points in time for each simulated metacommunity. Then, we sampled the species matrices changing the study duration but keeping constant the number of temporal sampling points. Consequently, we increased the time lag between sampling events as we extended the study duration (**Figures 2B,C**).

We used a model based on previous metacommunity simulations (Gravel et al., 2006; Sokol et al., 2017; Thompson et al., 2020). These models allow the observation of simulated metacommunity dynamics along different gradients of selection and dispersal. The model used had two parts differentiated in the simulation routine. First (Equation 1), species disperse among localities and then (Equation 2), the species compete at each locality depending on their relative abundances and the environmental conditions, determining the species composition for the next round. In the Equations 1 and 2, $N_{ij}(t)$ is the abundance of individuals of the species i in the site j at time t, $N_{ij}(t+1)_d$ is this abundance after dispersal (i.e., after Equation

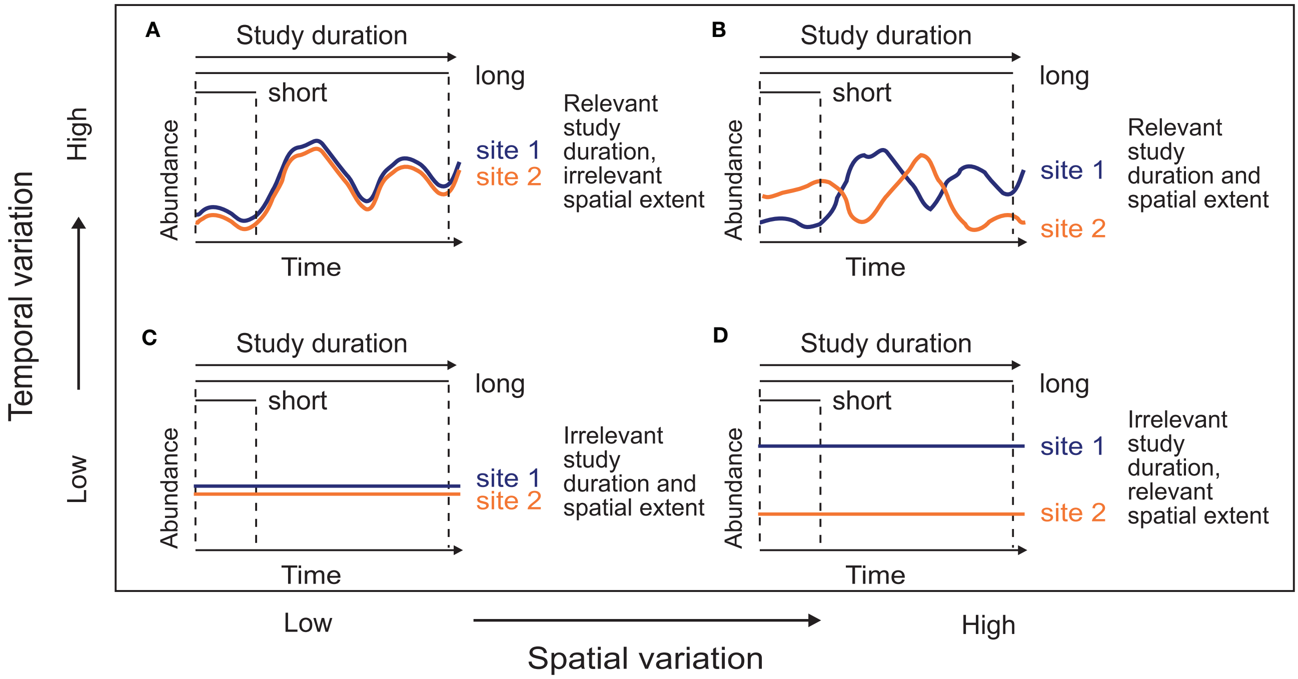

FIGURE 1 | Conceptual model of the variation distribution between the spatial and the temporal axes. Lines represent the abundance dynamics of an hypothetical species in two sites through time. When abundances temporally vary **(A,B)**, increasing the study duration is relevant because it allows encompassing more metacommunity variation. On the other hand, when abundances do not vary over time **(C,D)**, extending the temporal extent of observation (i.e., study duration) should not be relevant, because short and long-term studies show the same temporal variability. Similarly, spatial extent is important in the sampling design, depending on the spatial variation.

1), and $N_{ij}(t+1)_c$ after environmental filtering and competition (i.e., after Equation 2). M is the total number of localities (being k any other than j) and S the regional species richness (where g are different species than i).

$$N_{ij}(t+1)_d = N_{ij}(t) + \frac{a}{M-1}\sum_{k\neq j}^{M} N_{ik}(t) - aN_{ij}(t) \qquad (1)$$

$$N_{ij}(t+1)_c = \frac{r_i\lambda_i(E)N_{ij}(t+1)_d}{(1+\alpha_{intra}N_{ij}(t+1)_d + \alpha_{inter}\sum_{g\neq i}^{S} N_{gj}(t+1)_d)} \qquad (2)$$

In step 1, dispersal rates were determined by the proportion of potential emigrants (a; Loreau et al., 2003). We randomized the number of emigrants ($aN_{ij}(t)$) following a Poisson distribution (Thompson et al., 2020). Following Equation 1, all the localities received the same number of immigrants of each species. Additionally, we also considered an unequal distribution of emigrants relying on the distance among localities (Gravel et al., 2006; Sokol et al., 2017; Viana and Chase, 2019), increasing dispersal resistance with the distances among sites (see **Supplementary Material**). For simplicity, we only show here the results in a scenario where emigrants could reach all the localities with the same probabilities (i.e., very low distance limitation).

In step 2 (Equation 2), local dynamics were influenced by the abundance of each species after dispersal ($N_{ij}(t+1)_d$), the intrinsic growth rate (r_i) and competition (α). The intrinsic growth rate (r_i) relied on the performance of each species (λ_i) to the environmental conditions (E), which characterized the strength of the niche differentiation (Tilman, 2004; Gravel et al., 2006). The performance was defined by a Gaussian distribution, where μ_i is the optimal environmental value and σ_i is the niche breadth (Equation 3). We randomly modified the resulting $r_i\lambda_i(E)N_{ij}(t+1)_d$ following a Poisson distribution in each step, adding stochasticity to the model (Hubbell, 2001; Adler et al., 2007). We also considered intra- (α_{intra}) and interspecific (α_{inter}) competition in each locality (equation 2; Chesson, 2000; Adler et al., 2007).

$$\lambda_i(E) = exp(\frac{-(E-\mu_i)^2}{2\sigma_i^2}) \qquad (3)$$

2.2. Scenarios and Simulation Routine

The model ran in simulated landscapes of 10 localities with 10 species during 3,000 timesteps. Localities were randomly distributed in a square of 100 units of side. We simulated one environmental variable ranging from 0 to 1 for each landscape, which was spatially and temporally autocorrelated based on an exponential covariance model (Thompson et al., 2020). We set a spatial and temporal scale of autocorrelation of 50 and 500 units, respectively (see **Supplementary Material**). We generated different landscapes for each simulation.

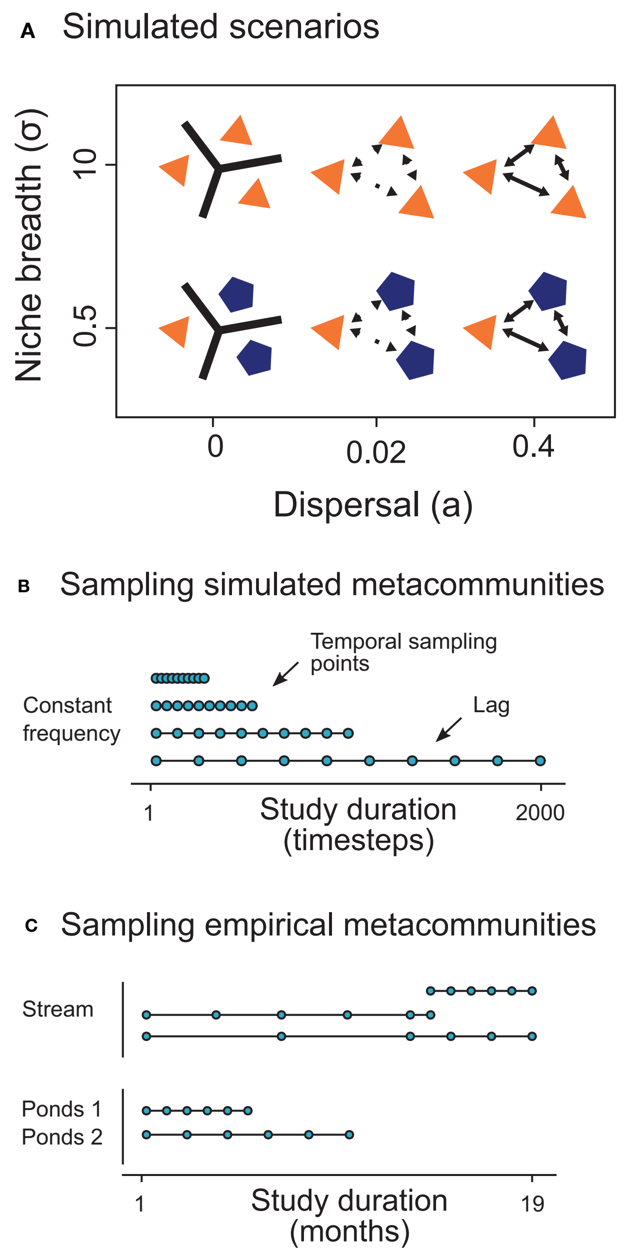

FIGURE 2 | Summary of the simulated scenarios across niche breadth (i.e., selection; σ) and dispersal rate (a) gradients **(A)** and a summary of the temporal sampling procedure in simulated **(B)** and empirical **(C)** metacommunities. In the conceptual models, polygons, and colors represent localities with different suitable conditions for an hypothetical species depending on its niche. The lines and arrows between the polygons show the connectivity among them.

The initial species matrix composition was randomly configured with a mean of 1 individual of each species per locality in a Poisson distribution. During the first 200 timesteps the environmental variable was kept constant in each locality (maintaining the spatial variability). In this period, we added each 10 steps more individuals following the same procedure as in the starting species matrix. After that, the environmental variable varied spatially and temporally and we did not add more individuals. We later removed the first 1,000 timesteps (200 + 800 steps) for further analyses to avoid the effect of the initial conditions on the results (Thompson et al., 2020).

We considered two levels of niche differentiation in the simulations (**Figure 2A**). In both scenarios, we set the same intrinsic growth rate for all the species ($r = 10$). The niche differentiation was determined by the niche breadth (σ_i) and it was the same for all the species in each metacommunity (Gravel et al., 2006; Sokol et al., 2017; Viana and Chase, 2019). In the neutral conditions ($\sigma = 10$), niche breadths were so wide to overlap species niches and cover the whole environmental gradient with the highest fitness (consequently all species have the same fitness at all the environmental values; Hubbell, 2001). Otherwise, with niche differentiation ($\sigma = 0.5$), niches were not totally overlapped and fitness was different for each species relying on their optimal environmental value (μ_i) and the environmental conditions at each site and time. We also assumed stable local coexistence in both scenarios. For this purpose, in the neutral scenario with equivalent fitness among species, stabilizing processes were weak ($\alpha_{intra} = 0.050$; $\alpha_{inter} = 0.048$). But we reinforced stabilization in the niche scenario due to established differences in fitness ($\alpha_{intra} = 0.050$; $\alpha_{inter} = 0.028$; Adler et al., 2007).

For each scenario, we explored 3 dispersal levels changing the proportion of emigrants (low: $a = 0$; intermediate: $a = 0.02$; high: $a = 0.4$; Loreau et al., 2003). Therefore, we studied 6 scenarios (2 niche × 3 dispersal levels; **Figure 2A**). We replicated 10 times the simulations of each scenario ($6 \times 10 = 60$ simulations).

2.3. Empirical Metacommunities

We used three databases of aquatic invertebrates from previous works, which were here reanalyzed with other purposes. The first database had 10 localities in a stream sampled on 11 occasions for 19 months (the first months were sampled seasonally and the last ones monthly; Mezquita et al., 1999; Rueda et al., 2002). The other two databases correspond to two groups of interdunal ponds, with 9 and 13 localities, respectively, sampled monthly during 12 months (Valls et al., 2013; Rueda, 2015). All the data originate from the eastern Iberian Peninsula, with an intra-annual fluctuation of temperatures and precipitations typical of Mediterranean regions (i.e., mild winters, hot and dry summers, and rainfalls concentrated in autumn months).

We selected four groups of arthropods (Ostracoda, Odonata, Coleoptera, and Diptera), each one corresponding to a taxonomic group with similar trophic features for the encompassed species, which potentially compete in a region for similar resources (Hubbell, 2001). Ostracods are benthic microcrustaceans which are predominantly omnivorous and they spread passively among ponds (Mesquita-Joanes et al., 2012). The other three groups have active dispersal with winged adults, although they have different dispersal capabilities and body sizes (Schmidt-Kloiber and Hering, 2015). Dragonflies and damselflies (Odonata) are predators, as well as the coleopterans (here, only family Dytiscidae). However, these two groups have different prey preference, attack strategies and life histories. Finally, dipterans (only families Stratiomyidae, Psychodidae, Ephydridae, and Dixidae) present aquatic larvae mostly consuming detritus. The criteria for selecting these groups were based on their abundance and species richness in the datasets. Overall, we analyzed nine datasets, separating the invertebrate groups in each landscape setting (3 in each landscape). More information of the empirical data is available in the **Supplementary Material**.

2.4. Sampling Metacommunities

We sampled the simulated and the empirical metacommunities across a gradient of study durations (i.e., temporal extents), maintaining the number of temporal sampling points or frequency (therefore varying the lag between samples; **Figures 2B,C**). In the simulated data, we sampled the metacommunities varying the temporal extent from 20 to 2,000 timesteps (**Figure 2B**), fixing the frequency at 10 times. In a similar way, empirical metacommunities were sampled at different study durations maintaining the number of temporal points at a frequency of 6 times (**Figure 2C**). After being sampled, the simulated and the empirical data have the same arrangement in matrices, and we applied the same analytical routine for both types of datasets, as follows.

2.5. Metacommunity Variation Partitioning

The empirical and the simulated data (after sampling) were analyzed by means of variation partitioning between environmental, spatial and temporal variables (Borcard et al., 1992; Anderson and Cribble, 1998; Peres-Neto et al., 2006). Environmental variables in the empirical dataset were previously log-transformed, and later we carried out a PCA to use the principal components as orthogonal environmental variables with all the environmental variability measured. In the simulated data, we used directly the simulated environmental variable (E).

We used Moran Eigenvector Maps (MEMs; Dray et al., 2006) to model spatio-temporal variables (see **Supplementary Material**). For this purpose, we created a three-dimensional network with the sampling points and the links among them, distributing them across space (x and y axes) and time (z axes). The links among samples were decided in two ways. In the spatial axes, the samples of each temporal point were connected following a Gabriel graph criterion, but never across time (Legendre and Legendre, 2012). In the temporal axis, we linked independently all the temporal points of each site separately, uniquely connecting each sample with the previous and the next one in the same site (Legendre and Gauthier, 2014). Therefore, we did not establish temporal connections between different sites. All the links were row standardized depending on the number of links of each point (e.g., 1 link = 1, 2 links = 0.5, and 0.5, 3 links = 0.3, 0.3, and 0.3, and so on), obtaining the weights of each link and calculating the MEMs (Dray et al., 2006).

With this method, the resulting MEMs modeled spatio-temporal patterns. We separated them in pure spatial and pure temporal MEMs by means of a two-way ANOVA, using each MEM as a response variable and spatial sites (space) and temporal points (time) as categorical explanatory variables (based on Legendre et al., 2010; Legendre and Gauthier, 2014). We considered spatial MEMs those with significant space, and temporal MEMs with significant time. Some of them could be significant for both space and time or for any of them. These MEMs were added into the two groups (spatial and temporal), and eventually, variation partitioning can attribute the explanation associated to these MEMs as the shared fractions among space and time (spatio-temporal fraction).

The variation partitioning procedure was based on RDA to calculate the fraction of variation of the species matrix explained by environmental, spatial, and temporal variables as R^2 (Peres-Neto et al., 2006; Legendre and Legendre, 2012). RDA presents some important limitations which could affect the explained fractions (Viana et al., 2019), although it is one of the most used in metacommunity analysis. For example, RDA uses linear regressions to obtain the R^2, although the species response to an environmental gradient could be non-linear (niches are usually Gaussian as in our simulation). In order to minimize this issue, we added a quadratic term for the environmental variables. In RDA, species matrices were transformed with the Hellinger method (i.e., the square-root-transformation of the relative abundance; Legendre and Gallagher, 2001). Additionally, we performed the same analyses by means of RDA without the quadratic term, so as with CCA and dbRDA (see **Supplementary Material**).

Variation partitioning has further limitations. Spurious correlations between environmental and spatio-temporal variables can occur due to spatio-temporal autocorrelation of the environment (Smith and Lundholm, 2010). This artificially increases the fractions (as R^2) shared between the environment and the spatio-temporal variables, whereas this spurious correlation is not associated with the environment. We corrected R^2 using a method based on MSR (Wagner and Dray, 2015), creating replicates of an environmental matrix with the same autocorrelation properties but removing their relationship with the species matrix (as a null model; Clappe et al., 2018). Previously to the variation partitioning, we selected subsets of each set of explanatory variables (environmental and all the MEMs with significant positive Moran's indices, before separating them in spatial and temporal) by means of forward selection, with a double stopping criterion (Blanchet et al., 2008a). We applied a Bonferroni correction for multiple testing to the p-values of the selected variables, i.e., those with adjusted p-values lower than 0.05.

All the simulations and metacommunity analyses were performed in R 3.6.3 (R Core Team, 2020), using the packages vegan (Oksanen et al., 2019), adespatial (Dray et al., 2020), spdep (Bivand and Wong, 2018), and RandomFields (Schlather et al., 2015). All the codes are available in https://github.com/andreucastillo/TemporalScalesMetacommunities.

3. RESULTS

In the simulated metacommunities, the explained fractions (adjusted R^2) varied across selection and dispersal levels (**Figure 3**). Generally, the effects of the temporal scale increased

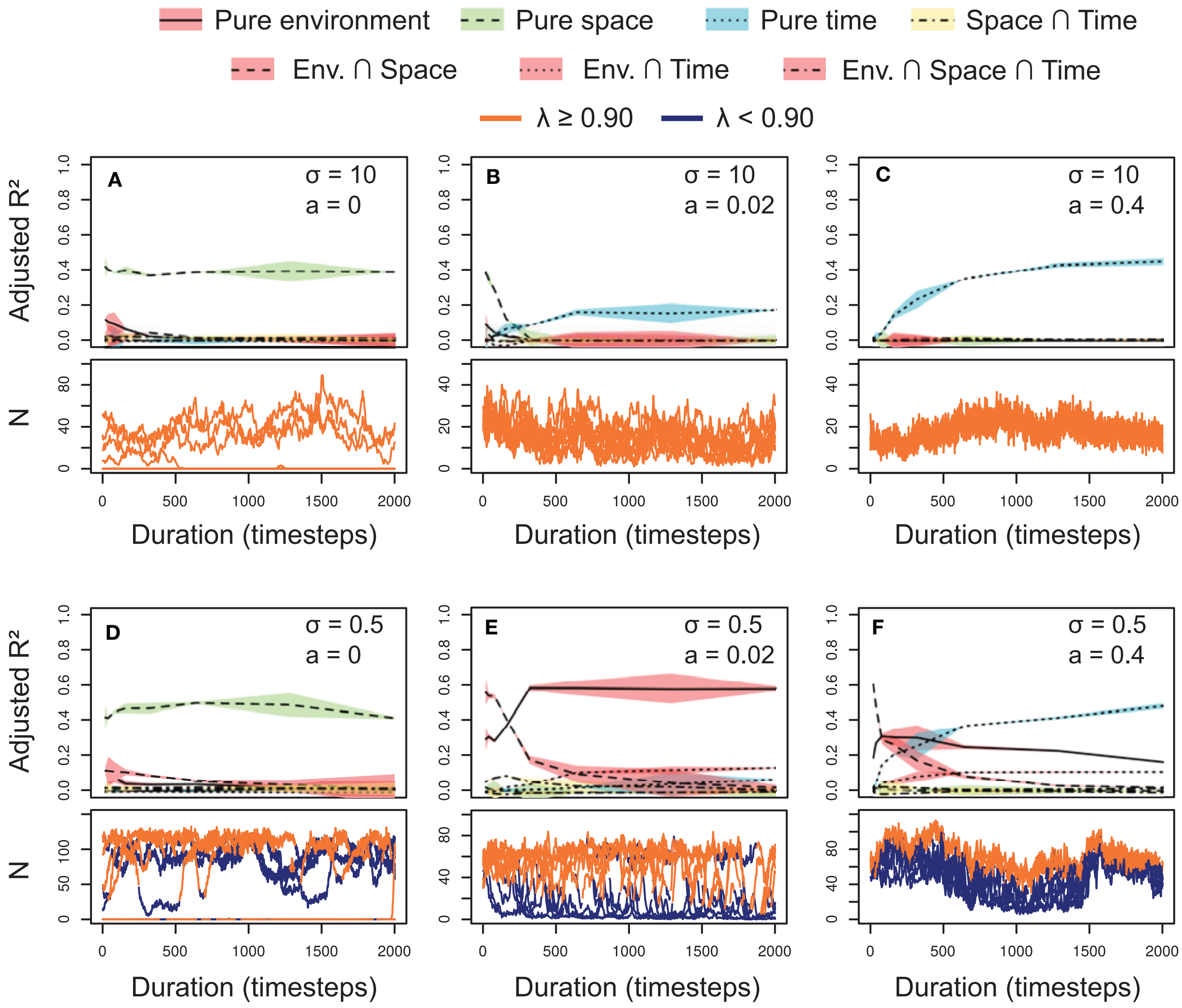

FIGURE 3 | Relative importance (adjusted R^2) of the explanatory sets on the variation of simulated metacommunities under different scenarios of niche differentiation (σ: broad in **A–C** vs. narrow in **D–F**) and dispersal rate (a: low in **A,D**, intermediate in **B,E** and high in **C,F**) in a gradient of study durations (top subpanels, **A–F**). The lines represent the mean, and the colored pattern the standard error of the adjusted R^2 of the 10 replicated simulations. The bottom subpanels display the associated temporal changes in abundance (N) of one random species in 10 localities represented with different lines. The color of the lines depend on the environmental performance of the species in each locality through time, being orange under favorable and blue under unsuitable conditions (with a threshold of $\lambda = 0.90$).

as we incremented the dispersal rates (a), for both niche breadth levels (σ). These temporal scale effects raised the relevance of the temporal variables, and reduced the fractions explained by other factors. The shared fraction between space and time was negligible in all the scenarios, indicating pure temporal or spatial patterns in the metacommunity structure due to the design of the simulations (e.g., equal distribution of emigrants among the localities).

With neutral conditions ($\sigma = 10$; **Figures 3A–C**, top subpanels), spatial variables dominated at low dispersal rates ($a = 0$), whereas temporal variables were prevalent at high dispersal rates ($a = 0.4$). At intermediate dispersal rates ($a = 0.02$), the pattern was a combination of the two extremes. Dispersal determined the main dimension (spatial or temporal) of change of the metacommunity. We can better understand this behavior if we observe the temporal dynamics of a single random species in each of the ten sites separately (**Figures 2A–C**, bottom subpanels). At low dispersal, spatial variation was high and maintained through time due to neutral dynamics. Therefore, space was relevant independently of the study duration. This spatial variation disappeared as we increased the dispersal rates (i.e., synchronizing the localities), until all the variation was concentrated in the temporal axis. However, the relevance of the temporal variables was not constant, increasing logarithmically with the study duration (**Figures 3B,C**).

When selection was included in the simulations by establishing narrower niches ($\sigma = 0.5$; **Figures 3D–F**) environmental effects appeared, and spatial and temporal variables exhibited a similar behavior to the neutral scenarios. However, the relevance of the environmental variable also depended on dispersal rate, accounting for larger fractions of metacommunity variation at intermediate dispersal rates ($a = 0.02$). Generally, the shared fraction between environment and space was higher at short study duration, whereas the shared fraction between environment and time slightly increased with the study duration (a pattern similar to pure spatial and temporal fractions). With low dispersal ($a = 0$), the species dynamics showed non-occupied suitable localities ($\lambda \geq 0.9$; see the orange line for $N = 0$ in **Figure 3D**, bottom subpanel). In these conditions, the environmental variable was less relevant than the spatial variables, which captured this spatial variation in species distribution. At intermediate dispersal rates ($a = 0.02$), the species abundances fitted the environmental suitability through time, according to a constant dominant relevance of the environmental variable (**Figure 3E**). At high dispersal rates (**Figure 3F**) the represented species (lower subpanel) survived even under unsuitable conditions. However, its abundances were higher in the suitable than in the unsuitable conditions, showing an important role for environmental effects at least at short and intermediate study durations. We can also observe a synchronization of the local populations, increasing the relevance of the temporal effects as we extended the study duration.

When exploring the empirical data on aquatic invertebrate metacommunities, explanatory variables accounted only for a relatively low proportion of the metacommunity variation, compared with the simulated scenarios, and their relative role depending on time extent varied widely among groups (**Figure 4**). Generally, pure environmental fractions were more relevant than the others, explaining about 5–25% of the metacommunity variation, particularly for the ponds (**Figures 4B,C**). In these data, the spatio-temporal position of the samples were more complex than in the simulations, and we can observe some relevance of combined spatio-temporal effects (i.e., the shared fraction between space and time). Extending the analyses of the empirical data at different temporal scales, while keeping the number of temporal sampling points fixed, we can observe changes in the variation partitioning results, but the effects of the study duration were unclear (**Figure 4**). Extending the study duration seems to generally increase the relevance of the environmental variables and decrease the spatio-temporal fractions. However, the opposite was true in some cases, and anyway these changes were relatively very low compared with the simulations.

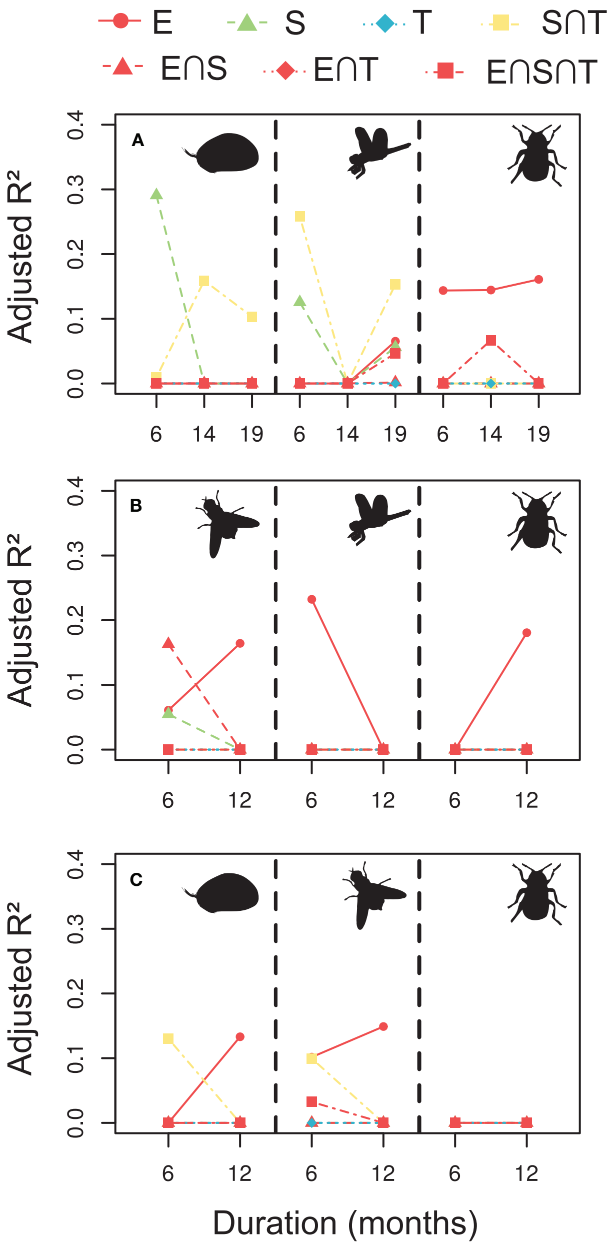

FIGURE 4 | Relative importance (adjusted R^2) of the explanatory sets on the variation of the empirical metacommunities in the Stream **(A)**, Ponds 1 **(B)**, and Ponds 2 **(C)** in a gradient of study durations from 6 to 19 months **(A)** or 6–12 months **(B,C)**, with six temporal sampling points. In the Stream **(A)**, we displayed ostracods (left), odonates (center), and coleopterans (right). In the Ponds 1 **(B)**, we represented dipterans (left), odonates (center), and coleopterans, and in the Ponds 2 **(C)**, ostracods (left), dipterans (center), and coleopterans (right).

4. DISCUSSION

Our results show that the temporal scale of observation affects our perception of the main processes contributing to metacommunity organization. Previous studies already highlighted the influence of spatial scale on the inference of these processes when analyzing communities sampled once (e.g., Condit et al., 2002; Heino et al., 2017; Viana and Chase, 2019), or comparing the spatial effects between several temporal points of the same metacommunity (e.g., Langenheder et al., 2012; Fernandes et al., 2014; Castillo-Escrivà et al., 2017). Other studies have focused on the effects of temporal scales on temporal turnover, but at one spatial point (e.g., Korhonen et al., 2010; Tomašových and Kidwell, 2010). Here, we integrated both perspectives, taking into account the spatio-temporal structure of the data as a whole and testing the influence of sampling period extent on the results of variation partitioning.

The simulations pointed out how dispersal and selection play a key role on metacommunity variation in both the spatial and temporal dimensions. Low dispersal rates allow maintaining the spatial variation through time, because local dynamics are spatially independent without a flux of organisms (Koelle and Vandermeer, 2004). In these cases, long study durations present the same results as short study durations in the simulations, suggesting to focus our sampling design only across space when dispersal is very limited (PD archetype), taking into account ranges of distributions and dispersal abilities of the organism studied (Wiens, 1989). On the other side, high dispersal reduces the spatial variation and temporally synchronizes all the local communities (Loreau et al., 2003; Gonzalez et al., 2009; Pandit et al., 2013). This synchronization implies that the whole metacommunity variation goes to the temporal axis (as expected with dispersal surplus in ME, and NT archetypes), and the longer the study duration, the higher the influence of time needed to capture these effects (e.g., ecological drift, progressive dispersal) on metacommunity variation.

The distribution of the environmental variation through time and space can also determine the importance of an adequate spatial or temporal scale of observation in niche-constrained metacommunities (SS archetype; Korhonen et al., 2010; Viana and Chase, 2019). In our simulations, the environmental variation was predominantly spatially distributed and the localities offered the whole environmental gradient at all the timesteps (even though the local environment was changing through time). Consequently, species always had available localities with suitable conditions when a locality became unsuitable; the key is an adequate dispersal to reach the optimal sites. Notwithstanding this environmental heterogeneity, extending the study duration affected the relevance of the shared fractions between environment and space-time, decreasing the fraction shared with space and slightly increasing the fraction overlapped with time. However, if the environmental variability would be expanded through time (as under climate change scenarios; Thompson et al., 2015), the temporal extent of observation would have a more important effect on detecting such environmental relevance.

In the empirical metacommunities, we observed relatively large differences when modifying the temporal scales of observation, usually increasing pure environmental effects and decreasing spatial pure and shared fractions. However, there was a large variation in this response among groups of organisms and landscape settings. According to the results of the simulations, the studied empirical metacommunities most probably rely on low to intermediate dispersal rates, combined with strong environmental filtering. However, the low explained proportion of metacommunity variation also suggests that fine-scale stochastic dynamics might have an important role in the empirical settings. Such low explained proportions are indeed very common in metacommunity studies (Cottenie, 2005), and may originate, among other sources, from the sampling design and methods used. First, the spatial and temporal scales could not be adequate to fully capture metacommunity variation, as we find in the simulations, emphasizing the importance of the sampling design (Viana and Chase, 2019). Second, we might have not acquired some relevant environmental information, failing to fully explain niche-related patterns and therefore increasing the unexplained fraction. Third, the statistical methods used might not be the best for the data being analyzed (e.g., linear models for non-linear environmental responses), although recent studies have developed new and promising methods (Clappe et al., 2018; Viana et al., 2019). Moreover, the large unexplained variation in empirical data demonstrates multiple and complex variation sources largely disregarded in the simulations, such as methodological errors when sampling or processing the samples, the influence of rare species (Magurran and Henderson, 2003) or trophic interactions (Guzman et al., 2019; García-Girón et al., 2020).

Previous empirical studies analyzing spatio-temporal patterns of metacommunities (Muylaert et al., 2000; Ysebaert and Herman, 2002; Padial et al., 2014) highlighted the relevance of the environment, even when environmental variables were temporally structured. According to our results, this also suggests a dependence on the temporal scale of observation, particularly whenever the environmental heterogeneity increases with the study duration. However, these studies only discussed pure spatial and temporal patterns, whereas we added explicitly mixed spatio-temporal patterns and the results could be different because of this combination (although some of the studies had indeed detected an overlap between space and time; Padial et al., 2014). Nevertheless, the spatio-temporal MEMs used here have some issues, such as their origin on symmetric connections, which may not be adequate for time (unlike AEMs, which consider an asymmetric relationship between points; Blanchet et al., 2008b).

In our empirical metacommunities, the shared fraction between space and time was important in some cases, indicating that the spatio-temporal variation in natural metacommunities might be more complex than that shown by our simulations. For example, ephemeral ponds do not disappear and appear always at the same time, creating spatio-temporal patterns in the data. The sampling design in these cases should take into account both spatial and temporal scales together. Therefore, the sampling design should be based on a previous knowledge of the temporal fluctuations of the landscape, this being important to find natural references of stable (such as tropical systems or stable interstitial zones; Hubbell, 2001; Dumas, 2002) and unstable landscapes (such as temporary ponds or intermittent rivers; Castillo-Escrivà et al., 2017; Cid et al., 2020) to test the theoretical predictions. This also encourages the use of more complex landscapes in the simulations for specific cases, taking into account different types of environmental variation (e.g., mosaic, gradient; Viana and Chase, 2019), the type of spatial distribution of localities (e.g., regular, random; Henriques-Silva et al., 2015), and regular or unexpected temporal events (e.g., droughts, seasonality; Tonkin et al., 2017).

We applied a basic model for the simulations that assumed that all the organisms of each metacommunity had the same population parameters. The study of metacommunity dynamics requires more complex models, considering the survival of the individuals through time (as a kind of temporal dispersal, such as diapause or lethargy) or the population structure (e.g., eggs, juveniles, adults). Simulating or monitoring metacommunities with different life-history strategies (Verberk et al., 2008) may allow comparisons at several temporal scales of observation among groups that differ in development time, synchronization in the reproduction, type of reproduction (e.g., semelparity or iteroparity) or with a population age-structure with changing dispersal capabilities among stages (e.g., juvenile and adult dimorphism). This type of comparison among organisms with different traits (e.g., body sizes and dispersal capabilities) has been a frequent approach in spatial studies of metacommunities (e.g., Soininen et al., 2011; Astorga et al., 2012; De Bie et al., 2012).

Another limitation of our simulations was to consider the same life-history traits (e.g., fecundity, survival, life cycle, dispersal capabilities) for all species. Natural communities are more complex, and variable life-history strategies within the community may allow the coexistence of species with similar trophic requirements (Amarasekare, 2003). For example, metacommunities could be composed by good competitors (with long life cycles, iteroparous, low dispersal rates, and niche dependence) and good colonizers (with short development times, semelparous, high dispersal rates, and low niche dependence; Chave et al., 2002). The prevalence of a trait could determine the relevance of the assembly processes in a metacommunity at different observational scales, whereas rare species may drive an increase in the amount of unexplained variation (Magurran and Henderson, 2003). Additionally, priority effects can also strongly influence the relevance of temporal factors in metacommunities (Fukami, 2015). As a process that is basically temporal, we can emulate historic and priority effects considering resistant stages to adverse transient environments (Wisnoski et al., 2019) and/or setting different inter-specific competition parameters for the modeled species (Thompson et al., 2020). Despite all these limitations, our model provides a general view of the effects of the temporal scale of observation on understanding metacommunity dynamics and methodological problems related to its study.

We focused on the temporal scale of observation using only one spatial scale, but the distribution of the metacommunity variation in the spatial and the temporal dimensions depends on both scales (increasing the extent of one of them decreases the relative relevance of the other). It is important to predict at which spatial and temporal scales the metacommunity variation is balanced in both dimensions, allowing to establish equivalences between spatial and temporal units (Adler and Lauenroth, 2003). We could find the equivalence by analyzing the data, but we need to develop deductive methods to estimate this equivalence taking into account the community structuring processes. This equivalence between space and time is crucial to plan research or conservation projects.

5. CONCLUSIONS

The inference of metacommunity structuring processes is influenced by the temporal scale of observation, depending on the distribution of the metacommunity variation between the spatial and the temporal dimensions. In our simulations, the variation was accumulated in the spatial dimension when dispersal rates were low, and in this case, an increase of the study duration did not have any effect on the inference of the underlying processes. On the other hand, high dispersal rates synchronized all the local communities, reducing the metacommunity variation to the temporal dimension. In this case, the study duration influenced our estimation of the metacommunity organization processes, logarithmically increasing the role of time-related effects (dispersal movements, ecological drift) when increasing the temporal extent of the study. In addition, we found the temporal scale effects to depend on the distribution of the environmental variation, which can generate more spatial or temporal variation in the metacommunity. In the empirical data, we observed only a slight influence of increasing temporal scale, mostly producing an increase of the role of environmental effects and decrease of spatial effects. This suggests metacommunity variation was rather distributed along the spatial axes and/or that the temporal scales considered were not adequate (maybe too short) to observe an increase in the role of time. However, the empirical data is expected to be more complex than the simulations, possibly including many unmeasured spatial, environmental, and stochastic effects. The present study highlights the importance of selecting an adequate observational scale to study or assess natural metacommunities, and the necessity to develop better methods to model and analyze spatio-temporal dynamics of natural systems.

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article/**Supplementary Material**.

AUTHOR CONTRIBUTIONS

FM-J, JR, and AC-E conceived the study. JR carried out the fieldwork and the identification of the organisms of the empirical data. JR and FM-J provided the empirical datasets. AC-E and FM-J designed the simulations. AC-E programmed the code and analyzed the data. AC-E wrote the first draft of the paper, with further revisions and contributions by FM-J. All authors approved the final version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.561838/full#supplementary-material

REFERENCES

Adler, P. B., HilleRisLambers, J., and Levine, J. M. (2007). A niche for neutrality. *Ecol. Lett*. 10, 95–104. doi: 10.1111/j.1461-0248.2006.00996.x

Adler, P. B., and Lauenroth, W. (2003). The power of time: spatiotemporal scaling of species diversity. *Ecol. Lett*. 6, 749–756. doi: 10.1046/j.1461-0248.2003.00497.x

Amarasekare, P. (2003). Competitive coexistence in spatially structured environments: a synthesis. *Ecol. Lett*. 6, 1109–1122. doi: 10.1046/j.1461-0248.2003.00530.x

Anderson, M. J., and Cribble, N. A. (1998). Partitioning the variation among spatial, temporal and environmental components in a multivariate data set. *Aust. J. Ecol*. 23, 158–167. doi: 10.1111/j.1442-9993.1998.tb00713.x

Astorga, A., Oksanen, J., Luoto, M., Soininen, J., Virtanen, R., and Muotka, T. (2012). Distance decay of similarity in freshwater communities: do macro- and microorganisms follow the same rules? *Glob. Ecol. Biogeogr*. 21, 365–375. doi: 10.1111/j.1466-8238.2011.00681.x

Azeria, E. T., and Kolasa, J. (2008). Nestedness, niche metrics and temporal dynamics of a metacommunity in a dynamic natural model system. *Oikos* 117, 1006–1019. doi: 10.1111/j.0030-1299.2008.16529.x

Bivand, R. S., and Wong, D. W. S. (2018). Comparing implementations of global and local indicators of spatial association. *Test* 27, 716–748. doi: 10.1007/s11749-018-0599-x

Blanchet, F. G., Legendre, P., and Borcard, D. (2008a). Forward selection of explanatory variables. *Ecology* 89, 2623–2632. doi: 10.1890/07-0986.1

Blanchet, F. G., Legendre, P., and Borcard, D. (2008b). Modelling directional spatial processes in ecological data. *Ecol. Model*. 215, 325–336. doi: 10.1016/j.ecolmodel.2008.04.001

Borcard, D., Legendre, P., and Drape, P. (1992). Partialling out the spatial component of ecological variation. *Ecology* 73, 1045–1055. doi: 10.2307/1940179

Cañedo-Argüelles, M., Gutiérrez-Cànovas, C., Acosta, R., Castro-López, D., Cid, N., et al. (2020). As time goes by: 20 years of changes in the aquatic macroinvertebrate metacommunity of mediterranean river networks. *J. Biogeogr*. 47, 1861–1874. doi: 10.1111/jbi.13913

Castillo-Escrivà, A., Valls, L., Rochera, C., Camacho, A., and Mesquita-Joanes, F. (2017). Metacommunity dynamics of ostracoda in temporary lakes: overall strong niche effects except at the onset of the flooding period. *Limnologica* 62, 104–110. doi: 10.1016/j.limno.2016.11.005

Chase, J. M., and Leibold, M. A. (2003). Ecological niches: linking classical and contemporary approaches. Chicago, IL: University of Chicago Press. doi: 10.7208/chicago/9780226101811.001.0001

Chave, J., Muller-Landau, H. C., and Levin, S. A. (2002). Comparing classical community models: theoretical consequences for patterns of diversity. *Am. Nat*. 159, 1–23. doi: 10.1086/324112

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst*. 31, 343–366. doi: 10.1146/annurev.ecolsys.31.1.343

Cid, N., Bonada, N., Heino, J., Cañedo-Argüelles, M., Crabot, J., Sarremejane, R., et al. (2020). A metacommunity approach to improve biological assessments in highly dynamic freshwater ecosystems. *Bioscience* 70, 427–438. doi: 10.1093/biosci/biaa033

Clappe, S., Dray, S., and Peres-Neto, P. R. (2018). Beyond neutrality: disentangling the effects of species sorting and spurious correlations in community analysis. *Ecology* 99, 1737–1747. doi: 10.1002/ecy.2376

Condit, R., Pitman, N., Leigh, E. G., Chave, J., Terborgh, J., Foster, R. B., et al. (2002). Beta-diversity in tropical forest trees. *Science* 295, 666–669. doi: 10.1126/science.1066854

Cottenie, K. (2005). Integrating environmental and spatial processes in ecological community dynamics. *Ecol. Lett*. 8, 1175–1182. doi: 10.1111/j.1461-0248.2005.00820.x

Datry, T., Bonada, N., and Heino, J. (2016). Towards understanding the organisation of metacommunities in highly dynamic ecological systems. *Oikos* 125, 149–159. doi: 10.1111/oik.02922

De Bie, T., Meester, L., Brendonck, L., Martens, K., Goddeeris, B., Ercken, D., et al. (2012). Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. *Ecol. Lett*. 15, 740–747. doi: 10.1111/j.1461-0248.2012.01794.x

Dornelas, M., Gotelli, N. J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., et al. (2014). Assemblage time series reveal biodiversity change but not systematic loss. *Science* 344, 296–299. doi: 10.1126/science.1248484

Dray, S., Bauman, D., Blanchet, G., Borcard, D., Clappe, S., Guenard, G., et al. (2020). *Adespatial: Multivariate Multiscale Spatial Analysis*. R package version 0.3-8.

Dray, S., Legendre, P., and Peres-Neto, P. R. (2006). Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecol. Model*. 196, 483–493. doi: 10.1016/j.ecolmodel.2006.02.015

Dumas, P. (2002). Stability of interstitial crustacean communities in an isolated alluvial aquifer. *Hydrobiologia* 468, 63–76. doi: 10.1023/A:1015226423335

Fernandes, I. M., Henriques-Silva, R., Penha, J., Zuanon, J., and Peres-Neto, P. R. (2014). Spatiotemporal dynamics in a seasonal metacommunity structure is predictable: the case of floodplain-fish communities. *Ecography* 37, 464–475. doi: 10.1111/j.1600-0587.2013.00527.x

Fukami, T. (2015). Historical contingency in community assembly: integrating niches, species pools, and priority effects. *Annu. Rev. Ecol. Evol. Syst*. 46, 1–23. doi: 10.1146/annurev-ecolsys-110411-160340

García-Girón, J., Heino, J., García-Criado, F., Fernández-Aláez, C., and Alahuhta, J. (2020). Biotic interactions hold the key to understanding metacommunity organisation. *Ecography* 43, 1180–1190. doi: 10.1111/ecog.05032

Gonzalez, A., Mouquet, N., and Loreau, M. (2009). "Biodiversity as spatial insurance: the effects of habitat fragmentation and dispersal on ecosystem functioning," in *Biodiversity, Ecosystem Functioning, and Human Wellbeing*, eds S. Naeem, D. E. Bunker, A. Hector, M. Loreau, and C. Perrings (New York, NY: Oxford University Press), 134–146. doi: 10.1093/acprof:oso/9780199547951.003.0010

Gravel, D., Canham, C. D., Beaudet, M., and Messier, C. (2006). Reconciling niche and neutrality: the continuum hypothesis. *Ecol. Lett*. 9, 399–409. doi: 10.1111/j.1461-0248.2006.00884.x

Guzman, L. M., Germain, R. M., Forbes, C., Straus, S., O'Connor, M. I., Gravel, D., et al. (2019). Towards a multi-trophic extension of metacommunity ecology. *Ecol. Lett*. 22, 19–33. doi: 10.1111/ele.13162

Heino, J., Melo, A. S., Siqueira, T., Soininen, J., Valanko, S., and Bini, L. M. (2015). Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. *Freshw. Biol*. 60, 845–869. doi: 10.1111/fwb.12533

Heino, J., Soininen, J., Alahuhta, J., Lappalainen, J., and Virtanen, R. (2017). Metacommunity ecology meets biogeography: effects of geographical region, spatial dynamics and environmental filtering on community structure in aquatic organisms. *Oecologia* 183, 121–137. doi: 10.1007/s00442-016-3750-y

Henriques-Silva, R., Boivin, F., Calcagno, V., Urban, M. C., and Peres-Neto, P. R. (2015). On the evolution of dispersal via heterogeneity in spatial connectivity. *Proc. R. Soc. B Biol. Sci.* 282:20142879. doi: 10.1098/rspb.2014.2879

Hubbell, S. P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton, NJ: Princeton University Press.

Huttunen, K.-L., Mykrä, H., Paavo, R., and Muotka, T. (2018). Estimates of benthic invertebrate community variability and its environmental determinants differ between snapshot and trajectory designs. *Freshw. Sci.* 37, 769–779. doi: 10.1086/700402

Koelle, K., and Vandermeer, J. (2004). Dispersal-induced desynchronization: from metapopulations to metacommunities. *Ecol. Lett*. 8, 167–175. doi: 10.1111/j.1461-0248.2004.00703.x

Korhonen, J. J., Soininen, J., and Hillebrand, H. (2010). A quantitative analysis of temporal turnover in aquatic species assemblages across ecosystems. *Ecology* 91, 508–517. doi: 10.1890/09-0392.1

Langenheder, S., Berga, M., Östman, O., and Székely, A. J. (2012). Temporal variation of β-diversity and assembly mechanisms in a bacterial metacommunity. *ISME J.* 6, 1107–1114. doi: 10.1038/ismej.2011.177

Legendre, P., de Cáceres, M., and Borcard, D. (2010). Community surveys through space and time: testing the space-time interaction in the absence of replication. *Ecology* 91, 262–272. doi: 10.1890/09-0199.1

Legendre, P., and Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia* 129, 271–280. doi: 10.1007/s004420100716

Legendre, P., and Gauthier, O. (2014). Statistical methods for temporal and space-time analysis of community composition data. *Proc. R. Soc. B Biol. Sci.* 281:20132728. doi: 10.1098/rspb.2013.2728

Legendre, P., and Legendre, L. F. J. (2012). *Numerical Ecology*. Amsterdam: Elsevier.

Leibold, M. A., and Chase, J. M. (2017). *Metacommunity Ecology*. Princeton, NJ: Princeton University Press. doi: 10.2307/j.ctt1wf4d24

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., et al. (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.* 7, 601–613. doi: 10.1111/j.1461-0248.2004.00608.x

Lindholm, M., Alahuhta, J., Heino, J., and Toivonen, H. (2020). No biotic homogenisation across decades but consistent effects of landscape position and pH on macrophyte communities in boreal lakes. *Ecography* 43, 294–305. doi: 10.1111/ecog.04757

Loreau, M., Mouquet, N., and Gonzalez, A. (2003). Biodiversity as spatial insurance in heterogeneous landscapes. *Proc. Natl. Acad. Sci. U.S.A*. 100, 12765–12770. doi: 10.1073/pnas.2235465100

Magurran, A. E., and Henderson, P. A. (2003). Explaining the excess of rare species in natural species abundance distributions. *Nature* 422:714. doi: 10.1038/nature01547

Mesquita-Joanes, F., Smith, A. J., and Viehberg, F. A. (2012). "The ecology of ostracoda across levels of biological organisation from individual to ecosystem: a review of recent developments and future potential," in *Ostracoda as Proxies for Quaternary Climate Change*, eds D. J. Horne, J. A. Holmes, J. Rodriguez-Lázaro, and F. A. Viehberg (Amsterdam: Elsevier), 15–35. doi: 10.1016/B978-0-444-53636-5.00002-0

Mezquita, F., Hernandez, R., and Rueda, J. (1999). Ecology and distribution of ostracods in a polluted mediterranean river. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 148, 87–103. doi: 10.1016/S0031-0182(98)00177-1

Mouquet, N., and Loreau, M. (2003). Community patterns in source sink metacommunities. *Am. Nat*. 162, 544–557. doi: 10.1086/378857

Muylaert, K., Sabbe, K., and Vyverman, W. (2000). Spatial and temporal dynamics of phytoplankton communities in a freshwater tidal estuary (Schelde, Belgium). *Estuar. Coast. Shelf Sci*. 50, 673–687. doi: 10.1006/ecss.2000.0590

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., et al. (2019). *vegan: Community Ecology Package*. R package version 2.5-6.

Padial, A. A., Ceschin, F., Declerck, S. A. J., Meester, L. D., Bonecker, C. C., Lansac-Tôha, F. A., et al. (2014). Dispersal ability determines the role of environmental, spatial and temporal drivers of metacommunity structure. *PLoS ONE* 9:e111227. doi: 10.1371/journal.pone.0111227

Pandit, S. N., Kolasa, J., and Cottenie, K. (2013). Population synchrony decreases with richness and increases with environmental fluctuations in an experimental metacommunity. *Oecologia* 171, 237–247. doi: 10.1007/s00442-012-2407-8

Peres-Neto, P. R., Legendre, P., Dray, S., and Borcard, D. (2006). Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* 87, 2614–2625. doi: 10.1890/0012-9658(2006)87[2614:VPOSDM]2.0.CO;2

R Core Team (2020). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Rueda, J. (2015). *Biodiversidad y ecología de metacomunidades de macroinvertebrados acuáticos de las malladas de la Devesa y del Racó de l'Olla (PN de l'Albufera de Valencia)* (Dissertation thesis). University of Valencia, Burjassot, Spain.

Rueda, J., Camacho, A., Mezquita, F., Hernández, R., and Roca, J. R. (2002). Effect of episodic and regular sewage discharges on the water chemistry and macroinvertebrate fauna of a mediterranean stream. *Water Air Soil Pollut*. 140, 425–444. doi: 10.1023/A:1020190227581

Sarremejane, R., Cañedo-Argüelles, M., Prat, N., Mykrä, H., Muotka, T., and Bonada, N. (2017). Do metacommunities vary through time? Intermittent rivers as model systems. *J. Biogeogr*. 44, 2752–2763. doi: 10.1111/jbi.13077

Schlather, M., Malinowski, A., Menck, P. J., Oesting, M., and Strokorb, K. (2015). Analysis, simulation and prediction of multivariate random fields with package randomfields. *J. Stat. Softw*. 63, 1–25. doi: 10.18637/jss.v063.i08

Schmidt-Kloiber, A., and Hering, D. (2015). www.freshwaterecology.info–an online tool that unifies, standardises and codifies more than 20,000 European freshwater organisms and their ecological preferences. *Ecol. Indic*. 53, 271–282. doi: 10.1016/j.ecolind.2015.02.007

Smith, T. W., and Lundholm, J. T. (2010). Variation partitioning as a tool to distinguish between niche and neutral processes. *Ecography* 33, 648–655. doi: 10.1111/j.1600-0587.2009.06105.x

Soininen, J., Korhonen, J. J., Karhu, J., and Vetterli, A. (2011). Disentangling the spatial patterns in community composition of prokaryotic and eukaryotic lake plankton. *Limnol. Oceanogr*. 56, 508–520. doi: 10.4319/lo.2011.56.2.0508

Sokol, E. R., Brown, B. L., and Barrett, J. E. (2017). A simulation-based approach to understand how metacommunity characteristics influence emergent biodiversity patterns. *Oikos* 126, 723–737. doi: 10.1111/oik.03690

Thompson, P. L., Beisner, B. E., and Gonzalez, A. (2015). Warming induces synchrony and destabilizes experimental pond zooplankton metacommunities. *Oikos* 124, 1171–1180. doi: 10.1111/oik.01945

Thompson, P. L., Guzman, L. M., De Meester, L., Horváth, Z., Ptacnik, R., Vanschoenwinkel, B., et al. (2020). A process-based metacommunity framework linking local and regional scale community ecology. *Ecol. Lett*. 23, 1314–1329. doi: 10.1111/ele.13568

Tilman, D. (2004). Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proc. Natl. Acad. Sci. U.S.A*. 101, 10854–10861. doi: 10.1073/pnas.0403458101

Tomašových, A., and Kidwell, S. (2010). The effects of temporal resolution on species turnover and on testing metacommunity models. *Am. Nat*. 175, 587–606. doi: 10.1086/651661

Tonkin, J. D., Bogan, M. T., Bonada, N., Rios-Touma, B., and Lytle, D. A. (2017). Seasonality and predictability shape temporal species diversity. *Ecology* 98, 1201–1216. doi: 10.1002/ecy.1761

Valls, L., Rueda, J., and Mesquita-Joanes, F. (2013). Dynamics of ostracoda (crustacea) assemblages in a mediterranean pond system (racó de l'olla, albufera nat. park) with focus on the exotic species *Candonocypris novaezelandiae* (Baird, 1843). *Ann. Limnol.-Int. J. Limnol*. 49, 237–247. doi: 10.1051/limn/2013053

Vellend, M. (2010). Conceptual synthesis in community ecology. *Q. Rev. Biol*. 85, 183–206. doi: 10.1086/652373

Verberk, W. C. E. P., Siepel, H., and Esselink, H. (2008). Life-history strategies in freshwater macroinvertebrates. *Freshw. Biol*. 53, 1722–1738. doi: 10.1111/j.1365-2427.2008.02035.x

Viana, D. S., and Chase, J. M. (2019). Spatial scale modulates the inference of metacommunity assembly processes. *Ecology* 100:e02576. doi: 10.1002/ecy.2576

Viana, D. S., Keil, P., and Jeliazkov, A. (2019). Partitioning environment and space in species-by-site matrices: a comparison of methods for community ecology and macroecology. *bioRxiv [Preprint]*. doi: 10.1101/871251

Wagner, H. H., and Dray, S. (2015). Generating spatially constrained null models for irregularly spaced data using moran spectral randomization methods. *Methods Ecol. Evol.* 6, 1169–1178. doi: 10.1111/2041-210X.12407

Wiens, J. A. (1989). Spatial scaling in ecology. *Funct. Ecol.* 3, 385–397. doi: 10.2307/2389612

Wisnoski, N. I., Leibold, M. A., and Lennon, J. T. (2019). Dormancy in metacommunities. *Am. Nat.* 194, 135–151. doi: 10.1086/704168

Wu, J., and Li, H. (2006). "Concepts of scale and scaling," in *Scaling and Uncertainty Analysis in Ecology*, eds J. Wu, B. Jones, H. Li, and O. L. Loucks (Dordrecht: Springer), 3–15. doi: 10.1007/1-4020-4663-4_1

Ysebaert, T., and Herman, P. M. J. (2002). Spatial and temporal variation in benthic macrofauna and relationships with environmental variables in an estuarine, intertidal soft-sediment environment. *Mar. Ecol. Prog. Ser.* 244, 105–124. doi: 10.3354/meps24410

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High Temporal Beta Diversity in an Ant Metacommunity, With Increasing Temporal Functional Replacement Along the Elevational Gradient

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Ecological communities vary considerably in space and time and understanding such changes has fundamental relevance for ecology and conservation sciences. Mountains provide an excellent scenario for studies addressing spatial and temporal variation, as they vary in conditions and resources in a small geographic region. Here, we aimed to understand the patterns of variation in ant metacommunity composition across time and along an elevational gradient in a tropical mountain, focusing both on the taxonomic and functional facets of diversity. We used a β-diversity metric and broke it into nestedness and turnover to estimate short-term temporal changes in ant metacommunity composition. We tested the following hypotheses: (i) taxonomic and functional temporal β-diversity increase along the elevational gradient and (ii) turnover is the main component driving taxonomic temporal β-diversity and nestedness for functional temporal β-diversity. Rejecting our first hypothesis, we found that both taxonomic and functional temporal β-diversity did not increase with elevation. Yet, the values were always high, indicating that both species and functional traits are highly variable over time. In accordance with our second hypothesis, we found that turnover was the main component of taxonomic β-diversity. Yet adding complexity to our hypothesis, the contribution of nestedness to functional β-diversity decreased with increasing elevation. These results suggest that at low elevations, the turnover in species composition may then cause changes in trait composition because of the loss of some traits, yet preserving the most common functions (nested functional communities), while at high elevations functional capabilities may change over time (turnover of traits). In the context of global warming, where tropical mountain insects are expected to change their distributional range upwards, it is extremely important to consider the importance of the turnover on the temporal variation in functional traits and functions of ant metacommunity at higher elevations.

Keywords: ***campo rupestre*, metacommunity, beta-diversity, nestedness, species turnover, rupestrian grassland, traits, environmental instability**

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INTRODUCTION

Understanding how communities are structured in space and time has fundamental relevance in ecology and conservation science (Gaston, 2000; Sutherland et al., 2013). There is abundant evidence in ecological studies that the spatio-temporal patterns we see in nature cannot be disentangled (Schiesari et al., 2019), as individuals and species can move both through space and time, forming metapopulations (Levins, 1969) and metacommunities (Leibold et al., 2004). Knowledge of complex spatial metacommunity dynamics have been advanced by using diversity partitioning analyses (e.g., Bishop et al., 2015; Heino et al., 2015), that partition diversity into local (α), and regional (γ) components, as well as the change among local communities (β) (Crist et al., 2003). However, most studies of this kind are based on one or a few samples in time, creating a gap in our knowledge of the importance of temporal variation of individuals and species in the structuring of metapopulations and metacommunities (Datry et al., 2016; Ruhí et al., 2017). In a changing world (Lewis and Maslin, 2015), there is an urgent need to understand the spatial and temporal distribution of diversity and the underlying mechanisms of these patterns, so we can predict and mitigate the effects of global change on biodiversity, ecosystem functions, and associated services (e.g., Legendre and Condit, 2019).

Since the classic work of von Humboldt and Bonpland (1805), numerous studies have investigated species distributions and the underlying mechanisms of these patterns along spatial and environmental gradients (e.g., Peters et al., 2016). Mountains are central to these studies, because they have significant environmental gradients in a relatively small geographical area (Körner, 2007). The small spatial scale means that all regional species can potentially access the whole gradient, minimizing the effects of the kinds of dispersal limitations seen over larger geographical areas (Longino and Colwell, 2011). Yet, species distribution patterns vary along mountains, with most taxa showing a decline in diversity with increasing elevation and associated changes in species composition (Fernandes et al., 2016; Perillo et al., 2017; Mota et al., 2018; Li et al., 2019). In this context, β-diversity metrics are useful for understanding how species composition changes across habitats or elevations and also attempt to reveal the assembly mechanisms that drive these differences (Bishop et al., 2015; Castro et al., 2019). Differences in habitat and resource use among species determine the spatial structure and maintenance of the β-diversity in mountains, where species turnover among elevations is the dominant component driving taxonomic spatial β-diversity of plants (Mota et al., 2018), birds (Li et al., 2019), termites (Nunes et al., 2017), dung beetles (Nunes et al., 2016), ants (Castro et al., 2020), and benthic invertebrates (Castro et al., 2019).

The abrupt spatial and temporal environmental changes in mountains provide a good experimental setting to study spatio-temporal dynamics of metacommunities. However, most studies on patterns of species and community distributions in mountains focus on the spatial rather than on the temporal dimension (e.g., Fernandes et al., 2016; Lasmar et al., 2020). Yet, the temporal variation in climatic conditions can be just as strong as the spatial variation, regulating plant resource availability and patterns of animal foraging in seasonal tropical systems (e.g., Basset et al., 2015; Costa et al., 2018; Novais et al., 2019). While the temporal variation in climatic conditions that is driven by seasonal variation could be similar to the variation found at different elevations in mountains (Rocha et al., 2016), it is less clear which drivers shape temporal β-diversity of communities on mountains. We have evidence that although spatial taxonomic diversity at the regional scale (γ-diversity) is mainly caused by differences in species compositions of local communities (β-diversity component), the functional regional diversity (γ-diversity) is mainly driven by patterns of local diversity (α-diversity component; species composition changes along the elevational gradient, but functions do not; Nunes et al., 2016; Castro et al., 2020). In contrast, there is a lack of information on how temporal variation structures communities that are subjected to different climatic conditions at different elevations, both taxonomically and functionally. In other words, we need to explicitly address how the temporal taxonomic and functional β-diversity within metacommunities vary in space, i.e., across the elevational gradient.

In this study, we explored the spatio-temporal dynamics of metacommunities in tropical mountains by investigating how communities respond to temporal variation in environmental conditions on an elevational gradient in south-eastern Brazil. We collected taxonomic and functional information on ant metacommunity quarterly over 3 years, totalling 12 temporal samplings at each of seven different elevations. We used ants (Hymenoptera: Formicidae) as a focal taxon, because they respond rapidly to changes in environmental conditions, both spatially (Castro et al., 2020) and temporally (Bishop et al., 2014) and perform important ecological functions such as nutrient cycling and seed dispersal (Farji-Brener and Werenkraut, 2017; Magalhães et al., 2018). We investigated how temporal taxonomic and functional β-diversity of ants vary along the elevation gradient and how turnover and nestedness contribute to overall temporal β-diversity. We tested the following hypotheses: (i) the temporal taxonomic and functional β-diversity increase with increasing elevation along the gradient (**Figure 1A**); and (ii) turnover is the main component driving taxonomic temporal β-diversity and nestedness for temporal functional β-diversity (**Figure 1B**). The first hypothesis predicts an increase in temporal β-diversity with increasing elevation because temporal variation in the environment is more pronounced at high elevations than at low elevations. Harsh climatic conditions, climatic instability, and lower resource availability (productivity) at higher elevations are therefore likely to favor higher taxonomic and functional variation of the metacommunity over time [e.g., Costa et al. (2018) for temporal variation in ant species activity among seasons]. With decreasing habitat heterogeneity and resource availability (e.g., during the dry season), we expect to find communities of ants with longer legs, since these communities would be composed mainly by generalist and predator species that usually walk longer distances to forage (Lenoir et al., 2009; Bishop et al., 2016; Fichaux et al., 2019). Accordingly, the communities would be composed mainly by species with longer mandibles, usually found in omnivore generalist and predator species (Gibb and Cunningham, 2013; Bishop et al., 2015). In addition, in harsher environments or seasons, we would expect higher polymorphism in ant colonies, because this would help colonies to deal with temperature and humidity variation through labor division (Lenoir et al., 2009). The second hypothesis predicts a higher contribution of turnover than nestedness to temporal taxonomic β-diversity, following the spatial pattern found for mountain insects (Nunes et al., 2017; Perillo et al., 2017; da Silva et al., 2018). Moreover, it also predicts a lower contribution of turnover compared to nestedness for temporal functional β-diversity, with communities showing a functional redundancy over time, as demonstrated spatially for insects in mountains (Bishop et al., 2015; Castro et al., 2020).

MATERIALS AND METHODS

Study Area

The study was conducted in the southern part of the Espinhaço mountain range (**Figure 2**), in the permanent plots of the Long Term Ecological Research Project Campos Rupestres (PELD CRSC/CNPq Project) along a gradient of elevation in the Serra do Cipó region, Minas Gerais State, Brazil (19°22′01′′S, 43°32′17 ′′W) (Silveira et al., 2019). The region has marked wet and dry seasons, and the mean annual precipitation is 1,300–1,500 mm, while the mean annual temperature is 20°C (highland tropical Cwb Köppen climate) (Fernandes et al., 2016). The Serra do Cipó region comprises private areas under environmental protection (APA Morro da Pedreira) and a National Park under full protection (PARNA Serra do Cipó), as well as being part of the Espinhaço Range Biosphere Reserve (Domingues et al., 2011; Fernandes et al., 2018). At the study location, soil and vegetation are very heterogeneous, with the core landscape being a vegetation mosaic dominated by *campo rupestre* (rupestrian grassland) intermingled by quartzitic outcrops, surrounding forest patches, gallery forests, and mixing with dry forests and cerrado at the lower elevations (Fernandes, 2016; Silveira et al., 2016; Morellato and Silveira, 2018).

Sampling Design and Explanatory Variables

We distributed our sampling sites every 100 m of elevation on a gradient that ranged from 800 to 1,400 m a.s.l. (**Figure 2**). At each of these sampling sites, we used three 200 m long transects separated by at least 250 m, totalling 21 transects (three × seven sampling sites). Within each transect, we placed five pitfall traps separated by 50 m (15 traps per sampling site, 105 in total for each temporal sampling) to collect ants foraging on the ground. Traps consisted of a plastic pot with a diameter of 14 cm and a depth of 9 cm, which was filled with 500 ml of a saline-detergent solution. The pots were set at ground level and covered with a plastic plate (20 cm from ground level) to prevent rain from entering the trap. All pitfall traps remained in the field for 48 h per survey (Bestelmeyer et al., 2000). We sampled quarterly (separated by 3 months), totalling 12 samples between April 2011 and January 2014 (January, April, July, and October); such that the samples spanned the beginning and end of both the wet and dry season each year. The transect represents independent sample replicates because the spacing of 50 m between samples is considered enough to avoid interference related to the foraging range of ants belonging to the same colony (Leponce et al., 2004) and we used five times this distance between transects. We pooled data from the five pitfall traps for each transect and each month (see Castro et al., 2020).

To explore the mechanisms behind the patterns we expected with our hypotheses, we accessed information on climatic and vegetation factors. For climatic factors, we used data from meteorological monitoring towers (equipped with the Onset HOBO® U30 data-logger) located at every 100 m of elevation, adjacent to the sampling sites of the PELD CRSC/CNPq Project (Silveira et al., 2019), between January 2012 and January 2014 (January, April, July, and October). We recorded air and soil temperature, humidity, and precipitation, and we calculated the mean and coefficient of variation of these variables for the whole sample period for each sample site (i.e., each elevation). We also used vegetation data from the same project at each elevation [see Mota et al. (2018) for more details] to assess the total plant richness per sample site.

Identification of Species and Definition of Functional Traits of Ants

To identify ants to species and morphospecies we used a comparison method with the Collection of Formicidae from *campo rupestre* of the Laboratory of Insect Ecology at the Universidade Federal de Minas Gerais, Brazil. In addition, all species were revised by experts of different ant taxa. Classifications were based on Baccaro et al. (2015) and Bolton's Ants of the World catalog (Bolton, 2020) classifications.

For all ant species collected, we measured key functional response traits related to diet, nesting ecology, foraging capacity, thermoregulation, and habitat association (Leal et al., 2012; Bishop et al., 2016; Paolucci et al., 2016; Tiede et al., 2017; Fichaux et al., 2019). Specifically, we quantified the following seven traits for each species: Weber's length, femur length, mandible length, predominant color (mesosoma), polymorphism, integument sculpture, and functional groups (six morphological traits and one ecological trait; **Table 1**).

Morphological measurements were taken following the guide for identification of functional attributes for ants (*The Global Ants trait Database* – GLAD; Parr et al., 2017), with exception for the variable "color." This trait was obtained from the HSV color model using only the variable V (color brightness), as proposed by Bishop et al. (2016). However, we performed the capture of HSV values of the predominant color on the mesosoma of each specimen, in contrast to Bishop et al. (2016), who considered the predominant color between head, mesosoma, and gaster. Since functional traits are not normally distributed (Arnan et al., 2018; Fichaux et al., 2019), all continuous data, except Weber's length and color brightness, were divided by Weber's length to correct for individual body size.

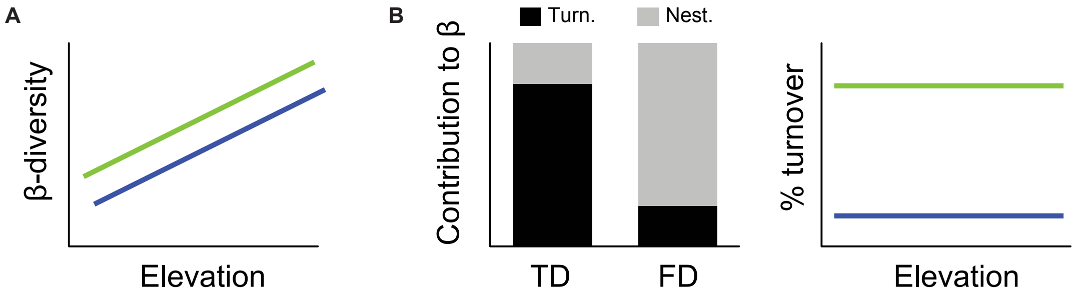

FIGURE 1 | Hypotheses of how temporal β-diversity and its turnover contribution varies in an elevational gradient. **(A)** Our first hypothesis is that both taxonomic (green line) and functional (blue line) temporal β-diversities increase with elevation, because in more harsh, higher elevation environments, the temporal variation in conditions and resources would be higher. **(B)** Our second hypothesis is that turnover (black bar) is the most important mechanism generating taxonomic temporal β-diversity (green line) and that nestedness (gray bar) is the most important component of functional temporal β-diversity (blue line) in general and along all the elevational gradient, because the communities would present functional redundancy over time.

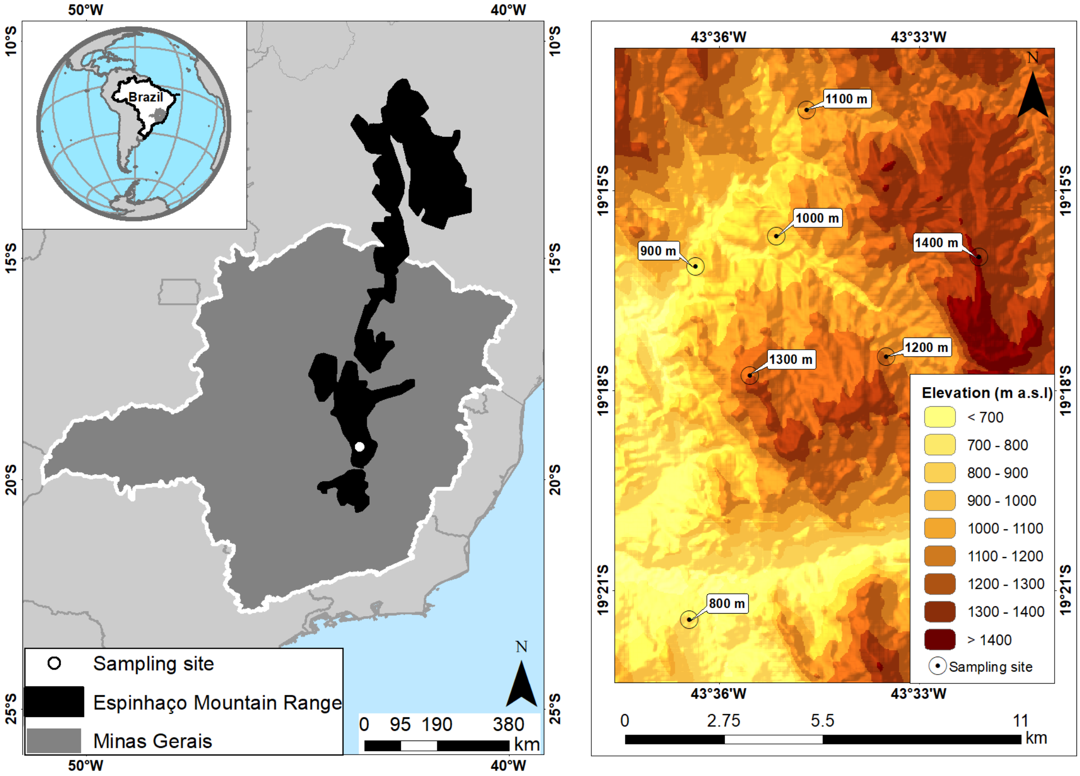

FIGURE 2 | Left panel shows a map with the location of the Espinhaço mountain range in Brazil, with our sampling area in the southern Serra do Cipó region, Minas Gerais. Right panel shows the distribution of the sampling sites along the elevational gradient.

Imaging was performed using Microscope Digital Camera LC30 OLYMPUS® mounted on a stereomicroscope SZ61 OLYMPUS®. Measurements were made with a digital capture micrometer (accurate to 0.01 mm) provided in the LC Micro 2.2 OLYMPUS® software. All measured specimens were selected at random from our dataset. When possible, at least six individuals were measured, and whenever it was not possible, we measured all the available individuals. Only minor workers were used, and a total of 2103 images were captured from 701 individuals, with an average of 4.52 individuals per species. Categorical and ordinal morphological traits (i.e., polymorphism and integument sculpture) were attributed using genera/species information available at AntWeb[1] and AntWiki website[2] (Guénard et al., 2017) and from our own observations.

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[1] www.antweb.org

[2] www.antwiki.org

TABLE 1 | List of response functional traits measured (morphological and ecological), their hypothesized ecological functions and the expected response of the traits to environmental change.

Traits	Measure	Abbrev. /Unit	Ecological functions	Expected response
Morphological traits				
Weber's length	Continuous	WL (μm)	Proxy for whole-length, related to metabolic characteristics (Weber, 1938; Kaspari and Weiser, 1999; Bishop et al., 2016).	As temperature decreases, we expect to find a community with larger individuals (e.g., Bishop et al., 2016).
Femur length	Continuous	HFL (μm)	Foraging speed indicator, related to habitat complexity (Feener et al., 1988; Yates et al., 2014).	Longer femur let ants move out rapidly, which allow then occurring in harsh environment conditions, as seen in seasonally flooded areas (Fichaux et al., 2019) or desert environments (Lenoir et al., 2009).
Mandible length	Continuous	ML (μm)	Diet's indicative (Brandão et al., 2009). Longer mandibles are associated with larger preys in predatory species (Gibb and Cunningham, 2013).	Due to the decrease in the complexity of the environment in the dry and cold season, we expect communities composed by species with larger mandibles; increase in predatory species frequency (e.g., Bishop et al., 2015).
Color (Mesossoma)	Continuous	V (%) *	Thermal melanism hypothesis (Trullas et al., 2007); Thermotolerance's indicative and, directly related to temperature variation and solar radiation (Bishop et al., 2016).	Dark ectothermic individuals have a benefit in cool climates compared to lighter ones (Trullas et al., 2007). We expected dark individuals in the dry and cold season (Bishop et al., 2016).
Polymorphism	Categorical	1 = monomorphic; 2 = dimorphic; 3 = polymorphic	Workers' polymorphism, related to the ability to develop different tasks in the colony (e.g., protection, foraging, or activities inside the nest; Wills et al., 2017).	Due to harsh conditions found in mountains, we expect more polymorphic species, which could be able to make labour division at a different time of the day in response to daily temperature variation (Lenoir et al., 2009).
Integument Sculpture	Ordinal	1 = cuticle smooth/shiny; 2 = superficial wrinkles/pits; 3 = surface heavily textured	Integument desiccation protection (Nation, 2008). Thickened cuticles enhanced the dehydration tolerance (Terblanche, 2012).	An intermediate tegument sculpture is expected, due to the lower temperatures during the dry season than the wet season, and due to the thermal amplitude commonly described in mountains between day and night.
Ecological trait				
Functional Groups	Categorical	AA = Army Ants; AD = Arboreal Dominant; AP = Arboreal Predator; AS = Arboreal Subordinate; CO = Cryptic Omnivores; CP = Cryptic Predators; DD = Dominant Dolichoderinae; EO = Epigeic Omnivores; EP = Epigeic Predators; Hatt = High Attini; Latt = Low Attini; Opp = Opportunist; SC = Subordinate Camponotini SH = Seed Harvester.	Functional groups based on ants' global-scale responses to environmental stress and disturbance. Indicative of ecological tasks, like nesting, foraging, and diet habits (Andersen, 1995; Leal et al., 2012; Paolucci et al., 2016). All groups were based on the classification used by Paolucci et al. (2016). Exception for Seed Harvester group (Johnson, 2015) here represented by *Pogonomyrmex naegelli*, which was not present in this list.	

Calculating Temporal β-Diversity

We calculated the variation of the taxonomic (TD) and functional (FD) composition of the ant community temporally using β-diversity (β_{SOR}) (Baselga, 2010). We used the data collected over the 12 sampling periods to calculate temporal TD and FD β-diversity for each transect (21 in total). We also partitioned TD and FD into the components derived from species turnover (β_{SIM}) and species gain/loss or nestedness (β_{SNE}). In this step, we partitioned β-diversity for the whole gradient and for each transect. In all β-diversity calculations, we used Sørensen dissimilarity index based on a presence/absence species composition matrix. To calculate temporal functional β-diversity, we first generated a distance matrix of species based on their functional traits using the Gower Distance, a useful method for combining categorical and continuous traits (de Bello et al., 2013). We then used this distance matrix to construct a functional space, using Principal Coordinates Analysis (PCoA), which in turn was used to calculate temporal functional β-diversity. We used the "beta.multi" and "functional.beta.multi" functions of the package "betapart" to partition TD and FD β-diversity,

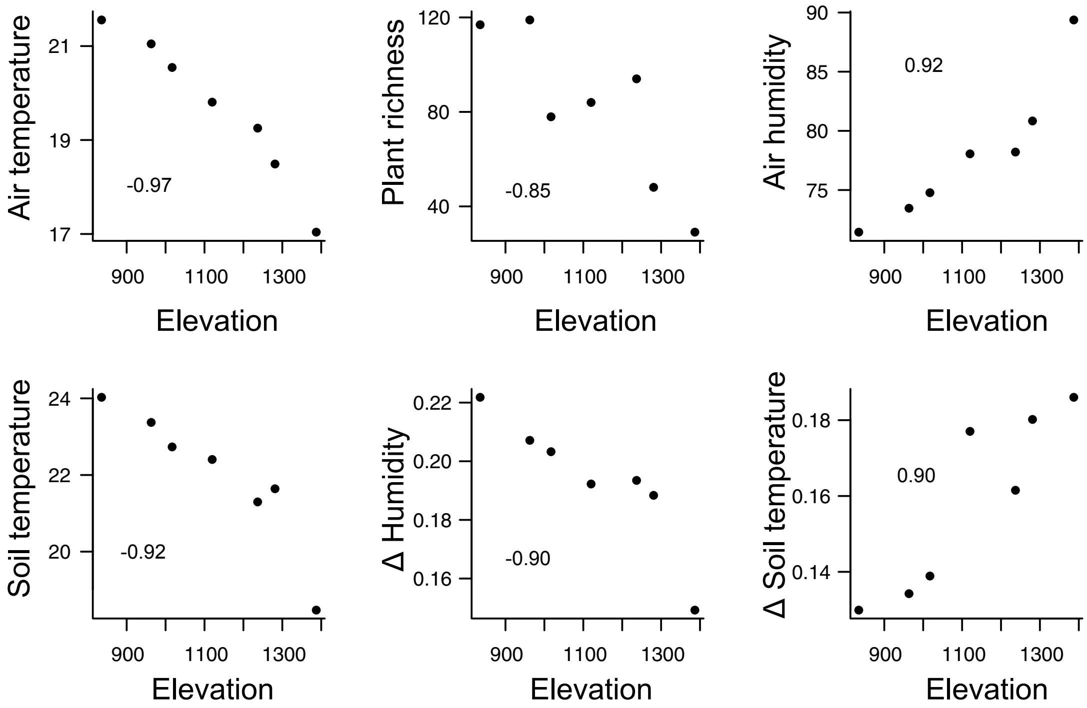

FIGURE 3 | Correlations between elevation and environmental variables. Mean air temperature, soil temperature, plant richness and the variation of air humidity decrease with elevation, while mean air humidity and the variation of soil temperature increase with elevation. All presented Pearson correlations are significant under $\alpha = 0.05$. Δ is coefficient of variation while the other variables represent mean values. Numbers inside the plots represent the coefficient of correlation. Data of plant richness from Mota et al. (2018). Data of climatic variables sampled using meteorological monitoring towers during 12 periods along an elevational gradient in Serra do Cipó, Minas Gerais State – Brazil.

respectively (Baselga and Orme, 2012), in the software R (R Core Team, 2019).

Statistical Analyses

We ran Pearson correlation analyses with all the environmental variables against elevation using the "psych" R package (Revelle, 2017). As elevation was correlated with mean air and soil temperature, air humidity, plant richness and the temporal variation of air humidity and soil temperature (see details in section "Results"), we used elevation as a proxy for all these variables in our analyses. To test our first hypothesis, we ran linear mixed-effect models (LMMs), one with TD β-diversity as response variable and other with FD β-diversity (β_{SOR}), and both had elevation as an independent variable and sampling site as a random variable. To test our second hypothesis, we used the turnover contribution (β_{SIM}/β_{SOR}) as the response variable and also ran separate LMMs for TD and FD, with elevation as an independent variable and sampling site as a random variable. We checked for the error distribution and over-dispersion of the data. All statistical analyses were performed in R (R Core Team, 2019).

RESULTS

We recorded a total of 155 ant morphospecies (species hereafter), belonging to eight subfamilies and 49 genera. Myrmicinae was the most representative subfamily with 25 of the identified genera, followed by Ponerinae (eight), Dolichoderinae (five), Dorylinae (four), and Formicinae (three). The subfamilies with the highest species richness were Myrmicinae (85 species), Formicinae (23 species), Ponerinae and Dolichoderinae (12 species each). These four subfamilies accounted for 85% of the species sampled. The genera with most species were *Pheidole* with 25 species, *Camponotus* 20 species, and *Solenopsis* with eight species. Across all samples, we recorded 13 doubletons and 23 singletons (23.2%).

We found that mean air and soil temperatures, plant richness, and coefficient of variation of air humidity were negatively correlated with elevation, whereas mean air humidity, and coefficient of variation of soil temperature were positively correlated with elevation (**Figure 3** and **Supplementary Table 1**). That is, mean air and soil temperature, plant richness and the temporal variation of humidity decrease with increasing elevation, while air humidity and the temporal variation of soil temperature increase with increasing elevation (**Figure 3**). We also found that precipitation dropped from ~170 mm to close to 0, while mean air temperature dropped from 21.1 to 17.2°C in the beginning of the wet season to the beginning of the dry season, respectively (**Figure 4**). Air and soil humidity mirrored this pattern of decrease from the wet to the dry season (**Figure 4**).

The main driver of temporal taxonomic β-diversity was the turnover component (β_{SIM}) with 86% of contribution. In contrast, nestedness (β_{SNE}) was the main component to temporal

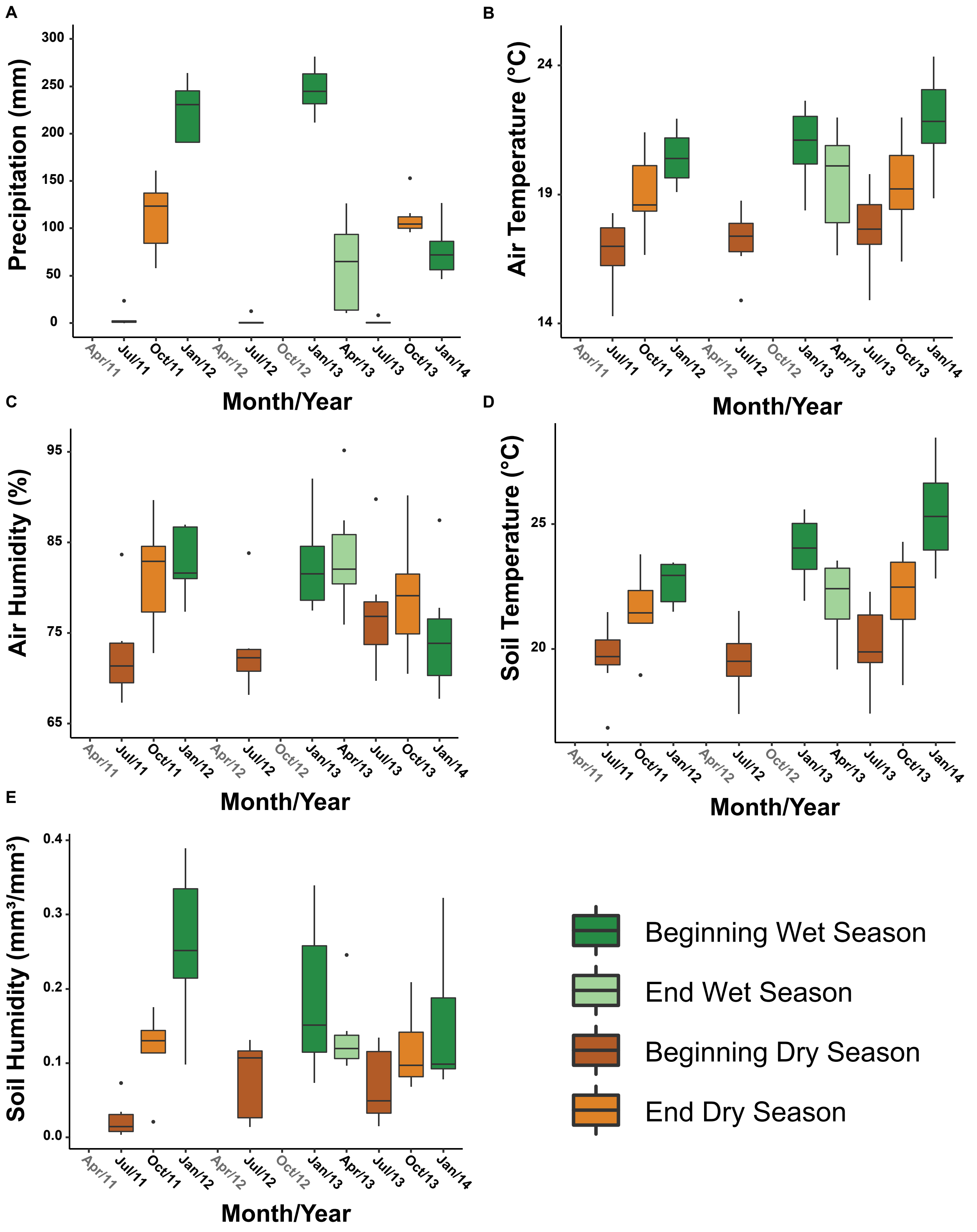

FIGURE 4 | Variation of **(A)** precipitation, **(B)** air temperature, **(C)** air humidity, **(D)** soil temperature, and **(E)** soil humidity over 12 periods in the beginning and end of wet and dry seasons. The boxplots represent the variation of the mean values of the seven sampling sites (different elevations) in each month/year. Data sampled using meteorological monitoring towers along an elevational gradient in Serra do Cipó, Minas Gerais State – Brazil.

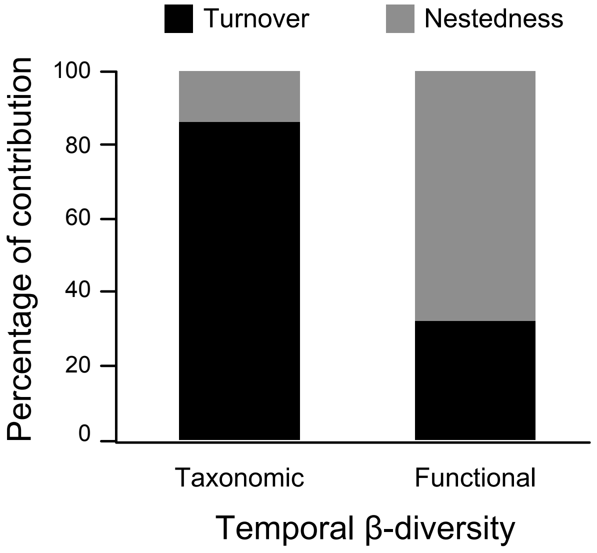

FIGURE 5 | Contribution of turnover and nestedness components to temporal taxonomic and functional β-diversity of ant metacommunity in Serra do Cipó, Minas Gerais State – Brazil. Data from 12 sampling periods between April 2011 and January 2014.

functional β-diversity with 67% of contribution across the entire gradient (**Figure 5**).

Neither temporal taxonomic nor functional β-diversity were influenced by elevation [TD: $\chi_{(1,19)} = 1.02$, $p = 0.31$; FD: $\chi_{(1,19)} = 1.86$, $p = 0.17$; **Figure 6A**]. Turnover (β_{SIM}) was the main driver of temporal taxonomic β-diversity with a consistent pattern along the entire elevation gradient [contribution always higher than 80%; $\chi_{(1,19)} = 0.24$, $p = 0.62$; **Figure 6B**]. In contrast, temporal functional turnover contribution increased with elevation [$\chi_{(1,19)} = 5.22$, $p < 0.05$, pseudo-$R^2 = 0.22$], going from less than 20% in lower elevations to more than 50% in higher elevations (**Figure 6B**).

DISCUSSION

We found that ant communities had remarkably high temporal taxonomic and functional β-diversity. Contrary to our first hypothesis, values of temporal taxonomic and functional β-diversity are high irrespective of their position along the elevational gradient. Partially in line with our second hypothesis, turnover was the main component of temporal taxonomic β-diversity along the gradient (above 80% of contribution). However, the contribution of nestedness to temporal functional β-diversity decreased significantly with elevation. We propose that ant activity is very sensitive to temporal variation in environmental conditions, and mainly temperature (Costa et al., 2018; Castro et al., 2020). The effect on ant community composition is then the same along the elevational gradient, with both species and functional traits highly variable over time at all elevations. Although ant metacommunities are changing over time, at low elevations the turnover in species composition may cause changes in trait composition because of the loss of some traits, but probably preserving the most common functions (nested functional communities). In contrast, at higher elevations, the turnover in species composition cause changes in the set of functions performed over time (i.e., temporal turnover of traits).

The *campo rupestre* has two well-defined seasons: a wet season that is also hot (∼170 mm/month and mean temperature of 21.1°C), and a dry season that is cold (close to 0 mm/month and 17.2°C). The changes in temperature and humidity impose changes in plant productivity (Rocha et al., 2016) and animal activity (especially the ectothermic animals; e.g., Costa et al., 2018). Indeed, temporal changes in temperature, humidity and resource availability are known to influence ant foraging activity (Calazans et al., 2020) and consequently the diversity and composition of communities. However, we found high levels of species and trait composition changes along the entire elevation gradient, contrary to our expectations. We propose two non-exclusive hypotheses to explain this result: (i) the sensitivity of ant communities in tropical mountains to changes in environmental conditions (Longino and Colwell, 2011; Castro et al., 2020; Lasmar et al., 2020) are enough to impose drastic changes in species and trait composition; ii. ant communities are regulated by the minimum humidity at low elevations, while the highland ant communities are regulated by the minimum temperature, consistent with our finding that the variation of temperature increases with elevation, while the variation in humidity decreases. Bishop et al. (2017) found that ants are constrained more by the critical thermal minimum temperature (CTmin) than by the maximum in a southern African mountain. Accordingly, Calazans et al. (2020) found, in a study in *campo rupestre*, that ant activity increased with temperature, but most species were not active under 20°C. Although highland ants would probably have a lower CTmin, the higher variation on temperature at high elevations could filter different species and traits in different seasons.

We found that turnover was the main mechanism generating temporal taxonomic β-diversity, as expected based on the spatial pattern for ants and many other organisms (Perillo et al., 2017; da Silva et al., 2018; Kaltsas et al., 2018; Castro et al., 2020). The spatial variation in conditions and resources provide an environmental filter for species that have pre-adaptations to survive in different places (Heino and Tolonen, 2017; García-Llamas et al., 2019) leading to high rates of turnover of species. In this sense, the same processes would be occurring to generate the temporal pattern but related to ant activity: environmentally filtering ant species to be active in different seasons along all the elevational gradient. In contrast, functional β-diversity is generated by a higher contribution of nestedness in spatial patterns (Nunes et al., 2016, 2017; Castro et al., 2020) especially on elevational gradients, showing high functional redundancy. In our study, at lowlands the temporal pattern mirrors the spatial and nestedness contributes 80% of functional β-diversity (i.e., 20% turnover, **Figure 6B**). However, the importance of turnover in functional diversity increases with elevation, reaching more than 50% in some highlands. The changes in species composition, caused by a change in the set of active species, lead to creation

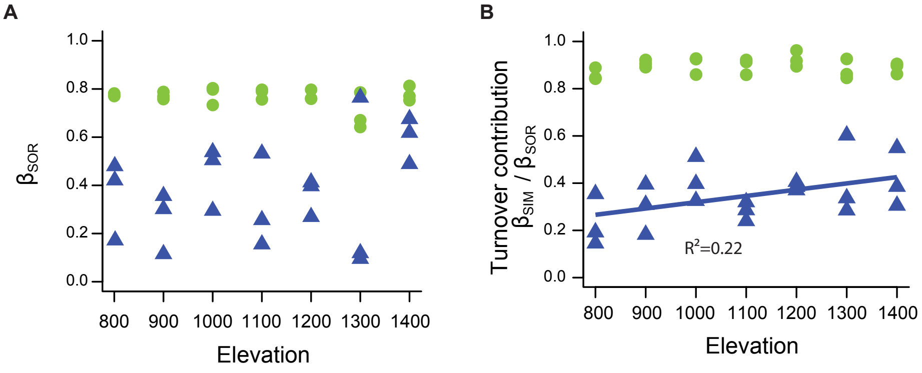

FIGURE 6 | Temporal taxonomic (green dots) and functional (blue triangles) β-diversity of ants along a tropical elevational gradient in Brazil. **(A)** Values of temporal β-diversity (β_{SOR}) were not correlated with elevation and were always high, both for temporal taxonomic and functional diversity. **(B)** Temporal turnover contribution (β_{SIM}/β_{SOR}) to β-diversity was always high for taxonomic diversity whereas it increased with elevation for functional diversity. Data from ant communities sampled in 12 periods along an elevation gradient in Serra do Cipó, Minas Gerais State – Brazil. The figure represents four separated models (see section "Materials and Methods").

of subsets of traits among seasons, with a more complete set in hot and dry season and a subset of the most common traits in dry and cold season. However, at higher elevations on the gradient, increasing trait turnover can create a greater variation in trait combinations over space and time. This means that lower elevation ant metacommunities are more functionally resistant to changes in species composition, having greater functional redundancy over time while higher elevation metacommunities are more functionally sensitive to changes in species composition across the seasons.

Contextualizing our results within the metacommunity framework, we can propose that ant diversity is explained by a combination of the species sorting and the mass effect models (Leibold et al., 2004; Soininen, 2014). We found a high β-diversity and turnover contribution in our study, showing that environmental conditions and resources are filtering the species comprising the ant metacommunity (i.e., species sorting; Leibold and Chase, 2018). Due to high environmental heterogeneity across the elevational gradient, if we are looking at different sites (e.g., different elevations or different habitats) or different times (e.g., different seasons) we expect to find different ant species compositions. Conversely, generalist ant species may have access to different habitats with different conditions through dispersal and can establish long term populations (e.g., Neves et al., 2020), maintaining the mass effect. Therefore, although environmental filters are strong in spatially and temporally regulating the ant metacommunity (species sorting), some ant species can disperse, overcoming local niche limitations and establish populations in different sites following close-to-optimal conditions (mass effects). In both cases, we observe a greater importance of environmental than dispersal-related factors, a pattern expected when there is high environmental heterogeneity (e.g., He et al., 2020).

Implications for Conservation

Our study builds on growing evidence that montane tropical insects are highly sensitive to local climatic and environmental changes (e.g., Longino and Colwell, 2011; Lasmar et al., 2020). The studied ant metacommunities are highly variable over time along the entire elevational gradient. Montane insect assemblages are thought to be very vulnerable to global warming (Laurance et al., 2011), because with increasing temperature, these organisms are expected to shift their elevational ranges, leading to mountaintop extinctions (Colwell et al., 2008). As there is growing evidence that climate change affects both temperature and precipitation regimes (e.g., Romero et al., 2020) and also the occurrence and intensity of extreme climatic events (e.g., Fischer and Knutti, 2015; Patricola and Wehner, 2018), we may expect that such increase in climatic variation and instability will drastically affect ant metacommunities. With this higher temporal variation in conditions and resources, we might lose the rarer and specialized species (Davies et al., 2004) that cannot survive the new environmental filter, leading to the homogenisation of the metacommunity (Newbold et al., 2019). In plants, generalist species tend to be functionally closer, i.e., have high functional redundancy (Denelle et al., 2020), and in assemblages with homogenized species composition we may observe a loss of functional traits and consequently, ecological functions (Newbold et al., 2019). In addition, species that show temporal shutdown in their activity, are likely to be more active year-round as the climate warms (Costa et al., 2018), potentially increasing competition, although the outcome of competitive interactions will likely be influenced by the prevailing combination of temperature and humidity. Furthermore, as we identified an increasing importance of functional temporal turnover along the elevational gradient, we expect that the higher climatic variation associated with climate change (Fischer and Knutti, 2015) will favor generalist species within communities. This, in turn, will result in the homogenisation of the set of functions performed in different seasons. With mountaintop extinctions, elevational range shifts, and taxonomic and functional homogenisation of assemblages, ecosystem functions provided by ants will be severely jeopardized in tropical mountains under global climatic changes.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

CAN, FN, SP, and RS: study design. GF and FN: project funding. HB and FC: data collection. CAN, FC, and FN: data analyses. CAN, FC, HB, SP, RS, GF, and FN: writing the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.571439/full#supplementary-material

Supplementary Figure 1 | Community weighted mean (CWM) values of continuous traits of ant metacommunities during four periods of the year: the beginning and end of wet and dry seasons.

Supplementary Table 1 | Correlations between environmental variables.

Supplementary Table 2 | Functional traits and temporal data used in data analyses.

REFERENCES

Andersen, A. N. (1995). A Classification of Australian Ant Communities, Based on Functional Groups Which Parallel Plant Life-Forms in Relation to Stress and Disturbance. *J. Biogeogr.* 22, 15–29. doi: 10.2307/2846070

Arnan, X., Andersen, A. N., Gibb, H., Parr, C. L., Sanders, N. J., Dunn, R. R., et al. (2018). Dominance-diversity relationships in ant communities differ with invasion. *Glob. Chang. Biol.* 24, 4614–4625. doi: 10.1111/gcb.14331

Baccaro, F. B., Feitosa, R. M., Fernandez, F., Fernandes, I. O., Izzo, T. J., Souza, J. L. P., et al. (2015). *Guia para os gêneros de formigas do Brasil.* Manaus: INPA. doi: 10.5281/zenodo.32912

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Glob. Ecol. Biogeogr.* 19, 134–143. doi: 10.1111/j.1466-8238.2009.00490.x

Baselga, A., and Orme, C. D. L. (2012). betapart?: an R package for the study of beta diversity. *Methods Ecol. Evol.* 3, 808–812. doi: 10.1111/j.2041-210X.2012.00224.x

Basset, Y., Cizek, L., Cuénoud, P., Didham, R. K., Novotny, V., Ødegaard, F., et al. (2015). Arthropod Distribution in a Tropical Rainforest: Tackling a Four Dimensional Puzzle. *PLoS One* 10:e0144110. doi: 10.1371/journal.pone.0144110

Bestelmeyer, B. T., Agosti, D., Alonso, L. E., Brandão, C. R. F., Brown, W. L. Jr., Delabie, J. H. C., et al. (2000). "Field Techniques for the Study of Ground-Dwelling Ants: An Overview, Description and Evaluation," in *Ants: standard methods for measuring and monitoring biodiversity*, eds D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz, (Washington, DC: Smithsonian Institution Press), 122–144.

Bishop, T. R., Robertson, M. P., Gibb, H., van Rensburg, B. J., Braschler, B., Chown, S. L., et al. (2016). Ant assemblages have darker and larger members in cold environments. *Glob. Ecol. Biogeogr.* 25, 1489–1499. doi: 10.1111/geb.12516

Bishop, T. R., Robertson, M. P., van Rensburg, B. J., and Parr, C. L. (2014). Elevation-diversity patterns through space and time: ant communities of the Maloti-Drakensberg Mountains of southern Africa. *J. Biogeogr.* 41, 2256–2268. doi: 10.1111/jbi.12368

Bishop, T. R., Robertson, M. P., van Rensburg, B. J., and Parr, C. L. (2015). Contrasting species and functional beta diversity in montane ant assemblages. *J. Biogeogr.* 42, 1776–1786. doi: 10.1111/jbi.12537

Bishop, T. R., Robertson, M. P., Van Rensburg, B. J., and Parr, C. L. (2017). Coping with the cold: minimum temperatures and thermal tolerances dominate the ecology of mountain ants. *Ecol. Entomol.* 42, 105–114. doi: 10.1111/een.12364

Bolton, B. (2020). *An online catalog of the ants of the world.* Available Online at: https://antcat.org (accessed February 6, 2019).

Brandão, C. R. F., Silva, R. R., and Delabie, J. H. C. (2009). "Formigas (Hymenoptera)," in *Bioecologia e Nutrição de Insetos. Base para o Manejo Integrado de Pragas*, eds A. R. Panizzi, and J. R. P. Parra, (Brasília: EMBRAPA), 323–369.

Calazans, E. G., Costa, F. V. d, Cristiano, M. P., and Cardoso, D. C. (2020). Daily Dynamics of an Ant Community in a Mountaintop Ecosystem. *Environ. Entomol.* 49, 383–390. doi: 10.1093/ee/nvaa011

Castro, D. M. P., Callisto, M., Solar, R. R. C., Macedo, D. R., and Fernandes, G. W. (2019). Beta diversity of aquatic invertebrates increases along an altitudinal gradient in a Neotropical mountain. *Biotropica* 51, 399–411. doi: 10.1111/btp.12660

Castro, F. S. d, Da Silva, P. G., Solar, R., Fernandes, G. W., and Neves, F. d. S (2020). Environmental drivers of taxonomic and functional diversity of ant communities in a tropical mountain. *Insect Conserv. Divers* 13, 393–403. doi: 10.1111/icad.12415

Colwell, R. K., Brehm, G., Cardelús, C. L., Gilman, A. C., and Longino, J. T. (2008). Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* 322, 258–261. doi: 10.1126/science.1162547

Costa, F. V., Blüthgen, N., Viana-Junior, A. B., Guerra, T. J., Di Spirito, L., and Neves, F. S. (2018). Resilience to fire and climate seasonality drive the temporal dynamics of ant-plant interactions in a fire-prone ecosystem. *Ecol. Indic.* 93, 247–255. doi: 10.1016/j.ecolind.2018.05.001

Crist, T. O., Veech, J. A., Gering, J. C., and Summerville, K. S. (2003). Partitioning species diversity across landscapes and regions: a hierarchical analysis of alpha, beta, and gamma diversity. *Am. Nat.* 162, 734–743. doi: 10.1086/378901 da Silva, P. G., Lobo, J. M., Hensen, M. C., Vaz-de-Mello, F. Z., and Hernández, M. I. M. (2018). Turnover and nestedness in subtropical dung beetle assemblages along an elevational gradient. *Divers. Distrib.* 24, 1277–1290. doi: 10.1111/ddi.12763

Datry, T., Bonada, N., and Heino, J. (2016). Towards understanding the organisation of metacommunities in highly dynamic ecological systems. *Oikos* 125, 149–159. doi: 10.1111/oik.02922

Davies, K. F., Margules, C. R., and Lawrence, J. F. (2004). A synergistic effect puts rare, specialized species at greater risk of extinction. *Ecology* 85, 265–271.

de Bello, F., Carmona, C. P., Mason, N. W. H., Sebastià, M.-T., and Lepš, J. (2013). Which trait dissimilarity for functional diversity: trait means or trait overlap? *J. Veg. Sci.* 24, 807–819. doi: 10.1111/jvs.12008

Denelle, P., Violle, C., and Munoz, F. (2020). Generalist plants are more competitive and more functionally similar to each other than specialist plants: insights from network analyses. *J. Biogeogr.* 47, 1922–1933. doi: 10.1111/jbi.13848

Domingues, S. A., Karez, C. S., Biondini, I. V. F., and Andrade, M. Â (2011). "Instrumentos económicos de gestión ambiental en la Reserva de Biosfera de la Serra do Espinhaço," in *UNESCO Regional Office for Science for Latin America and the Caribbean**, eds I. Sachs, M. Clüsener-Godt, and C. S. Karez Montevideo.

Farji-Brener, A. G., and Werenkraut, V. (2017). The effects of ant nests on soil fertility and plant performance: a meta-analysis. *J. Anim. Ecol.* 86, 866–877. doi: 10.1111/1365-2656.12672

Feener, D. H., Lighton, J. R. B., and Bartholomew, G. A. (1988). Curvilinear Allometry, Energetics and Foraging Ecology: A Comparison of Leaf-Cutting Ants and Army Ants. *Funct. Ecol.* 2, 509–520. doi: 10.2307/2389394

Fernandes, G. W., et al. (2016). *Ecology and Conservation of Mountaintop grasslands in Brazil*. Cham: Springer International Publishing.

Fernandes, G. W., Almeida, H. A., Nunes, C. A., Xavier, J. H. A., Cobb, N. S., Carneiro, M. A. A., et al. (2016). "Cerrado to Rupestrian Grasslands: Patterns of Species Distribution and the Forces Shaping Them Along an Altitudinal Gradient," in *Ecology and Conservation of Mountaintop grasslands in Brazil*, ed. G. W. Fernandes, (Dordrecht: Springer), 345–377. doi: 10.1007/978-3-319-29808-5_15

Fernandes, G. W., Barbosa, N. P. U., Alberton, B., Barbieri, A., Dirzo, R., Goulart, F., et al. (2018). The deadly route to collapse and the uncertain fate of Brazilian rupestrian grasslands. *Biodivers. Conserv.* 27, 2587–2603. doi: 10.1007/s10531-018-1556-1554

Fichaux, M., Béchade, B., Donald, J., Weyna, A., Delabie, J. H. C., Murienne, J., et al. (2019). Habitats shape taxonomic and functional composition of Neotropical ant assemblages. *Oecologia* 189, 501–513. doi: 10.1007/s00442-019-04341-z

Fischer, E. M., and Knutti, R. (2015). Anthropogenic contribution to global occurrence of heavy-precipitation and high-temperature extremes. *Nat. Clim. Chang.* 5, 560–564. doi: 10.1038/nclimate2617

García-Llamas, P., Rangel, T. F., Calvo, L., and Suárez-Seoane, S. (2019). Linking species functional traits of terrestrial vertebrates and environmental filters: A case study in temperate mountain systems. *PLoS One* 14:1–15. doi: 10.1371/journal.pone.0211760

Gaston, K. J. (2000). Global patterns in biodiversity. *Nature* 405, 220–227. doi: 10.1038/35012228

Gibb, H., and Cunningham, S. A. (2013). Restoration of trophic structure in an assemblage of omnivores, considering a revegetation chronosequence. *J. Appl. Ecol.* 50, 449–458. doi: 10.1111/1365-2664.12054

Guénard, B., Weiser, M. D., Gómez, K., Narula, N., and Economo, E. P. (2017). The Global Ant Biodiversity Informatics (GABI) database: Synthesizing data on the geographic distribution of ant species (Hymenoptera: Formicidae). *Myrmecol. News* 24, 83–89.

He, S., Soininen, J., Chen, K., and Wang, B. (2020). Environmental factors override dispersal-related factors in shaping diatom and macroinvertebrate communities within stream networks in China. *Front. Ecol. Evol.* 8:1–11. doi: 10.3389/fevo.2020.00141

Heino, J., Melo, A. S., Siqueira, T., Soininen, J., Valanko, S., and Bini, L. M. (2015). Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. *Freshw. Biol.* 60, 845–869. doi: 10.1111/fwb.12533

Heino, J., and Tolonen, K. T. (2017). Ecological drivers of multiple facets of beta diversity in a lentic macroinvertebrate metacommunity. *Limnol. Oceanogr.* 62, 2431–2444. doi: 10.1002/lno.10577

Johnson, R. A. (2015). A taxonomic revision of South American species of the seed-harvester ant genus Pogonomyrmex (Hymenoptera: Formicidae). Part I. *Zootaxa* 4029, 1–142. doi: 10.11646/zootaxa.4029.1.1

Kaltsas, D., Dede, K., Giannaka, J., Nasopoulou, T., Kechagioglou, S., Grigoriadou, E., et al. (2018). Taxonomic and functional diversity of butterflies along an altitudinal gradient in two NATURA 2000 sites in Greece. *Insect Conserv. Divers.* 11, 464–478. doi: 10.1111/icad.12292

Kaspari, M., and Weiser, M. D. (1999). The size–grain hypothesis and interspecific scaling in ants. *Funct. Ecol.* 13, 530–538. doi: 10.1046/j.1365-2435.1999.00343.x

Körner, C. (2007). The use of "altitude" in ecological research. *Trends Ecol. Evol.* 22, 569–574. doi: 10.1016/j.tree.2007.09.006

Lasmar, C. J., Ribas, C. R., Louzada, J., Queiroz, A. C. M., Feitosa, R. M., Imata, M. M. G., et al. (2020). Disentangling elevational and vegetational effects on ant diversity patterns. *Acta Oecol.* 102:103489. doi: 10.1016/j.actao.2019.103489

Laurance, W. F., Carolina Useche, D., Shoo, L. P., Herzog, S. K., Kessler, M., Escobar, F., et al. (2011). Global warming, elevational ranges and the vulnerability of tropical biota. *Biol. Conserv.* 144, 548–557. doi: 10.1016/j.biocon.2010.10.010

Leal, I. R., Filgueiras, B. K. C., Gomes, J. P., Iannuzzi, L., and Andersen, A. N. (2012). Effects of habitat fragmentation on ant richness and functional composition in Brazilian Atlantic forest. *Biodivers. Conserv.* 21, 1687–1701. doi: 10.1007/s10531-012-0271-279

Legendre, P., and Condit, R. (2019). Spatial and temporal analysis of beta diversity in the Barro Colorado Island forest dynamics plot, Panama. *For. Ecosyst.* 6:7. doi: 10.1186/s40663-019-0164-164

Leibold, M. A., and Chase, J. M. (2018). *Metacommunity ecology*. Princeton: Princeton University Press.

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., et al. (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.* 7, 601–613. doi: 10.1111/j.1461-0248.2004.00608.x

Lenoir, A., Aron, S., Cerdá, X., and Hefetz, A. (2009). Cataglyphis desert ants: a good model for evolutionary biology in Darwin's anniversary year - A review. *Isr. J. Entomol.* 39, 1–32.

Leponce, M., Theunis, L., Delabie, J. H. C., and Roisin, Y. (2004). Scale dependence of diversity measures in a leaf-litter ant assemblage. *Ecography* 27, 253–267.

Levins, R. (1969). Some Demographic and Genetic Consequences of Environmental Heterogeneity for Biological Control. *Bull. Entomol. Soc. Am.* 15, 237–240. doi: 10.1093/besa/15.3.237

Lewis, S. L., and Maslin, M. A. (2015). Defining the Anthropocene. *Nature* 519, 171–180. doi: 10.1038/nature14258

Li, N., Chu, H., Qi, Y., Li, C., Ping, X., Sun, Y., et al. (2019). Alpha and beta diversity of birds along elevational vegetation zones on the southern slope of Altai Mountains: Implication for conservation. *Glob. Ecol. Conserv.* 19:e00643. doi: 10.1016/j.gecco.2019.e00643

Longino, J. T., and Colwell, R. K. (2011). Density compensation, species composition, and richness of ants on a neotropical elevational gradient. *Ecosphere* 2:art29. doi: 10.1890/ES10-00200.1

Magalhães, V. B., Espírito Santo, N. B., Salles, L. F. P., Soares, H., and Oliveira, P. S. (2018). Secondary seed dispersal by ants in Neotropical cerrado savanna: species-specific effects on seeds and seedlings of Siparuna guianensis (Siparunaceae). *Ecol. Entomol.* 43, 665–674. doi: 10.1111/een.12640

Morellato, L. P. C., and Silveira, F. A. O. (2018). Plant life in campo rupestre?: New lessons from an ancient biodiversity hotspot. *Flora* 238, 1–10. doi: 10.1016/j.flora.2017.12.001

Mota, G. S., Luz, G. R., Mota, N. M., Silva Coutinho, E., das Dores, Magalhães Veloso, M., et al. (2018). Changes in species composition, vegetation structure, and life forms along an altitudinal gradient of rupestrian grasslands in south-eastern Brazil. *Flora* 238, 32–42. doi: 10.1016/j.flora.2017.03.010

Nation, J. L. (2008). "Integument: Structure and Function," in *Encyclopedia of Entomology*, ed. J. L. Capinera, (Netherlands: Springer), 2015–2019. doi: 10.1007/978-1-4020-6359-6_1557

Neves, F. D. S., da Silva, P. G., Solar, R., Nunes, C. A., Beirão, M. D. V., Brant, H., et al. (2020). Habitat generalists drive nestedness in a tropical mountaintop insect metacommunity. *Biol. J. Linn. Soc.* 2020:blaa059. doi: 10.1093/biolinnean/blaa059

Newbold, T., Adams, G. L., Albaladejo Robles, G., Boakes, E. H., Braga Ferreira, G., Chapman, A. S. A., et al. (2019). Climate and land-use change homogenise terrestrial biodiversity, with consequences for ecosystem functioning and human well-being. *Emerg. Top. Life Sci.* 3, 207–219. doi: 10.1042/ETLS20180135

Novais, S. M. A., Monteiro, G. F., Macedo-Reis, L. E., Leal, C. R. O., and Neves, F. D. S. (2019). Changes in the insect herbivore fauna after the first rains in a tropical dry forest. *Oecol. Aust.* 23, 381–387. doi: 10.4257/oeco.2019.2302.16

Nunes, C. A., Braga, R. F., Figueira, J. E. C., Neves, F. D. S., and Fernandes, G. W. (2016). Dung beetles along a tropical altitudinal gradient: environmental filtering on taxonomic and functional diversity. *PLoS One* 11:e0157442. doi: 10.1371/journal.pone.0157442

Nunes, C. A., Quintino, A. V., Constantino, R., Negreiros, D., Reis Júnior, R., and Fernandes, G. W. (2017). Patterns of taxonomic and functional diversity of termites along a tropical elevational gradient. *Biotropica* 49, 186–194. doi: 10.1111/btp.12365

Paolucci, L. N., Maia, M. L. B., Solar, R. R. C., Campos, R. I., Schoereder, J. H., and Andersen, A. N. (2016). Fire in the Amazon: impact of experimental fuel addition on responses of ants and their interactions with myrmecochorous seeds. *Oecologia* 182, 335–346. doi: 10.1007/s00442-016-3638-x

Parr, C. L., Dunn, R. R., Sanders, N. J., Weiser, M. D., Photakis, M., Bishop, T. R., et al. (2017). GlobalAnts?: a new database on the geography of ant traits (Hymenoptera: Formicidae). *Insect Conserv. Divers.* 10, 5–20. doi: 10.1111/icad.12211

Patricola, C. M., and Wehner, M. F. (2018). Anthropogenic influences on major tropical cyclone events. *Nature* 563, 339–346. doi: 10.1038/s41586-018-0673-672

Perillo, L. N., Neves, F. D. S., Antonini, Y., and Martins, R. P. (2017). Compositional changes in bee and wasp communities along Neotropical mountain altitudinal gradient. *PLoS One* 12:e0182054. doi: 10.1371/journal.pone.0182054

Peters, M. K., Hemp, A., Appelhans, T., Behler, C., Classen, A., Detsch, F., et al. (2016). Predictors of elevational biodiversity gradients change from single taxa to the multi-taxa community level. *Nat. Commun.* 7:13736. doi: 10.1038/ncomms13736

R Core Team (2019). *R: A language and environment for statistical computing*. Vienna: R Core Team

Revelle, W. R. (2017). *psych: Procedures for Personality and Psychological Research. R Package Version 1.8.4*.

Rocha, N. M. W. B., Carstensen, D. W., Fernandes, G. W., Le Stradic, S., Buisson, E., and Morellato, L. P. C. (2016). "Phenology Patterns Across a Rupestrian Grassland Altitudinal Gradient," in *Ecology and Conservation of Mountaintop grasslands in Brazil*, ed. G. W. Fernandes, (Cham: Springer International Publishing), 275–289. doi: 10.1007/978-3-319-29808-5_12

Romero, G. Q., Marino, N. A. C., MacDonald, A. A. M., Ceìrèighino, R., Trzcinski, M. K., Mercado, D. A., et al. (2020). Extreme rainfall events alter the trophic structure in bromeliad tanks across the Neotropics. *Nat. Commun.* 11:3215. doi: 10.1038/s41467-020-17036-17034

Ruhí, A., Datry, T., and Sabo, J. L. (2017). Interpreting beta-diversity components over time to conserve metacommunities in highly dynamic ecosystems. *Conserv. Biol.* 31, 1459–1468. doi: 10.1111/cobi.12906

Schiesari, L., Matias, M. G., Prado, P. I., Leibold, M. A., Albert, C. H., Howeth, J. G., et al. (2019). Towards an applied metaecology. *Perspect. Ecol. Conserv.* 17, 172–181. doi: 10.1016/j.pecon.2019.11.001

Silveira, F. A. O., Barbosa, M., Beiroz, W., Callisto, M., Macedo, D. R., Morellato, L. P. C., et al. (2019). Tropical mountains as natural laboratories to study global changes: A long-term ecological research project in a megadiverse biodiversity hotspot. *Perspect. Plant Ecol. Evol. Syst.* 38, 64–73. doi: 10.1016/j.ppees.2019.04.001

Silveira, F. A. O., Negreiros, D., Barbosa, N. P. U., Buisson, E., Carmo, F. F., Carstensen, D. W., et al. (2016). Ecology and evolution of plant diversity in the endangered campo rupestre: a neglected conservation priority. *Plant Soil* 403, 129–152. doi: 10.1007/s11104-015-2637-2638

Soininen, J. (2014). A quantitative analysis of species sorting across organisms and ecosystems. *Ecology* 95, 3284–3292. doi: 10.1890/13-2228.1

Sutherland, W. J., Freckleton, R. P., Godfray, H. C. J., Beissinger, S. R., Benton, T., Cameron, D. D., et al. (2013). Identification of 100 fundamental ecological questions. *J. Ecol.* 101, 58–67. doi: 10.1111/1365-2745.12025

Terblanche, J. S. (2012). "Thermal relations," in *The Insects: Structure and Function*, eds R. F. Chapman, S. J. Simpson, and A. E. Douglas, (New York: Cambridge University Press), 588–621.

Tiede, Y., Schlautmann, J., Donoso, D. A., Wallis, C. I. B., Bendix, J., Brandl, R., et al. (2017). Ants as indicators of environmental change and ecosystem processes. *Ecol. Indic.* 83, 527–537. doi: 10.1016/j.ecolind.2017.01.029

Trullas, S. C., van Wyk, J. H., and Spotila, J. R. (2007). Thermal melanism in ectotherms. *J. Therm. Biol.* 32, 235–245. doi: 10.1016/j.jtherbio.2007.01.013

von Humboldt, A., and Bonpland, A. (1805). *Essai sur la géographie des plantes*. Paris: Librarie Lebrault Schoell.

Weber, N. A. (1938). The biology of the fungus-growing ants. Part IV. Additional new forms. Part V. The Attini of Bolivia. Biología de las hormigas cultivadoras de hongos. Parte IV. Nuevas formas adicionales. Part V. Las Attini de Bolivia. *Rev. Entomol.* 7, 154–206.

Wills, B. D., Powell, S., Rivera, M. D., and Suarez, A. V. (2017). Correlates and Consequences of Worker Polymorphism in Ants. *Annu. Rev. Entomol.* 63, 575–598. doi: 10.1146/annurev-ento-020117-043357

Yates, M. L., Andrew, N. R., Binns, M., and Gibb, H. (2014). Morphological traits: predictable responses to macrohabitats across a 300 km scale. *PeerJ* 2:e271. doi: 10.7717/peerj.271

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Rethinking Biological Invasions as a Metacommunity Problem

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Perhaps more than any other ecological discipline, invasion biology has married the practices of basic science and the application of that science. The conceptual frameworks of population regulation, metapopulations, supply-side ecology, and community assembly have all to some degree informed the regulation, management, and prevention of biological invasions. Invasion biology needs to continue to adopt emerging frameworks and paradigms to progress as both a basic and applied science. This need is urgent as the biological invasion problem continues to worsen. The development of metacommunity theory in the last two decades represents a paradigm-shifting approach to community ecology that emphasizes the multi-scale nature of community assembly and biodiversity regulation. Work on metacommunities has demonstrated that even relatively simple processes at local scales are often heavily influenced by regional-scale processes driven primarily by the dispersal of organisms. Often the influence of dispersal interacts with, or even swamps, the influence of local-scale drivers like environmental conditions and species interactions. An emphasis on dispersal and a focus on multi-scale processes enable metacommunity theory to contribute strongly to the advancement of invasion biology. Propagule pressure of invaders has been identified as one of the most important drivers facilitating invasion, so the metacommunity concept, designed to address how dispersal-driven dynamics affect community structure, can directly address many of the central questions of invasion biology. Here we revisit many of the important concepts and paradigms of biological invasions—propagule pressure, biotic resistance, enemy release, functional traits, neonative species, human-assisted transport,—and view those concepts through the lens of metacommunity theory. In doing so, we accomplish several goals. First, we show that work on metacommunities has generated multiple predictions, models, and the tools that can be directly applied to invasion scenarios. Among these predictions is that invasibility of a community should decrease with both local controls on community assembly, and the dispersal rates of native species. Second, we demonstrate that framing biological invasions in metacommunity terms actually unifies several seemingly disparate concepts central to invasion biology. Finally, we recommend several courses of action for the control and management of invasive species that emerge from applying the concepts of metacommunity theory.

Keywords: biotic resistance, community ecology, dispersal, invasive species, invasibility, propagule pressure, mass effect hypothesis, sorting strength

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INVASION AS A METACOMMUNITY PROBLEM

By its very nature, invasion biology demands a partnership between the basic and applied aspects of ecology and environmental science. However, the field has also struggled since its inception to find generalizable concepts and approaches that both enhance our fundamental understanding of invasive species that can also be leveraged to aid in invasive species management. Much of the work in invasion biology has focused on identifying, characterizing, and limiting the spread of problem invaders (Pyšek and Richardson, 2007, 2010). This invader-focused perspective is often driven by policy, regulation, and funding, and has produced a huge amount of insight into the biology and impacts of invasive species (Vilà et al., 2011; Crystal-Ornelas and Lockwood, 2020). However, despite the successes of invader-driven research, this perspective is ultimately limited because it overlooks an important aspect of invasions: invasion is a community ecology problem (Shea and Chesson, 2002; Gallien and Carboni, 2017). Viewing invasions in isolation rather than in the community context within which invasion occurs risks missing or misidentifying many of the determinants that dictate invasion success and the emergence of problem invaders (Pearson et al., 2018). A mechanistic understanding of the process of invasion and the effects invasions produce in native ecosystems requires a community assembly context, and modern community assembly theory is built within the framework of metacommunity ecology.

Humans have moved species both intentionally and accidentally for millennia. These actions have provided resources, sustenance, and quality of life for humankind, but an unintended consequence of these actions is a global mixing of life that has resulted in unprecedented biotic homogenization affecting every landscape and ecosystem on Earth. For example, exotic mussels (Cárdenas et al., 2020) and vascular plants (Chwedorzewska et al., 2015) have now been identified on Antarctica, long considered immune or isolated from invasion. Similar concerns have now been raised about the inevitable likelihood of the melting Artic suffering a similar fate (Ricciardi et al., 2017). The ecological and economic impacts of invasive species are diverse, and in some cases irreversible, including extinction of native species, increasing intensity and frequency of wildfires, and alteration of nutrient and water cycles (e.g., Vilà et al., 2011). Despite decades of research and management, the rate of introductions of new species continues to rise across all taxonomic groups (Seebens et al., 2018), suggesting that invasion and their resulting ecosystem transformations are the new normal. Addressing this element of global change requires a robust conceptual framework that is broadly applicable across diverse species and ecosystems, and readily translates to applied management, because unlike many subdisciplines in ecology, invasion biology is both a basic and applied science.

The proportion of introduced species that are ultimately considered invasive, i.e., cause negative impacts, is a small fraction, estimated at <1% (Williamson, 1996), though the veracity of this number has been questioned (Jarić and Cvijanović, 2012). The small number of introduced species that become invasive presents a perplexing challenge that has driven decades of research: What is it about these select few species that result in problem invasions? There are two intertwined aspects of invasive species that have to be considered simultaneously: the biogeographic aspect that deals primarily with the distribution and abundance of non-native species (Richardson and Pyšek, 2006), and the impact of those species since invaders are often defined by agencies like the International Union for the Conservation of Nature by their impacts. These aspects can be difficult to reconcile. The overwhelming majority of work that followed focused on (i) what makes a species invasive (invasiveness), and (ii) what makes communities susceptible to invasion (invasibility) (Richardson and Pyšek, 2006). What resulted were dozens of hypotheses, each seeking to explain invasiveness and invasibility (Catford et al., 2009), and testing these hypotheses greatly enhanced our understanding of individual invasive species, but left the field fragmented chasing non-generalizable explanations (Hulme et al., 2013).

The frustration for investigators produced by this piecemeal approach, and resulting equivocal evidence (e.g., Jeschke et al., 2012), has led to the development of multiple syntheses (e.g., Catford et al., 2009), and conceptual frameworks (e.g., Barney and Whitlow, 2008). These approaches identified common themes that cut across diverse species and systems. While no unifying framework has emerged that is broadly applicable and lends itself to leverage improved management, due to the diversity of invaders and the communities and contexts to which they are introduced, several important trends have emerged. For example, Catford et al. (2009) evaluated the overlapping aspects of >20 individual hypotheses and found that they cluster around common elements: ecosystem invasibility defined by the abiotic and biotic characteristics of the system, and propagule pressure—all of which are modified by human interactions. This synthesis largely reflected the original conception of invasiveness and invasibility, modified to reflect the dominant influence of propagule pressure, or the number and frequency of introduction events, which has long been recognized as a through-line concept in invasion biology (Lockwood et al., 2005; Colautti et al., 2006). Despite major advances in our understanding of invasive species, our search for a conceptual synthesis continues with a large emphasis on increasingly sophisticated analyses (Enders et al., 2020). Here we suggest that approaching biological invasions as a community ecology problem (e.g., Shea and Chesson, 2002) and that applying a metacommunity lens will aid the development of a generalizable and readily applicable framework for invasion biology. Such improvements would enhance our basic understanding of invasion success, while also affording enhanced mitigation strategies—an important goal to address the biological invasion crisis.

The Intersection Between Invasion Biology and Metacommunity Ecology

Over the previous two decades, metacommunity ecology has produced a paradigm shift in community ecology by emphasizing that community assembly is dictated not only by local niche factors like environmental conditions and species interactions, but that dispersal between local communities can also be a major driving force in community assembly (Leibold et al., 2004; Holyoak et al., 2005). The goals of metacommunity ecology closely align with current needs invasion biology in two identifiable ways:

The Importance of Dispersal in Community Assembly and Membership

While dispersal has long been recognized as important in structuring ecological communities (e.g., MacArthur and Wilson, 1967; Lewin, 1986), metacommunity theory recognized that dispersal can be a more powerful driver of community assembly and structure than previously thought. Though much of the history of community ecology has been devoted to local niche-based controls on community structure, work on metacommunities has demonstrated that dispersal can be as or more influential on structuring communities than niche-based processes, and that there is often an important interaction between local and regional processes. This influence of dispersal has been documented in a wide range of both theoretical (e.g., Mouquet and Loreau, 2003; Calcagno et al., 2006) and empirical (e.g., Cottenie, 2005; Werner et al., 2007; Heino and Mykrä, 2008; Brown and Swan, 2010; Chase, 2010) studies.

A Multi-Scale Perspective on Community Assembly

Metacommunity ecology strongly emphasizes the role of multi-scale factors in driving community assembly and membership by making a distinction between “local” and “regional” processes (**Figure 1**). Local processes are traditional niche-based processes that limit species distributions and abundances like species interactions, environmental conditions, and localized disturbances. Regional processes are those driven by dispersal between local communities. Thus, a metacommunity is defined as a set of local communities linked by the regional process of dispersal between those localities (**Figure 1**). One major goal of metacommunity research is to estimate the relative influences of local vs. regional factors on community composition, as well as to examine the local x regional interaction (Logue et al., 2011; Brown et al., 2017). Along with this focus on multiple scales came tools designed to describe multi-scale assemblages; chief among those are the descriptors of diversity, α, β, and γ. α-diversity is the diversity of a local community (or average of all local communities), usually defined by species richness or a diversity index like Shannon or Simpson. γ-diversity is the accumulated diversity of the entire metacommunity, and β-diversity is the turnover in species composition between local communities, often interpreted as the number of distinct communities on a landscape (more detail on diversity metrics can be found in the glossary; Chao et al., 2012). These diversity parameters are intimately related to one another, and γ-diversity can be mathematically partitioned into independent contributions of α and β, usually in the form of $\alpha \times \beta = \gamma$, though other valid partitioning formulations exist (Jost, 2007; Chao et al., 2012). For example, in **Figure 1**, using species richness as a measure of α, $\gamma = 3$, $\alpha = 2.5$, and $\beta = 1.2$.

Because of a close alignment between focal questions in both metacommunities and invasion biology, metacommunity ecology is well-positioned to assist in the study of invasive species. The emphasis on propagule pressure in invasion biology (Simberloff, 2009) is closely mirrored by the emphasis on dispersal in metacommunity ecology (Leibold et al., 2004). Likewise, the need for a multi-scale perspective in invasion biology has been recognized and strongly advocated because the success of invasions is as reliant on the properties of the invaded community as it is on the properties of a specific invader (Shea and Chesson, 2002; Gallien and Carboni, 2017). These two foci also merge because it is dispersal among local communities that dictates assembly patterns in a metacommunity, and dispersal of native species may be as important in determining invasion outcomes as the dispersal of invasives (Howeth, 2017).

HOW METACOMMUNITY THEORY CAN ASSIST IN ADDRESSING INVASIVE SPECIES QUESTIONS

Decades of research in invasion biology have identified two key factors that are central to invasive species establishment and success: propagule pressure, and the characteristics of the community into which invaders are introduced (Simberloff, 2009). As suggested in Howeth et al. (2010), these factors in invasion biology directly parallel the regional and local forces addressed by metacommunity frameworks and suggest that invasions could benefit from a multi-scale concept. The multi-scale emphasis of metacommunity ecology can address invasive species spread and establishment in a realistic way by incorporating the movement of an invader from patch to patch across a landscape rather than focusing exclusively on a single-patch. Unlike single patch studies, which have dominated invasive species study systems (**Box 1**), a multi-scale approach can reveal details about the dynamics and limitations of invasive species. For example, **Figure 2** depicts the mechanisms and limitations of spread of an invader through a metacommunity, illustrating the multi-scale roles of dispersal and limitation through local community conditions. As **Figure 2** illustrates, the degree of spread of an invader is not just a product of local conditions or propagule pressure, but also depends on the interaction between those factors (**Figure 2**, spread from A to C).

Metacommunity theory can also address the human aspects of invasive species by partitioning the human influence on the process of invasion into influences on either local or regional processes (see below for more detail about the human element in invasions). For example, human movement of a species that contributes to invasion directly affects dispersal, i.e., a regional process, while human modification of the environment primarily affects local processes. Clearly many examples of human activity won’t fit easily into a facile local/regional dichotomy, but as illustrated before, metacommunity theory also emphasizes the interaction between local and regional processes.

A formidable body of theory has grown out of metacommunity ecology, complemented by an abundance of empirical tests of its efficacy. Metacommunity theory offers predictions about how biodiversity changes both locally and regionally (α and γ diversities) with rates of dispersal (e.g.,

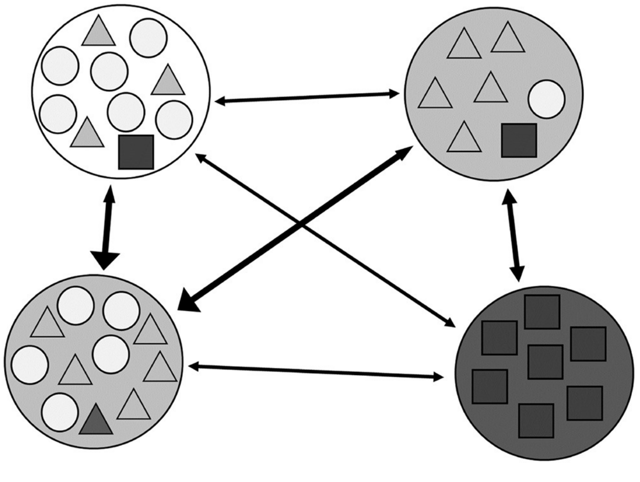


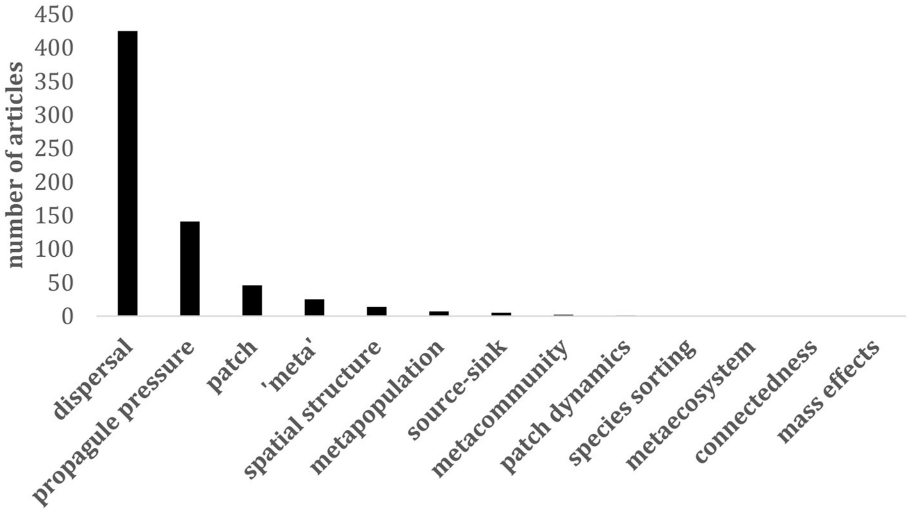
FIGURE 1 | Schematic representation of metacommunity dynamics. Circles indicate habitat patches (i.e., local communities) where increased shading represents increased local filtering on community composition. Shapes represent individuals of a species and congruent shading of species and patches represents a match between species and habitat. Arrows represent dispersal between local communities, with the thickness of the arrow shaft indicating overall dispersal rate between communities and size of the arrow head indicating possible asymmetry in dispersal.

Mouquet and Loreau, 2003; Gravel et al., 2011; Büchi and Vuilleumier, 2014), the consequences of local environmental filtering strength for community assembly (e.g., Chase, 2003; Sokol et al., 2011; Datry et al., 2016), how and why turnover (β-diversity) occurs across a landscape and what these patterns of β-diversity indicate about how communities are formed and maintained (e.g., Brown and Swan, 2010; Heino, 2011; Jamoneau et al., 2012), and how disturbance can affect metacommunity processes at both local and regional scales (e.g., Urban, 2004; Vanschoenwinkel et al., 2013; O'Neill, 2016). All of these efforts are largely directed at understanding the factors that control community composition and dynamics, including how they affect the entry of new species into a metacommunity. Accompanying the construction of this conceptual framework has been the development of methods and analyses for predicting and quantifying metacommunity patterns (e.g., Legendre et al., 1997; Nekola and White, 1999; Leibold and Mikkelson, 2002; Peres-Neto et al., 2006; Oksanen et al., 2020). Taken together, the conceptual framework of modern metacommunity ecology and the accompanying methodologies that have developed to support it offer a prodigious set of relevant tools for the study of invasions.

We will explore the application of metacommunity theory, approaches, and analyses to invasion biology, paying particular

BOX 1 | *Metacommunity theory and invasion biology*.

To estimate the extent to which metacommunity theory is currently being utilized in the field of invasion science we surveyed all published articles in the >20 year catalog of the primary journal in the field, *Biological Invasions*. We surveyed the titles, abstracts, and keywords of all 4,280 articles published in *Biological Invasions* from 1999 to January 2020 for 13 of the most common concepts and terms in metacommunity theory. These terms were selected for either their general usage in metacommunity parlance (e.g., dispersal), or because they identified one of the major metacommunity paradigms (species sorting, mass effects, patch dynamics; Leibold et al., 2004). Many metacommunity terms were used (9/13), with "dispersal" (9.9% of papers), and "propagule pressure" (3.3% of papers) the most common. It is not surprising that "spread" related terms were the most common, as spread dynamics is one of the defining characters of invasive species (Richardson et al., 2000). However, aside from these common movement-related invasive species terms, only the metacommunity concepts "patch" (1.1%) and the generic "meta" (0.6%) were included in 25 or more papers over >20 years. This suggests that metacommunity theory has played little role in the field to date.



Number of articles including metacommunity terms in the journal *Biological Invasions* from 1999-(early) 2020 (*N* = 4,280 articles).

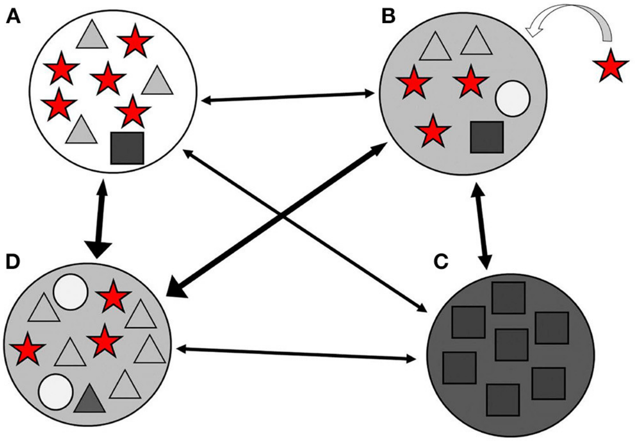


FIGURE 2 | Schematic representation of the mechanisms and limitations of spread of an invasive species through a metacommunity. The invasive species is depicted in red and initially propagates into patch A. Spread to patch B is facilitated by the more permissive local conditions and lack of local filtering. Despite a moderate amount of environmental filtering in patch C, establishment is facilitated by substantial dispersal from A to C. Finally, the invader fails to establish in patch D despite relatively strong dispersal because of impermissive local conditions.

attention to elements that can increase understanding of invader establishment, spread, and effects, thereby enhancing mitigation and management. Our goal is to both broaden the conceptual frameworks and toolkits for invasion biologists, but also to highlight that biological invasions present excellent systems in which to explore metacommunity concepts. To meet these objectives, we provide a glossary of invasion and metacommunity terms, survey the invasion literature for metacommunity concepts, explore examples of invasion concepts and their metacommunity counterparts, identify where application of metacommunity concepts allows novel exploitation for invasive species management, and conclude with development of novel hypotheses.

INVASION CONCEPTS IN A METACOMMUNITY FRAMEWORK

Foundational to the exchange of ideas across disciplines or sub-disciplines is common vocabulary (Holbrook, 2013). To elucidate the parallels and opportunities for explicit incorporation of invasions in a metacommunity framework, we explore several important invasion biology concepts; first from a traditional invasion biology perspective, then through the lens of metacommunity ecology. Topics were chosen based on reviews and syntheses to be representative of broad invasion topics as examples, and not to be an exhaustive survey. We identified several invasion biology concepts that are regularly discussed as base elements of the field of invasion biology, including propagule pressure, biotic resistance, enemy release, functional traits, and human influences (Catford et al., 2009; Gurevitch et al., 2011; Enders et al., 2020).

Propagule Pressure

Invasion Biology Perspective

Biological invasions are the result of intentional or accidental introduction of species propagules to locations outside their historical range. Propagule pressure is the number and magnitude of introduction events of a single species to a location (Lockwood et al., 2005). This composite measure of the number of individuals (or propagules) introduced to a location has been shown to be integral to the success of invading species at all stages of invasion, including transport, colonization, establishment, and landscape spread (Theoharides and Dukes, 2007). The role of propagule pressure in invasion success cannot be overstated–all syntheses, reviews, and conceptual frameworks (including our analysis of invasion literature in **Box 1**) have consistently identified the important role that propagule pressure plays in successful invasion, and a practical understanding of propagule pressure has been described as "…probably the biggest challenge facing invasion ecologists" (Richardson, 2004). Simply put, successful invasion is dependent on successful movement of viable propagules.

In their search for general principles, Colautti et al. (2006) found few consistencies aside from the strong predictive power of propagule pressure, stating that "propagule pressure should serve as the basis of a null model for studies of biological invasions when inferring process from patterns of invasion." As stated above, when Catford et al. (2009) reduced redundancies in the multitude of individual invasion hypotheses they found propagule pressure to be one of a tripartite of common elements. In his review of propagule pressure in invasion, Simberloff (2009) concluded that increasing the number of introduced propagules likely minimizes demographic stochasticity, while increasing the number of introduction events buffers against environmental stochasticity, hence partially explaining the mechanism of propagule pressure as fundamental to invasion success. In an under-appreciated proposal, Davis (2009) formalized the probability of invasion as a function of propagule pressure (N) and the probability of establishment of each propagule (P):

$$\textit{Probability of invasion} = 1 - (1 - P)^N$$

Davis' (2009) equation suggests that introduced species can successfully establish even with low individual propagule establishment potential, perhaps because of environmental mismatching or genetic bottlenecks, through a proportional exponential increase in the number of introduced propagules. In other words, successful invasion can result from either few introductions of propagules with high establishment potential, or large numbers of low establishment potential propagules. Increasing the number of introduced individuals, especially through multiple introduction events has been repeatedly found to increase invasion success, particularly when it increases genetic diversity (Simberloff, 2009). Though Barney et al. (2016) found that propagule pressure is not always a guarantor of establishment success, particularly in the face of strong biotic resistance of the receiving community. As with most aspects of biological invasions, successful establishment and spread is a result of complex interactions of many factors (e.g., Barney and

Whitlow, 2008). Despite the universal importance of propagule pressure in invasion, it is still largely viewed within single patches, or as a driver of genetic variation in introduced populations.

Metacommunity Perspective

Propagule pressure is closely aligned with the concept of dispersal in a metacommunity. While "dispersal" is a more general term (Glossary) that can be used to describe a variety of movements of organisms, its realized meaning in most metacommunity applications is almost identical to propagule pressure, i.e., both movement and establishment. The major factor that differentiates metacommunity ecology from traditional niche-based ecology is dispersal and how its consideration leads to a multi-scale perspective on biodiversity dynamics (Leibold et al., 2004; Holyoak et al., 2005; Logue et al., 2011). For example, metacommunity approaches have demonstrated that dispersal-driven dynamics lead to higher biodiversity in more productive environments (Chase, 2010), that spatial structuring of local communities interacts with dispersal to affect community assembly (Sokol et al., 2015; Resetarits and Silberbush, 2016), and that position of a local community within a river network metacommunity often predicts how influential dispersal-driven dynamics are to community composition (Tornwall et al., 2017; Tonkin et al., 2018). This congruence between the concepts of propagule pressure and dispersal in a metacommunity suggests that the theory, predictions, and tools of metacommunity theory can be readily applied to biological invasions. However, given the 2 distinct aspects of invasive species—the biogeographic aspect and the impact—Metacommunity ecology is best positioned to deal with invaders in a biogeographic sense, as members of a metacommunity of organisms.

Many of the predictions of metacommunity ecology are based on either dispersal rates, or the connectivity between local communities of the metacommunity. In the latter case, connectivity is actually a proxy for dispersal since dispersal is generally expected to decrease with distance between local communities (Nekola and White, 1999; Chase et al., 2005; Altermatt and Fronhofer, 2018). Some of the most foundational predictions of metacommunity ecology regard how α, β, and γ-diversities change within a metacommunity across a gradient of dispersal (Mouquet and Loreau, 2003; Chase et al., 2005; Swenson et al., 2012; Matias et al., 2013). Likewise, dispersal is predicted to directly influence how communities assemble. Classic-niche based processes control community assembly at low rates of dispersal or connectivity, but become less important as dispersal increases and dynamics driven by propagule pressure overwhelm local niche-based processes (Mouquet and Loreau, 2003; Leibold et al., 2004; Chase et al., 2005). Importantly, these predictions have also received strong empirical support from subsequent studies (e.g., Cadotte, 2006; Hunt and Bonsall, 2009; Steiner et al., 2011; Carrara et al., 2012; Frisch et al., 2012; Heino et al., 2015), including some studies of invasive species. For example, Smith et al. (2020) demonstrated that human-mediated repeated introductions, even over long distances, allowed a widespread invasive plant to overcome genetic and environmental constraints. Both theoretical and empirical studies have extended these concepts to more complex metacommunities by using connectivity within networks to precisely map connectivity and predict how α, β, and γ-diversities will change at multiple scales in the metacommunity (e.g., Economo and Keitt, 2008; Brown and Swan, 2010; Carrara et al., 2012; Moritz et al., 2013). Indeed, some frameworks for invasion ecology also emphasize the role of invader propagule pressure in a community context, most notably Catford et al.'s PAB framework (Propaule pressure, Abiotic characteristics, Biotic characteristics; Catford et al., 2009), and the invasiability predictive framework presented in Hui and Richardson (2017).

One potential mismatch between current metacommunity approaches and the focus of invasive species work is that metacommunity models tend to consider the dispersal rates of communities as a whole rather than with a focus on individual species like an invader. However, some metacommunity models allow for flexibility or individuality in species' dispersal rates (Sokol, 2016; Sokol et al., 2017), and these models could be easily adapted for the purposes of generating predictions regarding invasives. However, we submit that the tendency of metacommunity work to focus on whole communities rather than individual species should be adopted by invasion ecology, particularly with regard to understanding the community context into which an invader is moving (see below for development of this idea).

Biotic Resistance

Invasion Biology Perspective

It has long been thought that not all communities are equally susceptible to invasion, a result of the unique combination of abiotic and biotic properties comprising individual ecosystems. The susceptibility of a community to invasion is termed invasibility, while the communities that are less susceptible to invasion are said to have "biotic resistance." The concept of biotic resistance harks back to Darwin and the "father" of invasion biology Charles Elton. The general concept is that resident species with long co-evolutionary histories are best adapted to a locality and will exclude invaders through a combination of competitive exclusion and niche filling (Elton, 1958; Levine et al., 2004). Thus, Elton's proposal was that communities with large numbers of native species will better resist invasion than communities with fewer natives. However, there has also been contrasting evidence that supports a concept of Biotic Acceptance, essentially a "rich get richer" paradigm in which species rich communities are more susceptible to invasion because the environment is favorable for both natives and invasives (Stohlgren et al., 2006).

A growing body of research shows equivocal evidence for Biotic Resistance, finding both positive and negative relationships between exotic and native species richness (Fridley, 2010), which was largely attributed to the scale and method (experimental vs. observation) at which the study was conducted (Shea and Chesson, 2002). In an attempt to reconcile this seeming "invasion paradox," Fridley et al. (2007) conclude that native-rich communities are more invasible than native-poor communities, and that threats to native residents will accelerate further invasion. However, a recent expansive meta-analysis found strong support that more native-rich communities supported fewer exotic species across a wide range of communities and ecoregions (Beaury et al., 2020).

Expanding the scope of propagule pressure, Lockwood et al. (2009) propose the concept of colonization pressure, or the number of species introduced to a single location, as a key explanatory parameter describing exotic species richness. Similar to propagule pressure, they argue that the probability of exotic species establishing is proportional to the number that are introduced. This concept unites both propagule/colonization pressure and biotic resistance because there is always an element of stochasticity in colonization by non-native species, and increasing the number of chances at successful invasion ultimately results in higher numbers of invasions. Thus, propagule pressure and community composition of the target community in invasions are inherently integrated concepts that interact in a complex network, partially determining the success of introduced species.

Metacommunity Perspective

One of the major goals of metacommunity ecology is to understand how communities are assembled and the mechanisms underlying the distributions of species. Classical ecological approaches have largely attempted to explain the presence of a species in a particular locale using local niche-based factors like environmental conditions and species interactions, often with the implicit assumption that presence of a species indicates favorable conditions (e.g., Hutchinson, 1959; MacArthur, 1970). This "overwhelming emphasis on localness" (Lawton, 1999) dominated ecological thought for decades and continues to be the standard paradigm for much of ecology, environmental science, and conservation. Approaches that focus on localness have also formed the foundational basis for invasion biology (Peterson, 2003), and local niche-based mechanisms lie at the heart of the Biotic Resistance hypothesis. To be clear, these niche-based processes are fundamental to understanding community assembly, and density-dependent interactions between species often play a strong role in dictating community composition, even when dispersal is high (Thompson et al., 2020). However, metacommunity theory recognizes that species presence in a local community is the product of multiple factors, both local and regional, and that the occurrence of a species does not always reflect favorable local niche-based conditions (Leibold et al., 2004).

The application of metacommunity theory to the topic of biotic resistance begins with the recognition that species presence or absence from a local community is not dictated by local factors alone. In some ways, invasion biology has already made this acknowledgment through its emphasis on the importance of propagule pressure. However, from a metacommunity perspective, propagule pressure isn't necessarily just a vehicle for the introduction of a species to a site, after which local factors take over. Rather, propagule pressure is a dynamic force of community assembly that interacts with local factors like density-dependent population growth and species interactions, and it is this interplay that dictates a species inclusion or exclusion from any locality (Thompson et al., 2020). In other words, the mechanisms through which an invader successfully establishes in a local community will depend on the assembly mechanisms of that community. In a species sorting metacommunity (glossary), propagule pressure is just a vehicle for arrival of an invader, and successful establishment occurs though local density-dependent interactions like environmental suitability and interactions with currently residing species. This process of community membership being limited by local factors like environmental conditions and species interactions is collectively termed "species sorting" in metacommunity parlance. However, in metacommunities where assembly follows a patch dynamics (glossary) or mass effects (glossary) pattern, dispersal will play a more active role in establishment and maintenance of local species composition. Additionally, these latter paradigms emphasize multi-scale dynamics that will not be obvious by a focus on a single local patch. In fact, a recent experiment in which native species reduced invader propagule pressure because invader dispersal was density-dependent clearly demonstrates the interaction between local-scale competition and propagule pressure of invaders (Legault et al., 2020).

Much of invasion biology has been based on single-patch approaches (**Box 1**), and seeking local explanations in cases when dynamics are actually driven by regional-scale processes could be potentially confounding to studies of invasive species establishment, resulting in erroneous, or nonsensical conclusions. Thus, applying multi-scale approaches to invasion has the potential to reveal mechanistic insights that would be difficult or impossible to derive from single-patch studies.

One particularly effective example of this multi-scale approach applies community coexistence theory (Chesson, 2000) in a spatial context to create a framework for understanding successes and failures of invaders by viewing invasion as a successional process (Hui and Richardson, 2017). The framework uses two traits of invaders to categorize possible outcomes: the fitness differences between natives and invaders, and the degree to which the invader niche overlaps those of resident species, and suggests that, early in the process of invasion, a Neutral Paradigm (glossary) is more likely to dictate community assembly than niche-based processes due to the more stochastic nature of propagule pressure. The framework identifies not only three possible outcomes—coexistence, invader excluded, invader excluding residents—but also the rates at which these outcomes are expected to materialize (Hui and Richardson, 2017).

The ability of a species to invade an established local community has long been a focus of community ecology. In fact, a metric known as the *invasibility criterion* is often used as a definitive test of the ability of species to coexist in communities (MacArthur, 1972; Holt, 1977; Chesson, 2000). In this case, coexistence is distinguished from co-occurrence, though they are often incorrectly used interchangeably (Siepielski and McPeek, 2010). True coexistence doesn't simply imply that two species appear together; both species must both be able to persist together indefinitely (Holt, 1977; Blanchet et al., 2020). The invasibility criterion stipulates that in order for a species to truly coexist with other species in a community, it must be able to increase its abundance when rare, in the presence of other community members (Chesson, 2000; Siepielski and McPeek, 2010). The name of the criterion clearly derives from the scenario of a species invading, at low abundance, a locality within an extant community. Therefore, one potential mechanism of biotic resistance is that interactions with other species in a community cause an invader to fail the invasibility criterion. However, metacommunity approaches demonstrate that even if a species fails to meet the invasibility criterion, the species may still co-occur and even spread to new patches if dispersal of an invader is high, and their dynamics more resemble a mass effect or patch dynamic paradigm than a species sorting (i.e., niche based) paradigm. Thus, presence of an invader does not necessarily imply that a species is coexisting with native species, nor that an invader is even gratified by local conditions, shifting the burden of proof for biotic resistance (or acceptance) to a demonstration of local control on community membership.

Enemy Release

Invasion Biology Perspective

Perhaps the most commonly cited explanation for the success of invasive species is escape from their suite of herbivores, pathogens, predators, and other biotic limitations in the introduced range. Termed Enemy Release (Keane and Crawley, 2002), this hypothesis serves as the basis for classical biological control whose modus operandi is to introduce native enemies of the invader into the introduced range to limit population growth, as well as the basis for a range of additional hypotheses expanding on this basic tenet (e.g., Evolution of Increased Competitive Ability, Blossey and Notzold, 1995). Enemy release is also an element of biotic resistance broadly interpreted, comprising elements of an ecosystem that may limit exotic species success.

In a meta-analysis, Levine et al. (2004) found little evidence that resident competitors, their diversity, and the resident suite of limiting herbivores and facilitating soil fungal communities curb exotic species introductions, but do play a role in limiting population growth once established, and thus may contribute to invaders failing the Invasibility criterion. Evidence for enemy release remains weak, with some studies showing strong support for release from plant pathogens and viruses (Mitchell and Power, 2003), while a meta-analysis showed reduced herbivore damage especially of specialists (Liu and Stiling, 2006) and higher insect diversity on native plants (Meijer et al., 2016). As with most aspects of invasion biology, testing outside the plant kingdom remains scant (e.g., Roy et al., 2011), precluding broad, empirically-supported, general statements.

Metacommunity Perspective

As with Biotic Resistance, the Enemy Release hypothesis highlights local factors as a mechanism for success or failure of an invasion. In the case of Enemy Release, local filters on community membership that are created by natural enemies present in the home range of an invader are absent in the colonized community. From a metacommunity perspective, Enemy Release differs from Biotic Resistance because it necessarily invokes complex trophic structure, with invaders in their natural ranges serving as a food resource. However, the majority of metacommunity theory was developed around concepts of competitive metacommunities (e.g., Mouquet and Loreau, 2003; Chase et al., 2005; Mouquet et al., 2005) and the incorporation of more complex trophic structure into metacommunity frameworks is a relatively new advance (Leibold and Chase, 2018; Guzman et al., 2019). Despite the relative youth of multi-trophic metacommunity concepts, there are already considerable insights that may benefit invasion biology.

As with the Biotic Resistance Hypothesis, the appeal to strictly local mechanistic explanations misses the potential for larger-scale, dispersal-driven dynamics. While release from natural enemies in a local community may explain some of the successes and failures of invasion, dispersal-driven dynamics of both the invader, and the metacommunity into which it is invading, may play a larger role than local-scale species interactions. Predators and parasites move; prey move, and plants disperse to new areas. The dynamics produced by those movements on a landscape can rarely be captured in single-patch studies. Simulation models show a complex interplay between trophic level persistence and the spatial properties of a metacommunity, illustrating that overlooking the spatial properties of metacommunity trophic construction risks missing key mechanisms that shape predator-prey dynamics (Baiser et al., 2013; Guzman et al., 2019). Simulation models that included spatial dynamics also accurately represented realistic patterns in focal systems like pitcher-plant communities (Baiser et al., 2013). Dispersal in metacommunities has also been demonstrated, both theoretically and empirically, to provide a sort of "spatial insurance" that buffers communities against perturbations by promoting rescue effects and resource complementarity (Loreau et al., 2003; Limberger et al., 2019), and experiments have confirmed that these same spatial insurance effects can lower the invasibility of local communities when invasive species are the "perturbation" (Howeth, 2017). Intermediate levels of dispersal in a metacommunity also maximize food web linkages and species diversity, the latter of which has been shown to be a deterrent for invaders (Beaury et al., 2020).

These early results from a metacommunity approach to food webs have clear implications for the Enemy Release Hypothesis: spatial properties of metacommunities can have large effects on food-web dynamics, and therefore, for how robust a mechanism Enemy Release is likely to be in a particular metacommunity. A strategy for exploring the effect of Enemy Release in a metacommunity context is to examine the dynamics of multi-trophic metacommunities with vs. without predators/parasites. Of particular interest is that intermediate rates of dispersal maximize community diversity and therefore, resistance of a (meta)community to invasion (Beaury et al., 2020). As with Biotic Resistance, a mechanism like Enemy Release that is predicated solely on local effects may have some successes, but is likely missing important mechanistic links in a metacommunity context where dispersal of natives is moderate to high.

One way in which metacommunity theory can be more finely tuned to address issues of invasive species is that most metacommunity models and theory include the general assumption that either dispersal is a stochastic, probabilistic process with regards to which species colonize and at what rate, or dispersal is probabilistically equivalent across all species in a metacommunity (e.g., Loreau et al., 2003; Dallas et al., 2019). However, dispersal has been demonstrated to be distinctly non-random in both food webs (Melián et al., 2015) and in metacommunities (Lowe and McPeek, 2014). Specifically in an invasion context, non-random dispersal can benefit invaders who show distinct "dispersal syndromes" that facilitate invasion (Cote et al., 2017). However, a number of metacommunity models and simulations, allow for flexible dispersal kernels in models, including freely-available simulation packages (e.g., Sokol, 2019) and these platforms can provide an excellent tool for generating and evaluating hypotheses about multi-trophic Enemy Release effects.

Functional Traits

Invasion Biology Perspective

Increasing attention is being paid to functional traits, the morpho-physio-phenological traits that impact fitness (Violle et al., 2007), broadly in community ecology, and especially in invasion biology. Drenovsky et al. (2012) expand the functional trait framework beyond those that affect individual fitness, to include those that play a role in invader abundance and impacts, two defining elements of biological invasions. This attention to traits that influence performance and fitness affords an opportunity to add quantifiable elements in complex systems, again in a search to understand the mechanisms resulting in invasiveness.

In a meta-analysis of plant invaders, Van Kleunen et al. (2010b) found that invasive plants had significantly higher values than natives for six performance-related traits. A complementary analysis found that invasive species show higher phenotypic plasticity than native species across a range of traits (Davidson et al., 2011). A similar approach is being applied to ecosystems by viewing not just the richness/diversity of the community, but the functional trait diversity of the community and its relationship to ecosystem processes (Diaz and Cabido, 2001). This functional trait diversity approach also informs community susceptibility to invasion through "trait space," the uniqueness of invader traits relative to the breadth of resident traits (Funk et al., 2008). Despite these advances, many challenges remain to fully realize and generalize a functional trait approach in invasion biology and community and ecosystem processes (Funk and Wolf, 2016).

Metacommunity Perspective

Functional traits have played a large role in metacommunity investigation in much the same way they have in invasion biology, and they have been employed in a variety of ways. Many studies use community trait indices as a metric in place of, or in addition to, taxonomic identity to examine how communities are assembled from a functional perspective (Ackerly and Cornwell, 2007; Cadotte et al., 2013; Biswas et al., 2016; Falster et al., 2017; Tolonen et al., 2018), while others have used traits as evidence supporting various community assembly paradigms (e.g., Brown and Swan, 2010; Sokol et al., 2011; Zhang et al., 2015). Trait metrics have also shown predictable relationships with other diversity metrics like α, β, and γ diversity (Patrick and Brown, 2018). Fourth Corner Analysis is a common method in metacommunity studies that simultaneously relates data on species abundances, spatial data, and traits to test trait-environment relationships in a spatial context (Legendre et al., 1997; Dray and Legendre, 2008; Peres-Neto et al., 2012), a method that could prove particularly useful in deciphering the mechanics of invasions by elucidating the relationships between community composition, functional traits, and spatial dynamics driven by dispersal.

The combination of species traits and the multi-scale perspective of metacommunity ecology has great potential for producing insights about the success and effects of invasions. A rapidly growing literature suggests that invader traits, rather than simply species identities, are the best predictors of invasion success (Berg and Ellers, 2010; Van Kleunen et al., 2010a; Davidson et al., 2011; Drenovsky et al., 2012), particularly because traits are best suited for defining the trade-offs that allow invasion success in a particular target community. For example, while high propagule pressure is often associated with invasion success, high propagule pressure alone cannot ensure successful invasion in some systems due to ecological mismatches or innate biotic resistance that ultimately depend on the local-scale traits of the invader like competitive ability and predator/herbivore resistance (Barney et al., 2016). Some investigations have even focused on the composition of target communities in an effort to predict what traits would allow invasion into that system (Moles et al., 2008). Metacommunity approaches can add a layer of explanatory power to these investigations by considering how these same trait combinations of natives and invaders play out in a more complex spatial environment. In a metacommunity context, the trade-offs defined by species traits like competitive ability and propagule pressure exist not just at the local scale, but also within the whole metacommunity. Thus, regional properties—like the regional abundance of invaders or habitat heterogeneity across patches within the metacommunity—can interact with species traits and exert a strong influence over invasion success and effects in any single local community.

A number of perspectives on trade-offs in a multi-scale environment have emerged from the metacommunity literature (e.g., Kneitel and Chase, 2004; Hillebrand et al., 2008). Of these perspectives, Hillebrand et al.'s (2008) investigation of dominance effects is of particular significance. Hillebrand et al. define "dominance" by the distribution of traits within a community, with "dominance" characterized by a lack of trait evenness (2008), and they distinguish two distinct scenarios for dominant species: locally dominant but regionally rare, and both locally and regionally dominant (Hillebrand et al., 2008). From the perspective of the invader, in the case of locally dominant and regionally rare, invader persistence depends on an invader possessing trait combinations that allow it to occupy a local niche and exceed the invasion criterion. However, in a locally and regionally dominant scenario, invader persistence may occur in less advantageous patches through mass effects which can rescue an invader from local extinction. The local/regional dominance perspective can also address biotic resistance of a local community. Theoretically, low dominance in a native community should result in lower invasibility since a higher evenness in community traits should mean that a greater number of niches are filled in community niche space (Hillebrand et al., 2008). These theoretical predictions have been supported empirically (Mwangi et al., 2007; Zavaleta and Hulvey, 2007) with at least one study demonstrating that invasion is actually facilitated by dominance in the native community (Smith et al., 2004).

Human Influence

Invasion Perspective

Unlike many aspects of classic ecology, humans are a fundamental element of invasion. Not only are humans the initial source of invasion, through direct or indirect action, but affect invasion nearly all stages of invasion (Theoharides and Dukes, 2007). As Catford et al. (2009) noted, humans also modify the biotic and abiotic environment of the receiving environment through both direct (e.g., habitat destruction) or indirect (e.g., climate change) actions. And of course, humans are the source of propagule introduction through a diverse variety of pathways. Thus, there can be no realistic discussion of invasive species without considering the influences that humans exert on the specific species that invade ecosystems, the movement of species across large and small spatial distances, and the mechanisms of their invasion.

Metacommunity Perspective

From a metacommunity perspective, humans influence both local and regional processes. Local influence is felt primarily through habitat modification and land-use change, though in more built environments, humans may also exert a strong direct influence over the local species pool through horticultural and agricultural practices (e.g., Knapp et al., 2012; Johnson et al., 2015). Humans also affect regional-scale processes by influencing the dispersal of invasives and augmenting the regional species pool (e.g., Gilroy et al., 2017). Both sets of effects can be accommodated by metacommunity approaches which have a rich history of analytical methods designed to partition the influences of diverse effects on community composition (Leibold and Mikkelson, 2002; Peres-Neto et al., 2006). Despite the recognition of the role humans play in invasion, explicit incorporation of that role is rarely measured as an explicit component of the community assembly process. Assuming human influence can be accurately measured, metacommunity theory and tools provide a number of mechanisms for incorporation of those effects into empirical research, either through implicit incorporation of human elements as covariates in the local/regional partitioning of metacommunity drivers, or though explicit incorporation using methods like variation partitioning (Peres-Neto et al., 2006). These approaches may show not only the clear, direct effect of human agency in invasion, but also reveal much about the interaction between human influence on local conditions like environmental conditions and land use change, and regional factors like human movement of species and introduction of non-natives to the regional species pool.

From a conceptual metacommunity perspective, human involvement in invasions has one major effect on community processes: decoupling the tradeoffs that promote coexistence in communities. Tradeoffs have formed a central tenet of community ecology for decades (MacArthur, 1972), and species coexistence in a community is thought to depend on tradeoffs between traits of species with overlapping niche space (MacArthur, 1972; Tilman, 1982, 2000; Chesson and Huntly, 1997; Grover, 1997). Trade-offs are negatively correlated fitness-related traits in a species, developed through the serially optimizing force of natural selection, constrained by the physiological limits of organic life (Garland, 2014). Tradeoffs impose constraints that prohibit the evolution of "superspecies" and allow for coexistence of species through the employment of alternative tradeoff strategies (Kneitel and Chase, 2004). Common trade-offs in communities include growth rate vs. carry capacity (Pianka, 1970; Boyce, 1984), differential resource use (MacArthur, 1972; Tilman, 1982), predator/herbivore tolerance vs. competitive ability (Holt et al., 1994; Leibold, 1996), and competition vs. colonization (Levins and Culver, 1971; Hastings, 1980). The influence of humans on invasive species effectively decouples traits involved in tradeoffs in two distinct ways. The most obvious is the alleviation of dispersal limitation. For example, given a classic competition vs. colonization tradeoff, a species with high competitive ability would have low rates of colonization/propagule pressure. If that limitation on colonization is removed via human agency, then a species' competitive ability is left unchecked. Humans can also alter the other side of the equation, competitive ability, by selectively promoting or eliminating species. Intentional cultivation of invasive species is common, particularly in built environments and agricultural settings (Johnson and Swan, 2014), and horticulture is a major vehicle for the introduction of invasive species (Reichard and White, 2001). Surveys from non-governmental organizations suggest that possibly as many as 83% of invasive plants in the United States had horticultural origins (Niemiera and Von Holle, 2009). Promoting a species' competitive ability can also occur without intent through the indirect effects of land use changes that favor invasives (e.g., Lenda et al., 2018). In a metacommunity of interconnected patches, the intentional cultivation of invasive species can also have trait-decoupling effects that range far beyond a local patch because maintenance of invasives in the regional species pool not only subverts local competitive hierarchies, but also facilitates the dispersal of invaders into non-target patches. A recent publication from urban ecosystems demonstrates how human activity can be incorporated in a metacommunity framework to holistically describe the factors that structure communities in cities (Andrade et al., 2020). Another prominent example of human activity altering the course of invasions through both local and regional effects is the "bridgehead effect" in which invasions beget additional invasions (Lombaert et al., 2010). While first descriptions of the bridgehead effect postulated that adaptation in the initially invading population was the driver of subsequent invasions, further analysis suggests that a more parsimonious explanation is that human agency either (1) subverts limitations of the competition-colonization tradeoff structure to allow establishment of an invasive population that continues to spread, or (2) that the structure of networks of human transport result in multiple introductions that can exacerbate one another (Bertelsmeier and Keller, 2018), and these mechanisms have been supported by subsequent empirical investigations (e.g., Oficialdegui et al., 2019).

EMERGENT INVASION PREDICTIONS VIA METACOMMUNITY APPROACHES

Translating invasion terms and concepts into the vocabulary of metacommunity theory is a practical first step toward a metacommunity approach to invasive species. However, simply rephrasing well-known concepts has little utility unless new and interesting principles, predictions, and hypotheses emerge. A recurring theme in this paper–and especially in this section—is the importance of a multi-scale perspective. Just as metacommunity theory explicitly incorporates both local and regional scales, invasions should be similarly viewed, moving beyond the focus on single-patch studies that do not incorporate interconnectedness and regional processes. Likewise, we continue to focus not only on a particular invasive species and their traits, but rather on the community into which an invader is attempting to colonize. More so, expanding our approach to the total suite of exotic and native species within and among patches that interact with each other, as well as the local environment. This perspective has been encouraged by previous researchers (e.g., Shea and Chesson, 2002; Preston et al., 2012; Gallien and Carboni, 2017), but its adoption has been sluggish. Here we present several ideas and testable hypotheses that result from a metacommunity approach to invasions, and suggest approaches through which these ideas can be tested. This list is by no means exhaustive and serves more as an illustration of what a metacommunity approach to invasions may accomplish rather than a comprehensive list of ideas.

The Relationship Between Local Sorting Strength and Invasion Success

Two major invasion hypotheses, Biotic Resistance and Enemy Release, implicate local sorting strength in determining invasion success. However, a metacommunity approach strongly suggests that local sorting strength is often only part of the equation when it comes to community assembly, and that regional dispersal-driven factors can be just as important, or more important in structuring communities (Leibold et al., 2004). Previous work on metacommunities has demonstrated that when local sorting strength is the primary driver of community assembly, resultant communities tend to be far more predictable and deterministic (Chase, 2003, 2007). The converse of that result is that when communities are significantly influenced by dispersal-driven dynamics, resulting communities are more stochastic in structure and more permissible to the introduction of new species (Sokol et al., 2017; Brown et al., 2018). Taken together, these suggest a powerful hypothesis about the relationship between local sorting strength and the invasibility of a community: probability of invasion decreases as the importance of local sorting strength increases (**Figure 3A**).

This hypothesis is both imminently testable and useful. A rich history of metacommunity investigation provides both the conceptual foundation and analytical tools for evaluating the relative contributions of local sorting strength and dispersal for community assembly. Experimental approaches are the most powerful for evaluating assembly mechanisms because they allow for direct evaluation of the outcome of assembly processes (e.g., Cadotte, 2006; Chase, 2007; Steiner et al., 2013; Resetarits and Silberbush, 2016; Tornwall et al., 2017; Brown et al., 2018), and when experimental approaches are practical, they are encouraged. Experimental approaches use replicated communities to examine the repeatability of species compositions after assembly, with high levels of repeatability being an indicator of deterministic, niche-based local control (Chase, 2007; Swan and Brown, 2017; Brown et al., 2018). However, experimental approaches may prove intractable, since available data are often the work of surveys outside of a designed context. Nevertheless, these sorts of survey data have been employed in a wide range of metacommunity studies to great effect. While methods to evaluate the relative balance of local vs. regional effects in assembling communities are numerous, two common methodologies are distance-decay and variation partitioning. Distance-decay studies examine how similarity between multiple local communities changes as a function of environmental distance and physical distance (Nekola and White, 1999). Stronger relationships with environmental parameters indicate more local, niche-based control, while strong relationships with distance indicate dispersal-driven dynamics (Chase et al., 2005). These methods have been used to evaluate diverse ranges of communities including stream invertebrates, frogs, microbiota, plants, lentic algae, and internal parasites (Morlon et al., 2008; Brown and Swan, 2010; Diniz-Filho et al., 2012; Warburton et al., 2016; He et al., 2020). Variation partitioning is a method based on constrained ordination that simultaneously uses community composition data (taxonomic or trait-based), spatial data, and environmental data across multiple sites to evaluate the factors that most strongly structure communities (Borcard et al., 1992; Peres-Neto et al., 2006). Similar to distance-decay relationships, the degree of local vs. regional control is inferred based on the relative influences of environmental and spatial variables, but in the case of variation partitioning, statistical significance of the various partitions can be simultaneously evaluated (Peres-Neto et al., 2006). Variation partitioning has been used in a wide range of systems in both an exploratory (e.g., Grönroos et al., 2013; Sokol et al., 2013) and a hypothesis-testing framework (e.g., Cottenie and de Meester, 2003; Resetarits and Silberbush, 2016). It is also worth noting that while the most common predictor matrices in variation partitioning are spatial and environmental variables, other predictor matrices can be incorporated into the analysis if appropriate, such as phylogenetic (Perez Rocha et al., 2018) and functional trait data (De Bie et al., 2012). Any or all of these approaches can be used effectively to evaluate the drivers of community assembly and evaluate risk of invasion.

To be clear, even without assessing the impact of an invasive species, we posit that a community's degree of sorting strength may be a useful predictor of invasion success in that community. Invasive species need not necessarily be involved in the studies, since the focus is on what structures the pre-invasion community, so these studies can be used as assays to evaluate the potential for invasion before invasion occurs in a locality. One caveat for all of these approaches is that they necessarily involve the evaluation of multiple patches within a metacommunity. In metacommunity ecology, there are no single-patch studies since regional scale processes cannot be evaluated from a single locality. Again, this point underscores a major argument of this contribution: that invasion biology can benefit greatly from larger scale or multi-site studies. Different sets of community processes occurring at different scales may also help explain discrepancies in results of studies on Enemy Release and Biotic Resistance. The search for strictly local explanations of species' membership in communities is destined to produce negative or confounded results when assembly is strongly influenced by regional, dispersal-driven dynamics. In fact, the vast majority of studies of community assembly in metacommunities find that, when evaluating the relative influences of local vs. regional processes in structuring communities, there is rarely an either/or explanation and more often than not, the two sets of forces interact (e.g., Forbes and Chase, 2002; Cottenie et al., 2003; De Bie et al., 2012; Göthe et al., 2013). Thus, for both Biotic Resistance and Enemy Release hypotheses, an interaction between local and regional processes is likely, and mechanistic understanding of successful invasion into a community will likely be elusive without considering both sets of forces.

The Importance of Native Dispersal in Invasion Resistance

Higher rates of dispersal do not always result in stochastic community assembly. When local sorting strength is high and dispersal rates are moderate, dispersal can "fuel" deterministic processes by providing a steady source of colonists that are then sorted into largely deterministic communities by local forces (Cottenie and De Meester, 2004). Under this scenario, high rates of native dispersal may also act as a deterrent to invasion by maximizing local species richness (Cadotte, 2006; Grainger and Gilbert, 2016; **Figure 3A**). Howeth (2017) tested this scenario using zooplankton mesocosms and the invasive cladoceran zooplankton, *Daphnia lumholtzi,* and found that, while holding environmental conditions constant across treatments, experimentally increasing dispersal of native species decreased rates of invasion of *D. lumholtzi*. There appear to be two non-exclusive mechanisms contributing to this effect. The first was that higher rates of dispersal produced *rescue effects* (Brown and Kodric-Brown, 1977) that allowed locally extinct native species to rapidly recolonize. Secondarily, rescue effects resulted in higher species richness of natives in higher-dispersal treatments which resulted in higher niche complementarity, reduced niche space available for the invader, and lower rates of invasion. In the highest dispersal treatments (equating to highest propagule pressure), *D. lumholtzi* had negative growth rates, indicating that native dispersal had resulted in failure of the invader to meet the Invasibility criterion and therefore not be able to coexist with native species (Howeth, 2017).

However, a high rate of dispersal (i.e., high propagule pressure) is also a mechanism that allows many invasive species to colonize and eventually dominate native communities (Simberloff, 2009). Therefore, operationalizing a native dispersal mechanism for invasion resistance will necessarily involve simultaneous consideration of dispersal of both natives and invaders. **Figure 3B** illustrates four bookend scenarios when considering both native and invasive dispersal. Assuming similar local environmental conditions across all four scenarios, scenario a—high invader propagule pressure and low native dispersal—would present the highest invasion risk, while scenario d would present the lowest risk of invasion (high native and low invasive dispersal), with scenarios b and c posing intermediate risk.

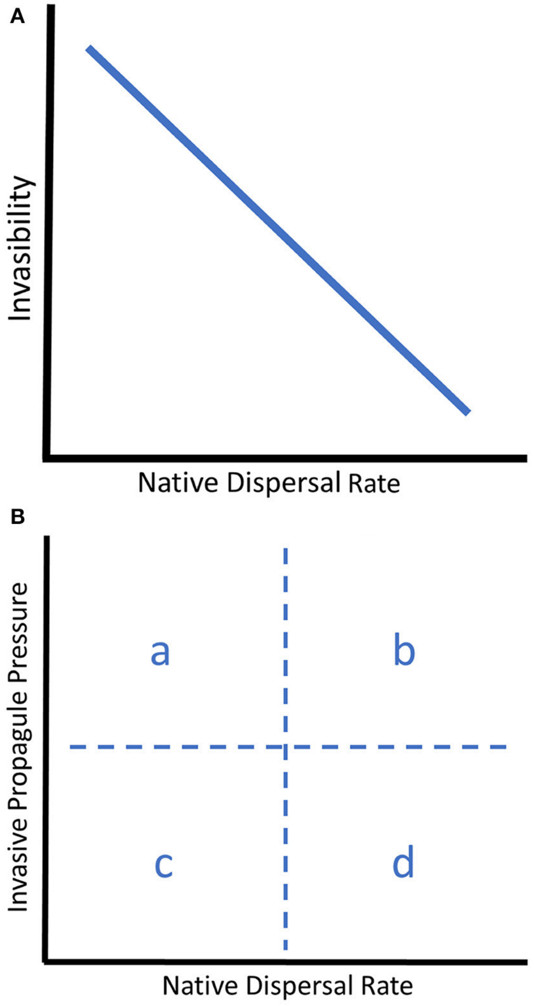


FIGURE 3 | Hypothesized relationships between dispersal and invasibility. **(A)** Hypothesized effect of native dispersal rate of species in a community on the invasibility of that locality. **(B)** Four invasion scenarios defined by propagule pressure of a potential invader and dispersal rates of native species. Scenario *a* represents the highest potential for invasion while scenario *d* represents the lowest potential for invasion. Scenarios *b* and *c* have intermediate potential for invasion and specific outcomes will largely depend on specifics of the local community.

Native-Invasive Diversity Relationships

One of the most controversial and frustrating topics in invasion biology has been the relationship between native and invasive diversity (the so-called Invasion Paradox; Fridley et al., 2007). The two extreme positions in this controversy are Biotic

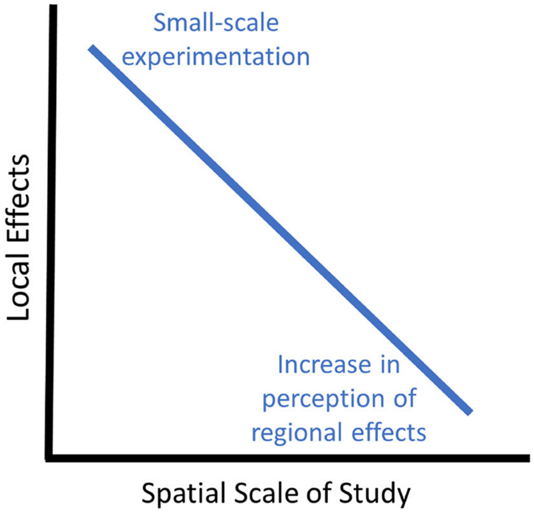


FIGURE 4 | Hypothesized explanation for scale discrepancies in native-invasive relationships. Studies at small spatial scales are only able to perceive local effects and often encourage exacerbated local effects through study design or experimental control. Given the hypothesized relationship between local sorting strength and invasibility (**Figure 5**), signs of Biotic Resistance are frequently detected. Studies at larger spatial scales or spanning multiple spatial scales are better able to perceive regional-scale effects on community assembly and are more likely to observe positive relationships between native biodiversity and invader biodiversity, especially in heterogeneous landscapes.

Resistance, and Biotic Acceptance. We previously defined and discussed Biotic Resistance, and the prediction that emerges from Biotic Resistance is that diversity of native and invasive species should be negatively correlated on a landscape. On the other hand, Biotic Acceptance posits that environmental conditions that are good for natives are also good for invasives, and therefore their abundances should be positively correlated (Stohlgren et al., 2006). While these predictions are straightforward, testable, and easily distinguishable, the issue of scale has complicated a seemingly simple question. At smaller spatial scales, particularly in experimental studies, evidence for Biotic Resistance has been substantial (e.g., Levine et al., 2004; Fridley et al., 2007). In contrast, studies incorporating larger spatial scales have found considerable evidence for Biotic Acceptance (e.g., Stohlgren et al., 2006; Iannone et al., 2016). This difference in results across spatial scales has long been a source of debate for invasion biologists (Shea and Chesson, 2002; Fridley et al., 2007), though some recent work has claimed to resolve this debate in favor of Biotic Resistance by incorporating covariates not included in prior analyses (Beaury et al., 2020), and a global meta-analysis of observational data found no paradox across scales (Peng et al., 2019).

Here we pose another potential explanation for the discrepancy in results across scales, i.e., that different metacommunity processes are being evaluated at different scales. This explanation operates in tandem with our prediction that invasion success will decrease with local sorting strength. At smaller spatial scales—particularly in experiments, which often have limited spatial extent (e.g., Chen et al., 2010; Sandel and Corbin, 2010)—local factors that contribute to sorting strength are readily observable and, in the case of experiments, “localness” may even be strictly maintained. These circumstances create the highest probability of observing local control over community composition, and thus, a decreased probability of invasion success (**Figure 5**). Larger scale studies tend to be observational. As such, both the lack of control of local conditions and the ability to observe dispersal-driven, regional-scale effects are inherent in study design. Taking these points together, we suggest that the scale related discrepancy in results of native-invasive relationships may be an artifact of study designs, that localized studies, especially experiments, are more likely to identify local sorting strength as a driver of community assembly, while larger scale, less controlled studies capture the dispersal-driven regional processes that are fundamental to many metacommunities (**Figure 4**).

Does this potential explanation offer an answer as to whether Biotic Resistance or Biotic Acceptance should be the dominant paradigm? No. Rather, this idea emphasizes the multi-scale processes that are involved in community assembly and suggests that the search for a single, unvarying answer regarding native-invasive relationships is illogical. As predicted in our first hypothesis, invasibility will likely depend on the relative balance of local sorting strength and dispersal-driven dynamics in any single metacommunity. However, this idea does present testable predictions and potential solutions for resolving this “Invasion Paradox” (Fridley et al., 2007). One imminently testable prediction is that the variability in native-invasive relationships should increase with the spatial scale of study because increasing incorporation of regional-scale effects will introduce stochasticity (Leibold et al., 2004; Chase and Myers, 2011). Another way to address this idea is through controlled experiments or designed studies that span scales and can thus be evaluated for both local and regional community dynamics. In the case of direct experimentation, either dispersal or local conditions could be manipulated across a spatial array of study sites. However, similar goals can be accomplished in well-designed survey studies that use observation of communities across spatially arranged sites.

APPLICATIONS OF A METACOMMUNITY APPROACH TO MITIGATE INVASIONS

One of the most intriguing outcomes of integrating metacommunity concepts into invasion biology is the possibility for improved management, which has been a long-term goal of the field. Invasion biologists have long posited that enhanced understanding of basic invasion biology, ecology, and the underlying causes and consequences of invasiveness would collectively lead to our ability to mitigate the current invasion threat and limit future invasion. There are certainly success stories, including weed risk assessment (WRA, Pheloung et al., 1999) and fish invasiveness scoring kit (FISK, Copp et al., 2005),

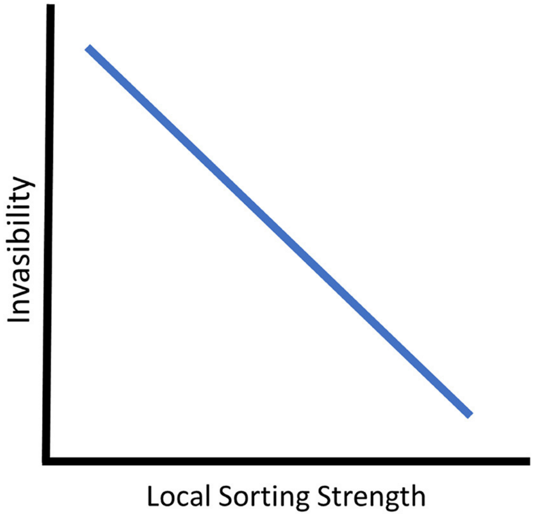


FIGURE 5 | Hypothesized relationship between local sorting strength and invasibility of a local community.

which were designed to identify invasive weed and fishes, pre-introduction, to minimize new invaders. Despite these limited successes, the number of new species introductions continues seemingly unabated (Seebens et al., 2017), necessitating continued development of theory and practice that mitigate current invasion impacts and limit future spread of invaders. We contend that application of the metacommunity concepts outlined above present several key opportunities to enhance invasive species management.

Dispersal Disruption of Invasive Species

Dispersal and propagule pressure are fundamental aspects of invasion that most clearly lend themselves to mitigation. Since invasion is contingent on movement of propagules, disrupting the production and movement of propagules would result in immediate benefits. For example, with emergence of devastating herbicide resistant agricultural weeds, many of which are spread through seed and equipment contamination, many farmers are adopting a "no weed seed" approach that is designed to prevent weed seed production, diversifying weed management tactics, eliminating pollen production, and equipment sanitation (e.g., Norsworthy et al., 2012; Riar et al., 2016). However, effective disruption must consider the interconnectedness of patches, as it is clear that regional propagule dispersal can "rescue" local extinction. Thus, propagules should be managed in a broader spatial context.

Dispersal disruption is also a powerful, yet underutilized tool, to mitigate the spread of invasive species. This technique is currently being recommended for limiting the spread of wavyleaf basketgrass in the Mid-Atlantic US through land management practices and limitations on access to hikers and hunters. The seeds of wavyleaf basketgrass can stick to animals and clothes, easily transporting propagules over large distances (Beauchamp, 2014). Thus, dispersal disruption tactics of avoiding infested areas during seed production, or thoroughly cleaning clothes and equipment have been recommended (Swearingen et al., 2014). This tactic is particularly useful when the introduction/dispersal pathway of the invasive species is known. For example, live bait was identified as a common dispersal pathway in many freshwater systems, and has been targeted to reduce use and release of exotic live bait (Kilian et al., 2012). Recent work has also demonstrated variability in the efficacy of propagule interception using simulation modeling (Latombe et al., 2020). Of course, the management of propagules is not new, but the metacommunity perspective warrants clear identification of patch interconnectedness and dispersal pathways, identifying invasive species functional traits enhancing fitness, as well as an understanding of the dispersal of resident native species as well as invaders and parsing the effects on community dynamics of each.

Community Risk Assessment

Perhaps the most unique management suggestion that emerges from this work is using assessment of native communities as a way to evaluate invasion risk. Risk assessment is not new to invasion biology, and has been used with no small degree of success (Keller et al., 2007). However, current risk assessments focus on the particular invasive species of interest, rather than on the community into which an invader may attempt to colonize. Our invasibility x sorting strength prediction (**Figure 5**), derived from principles of metacommunity ecology, suggests that understanding the assembly mechanisms of an extant metacommunity will provide strong evidence for how invasible that community will be. Communities strongly influenced by regional forces like dispersal should be more vulnerable to invasion, while metacommunities more influenced by local controls should resist invasion. As previously described, metacommunity ecology provides a powerful conceptual framework and a large range of analytical tools for making such evaluations. We should stress, however, that while our prediction emerges as a natural consequence of metacommunity theory, it is still just a prediction and requires empirical evaluation prior to any attempts to operationalize it as a management strategy.

Resilient Communities

The relationship between native and exotic richness remains empirically equivocal, but tactics that enhance native species abundance, dispersal, and connectivity are likely to enhance community resilience to invasive species. Management actions that encourage native species may be more effective than eradicating invasions, the latter of which is relatively rare and often expensive and limited to small infestations (Rejmanek and Pitcairn, 2002). Managing *for* native-rich assemblages should be holistic and multi-scale in nature to manage for both local and regional effects. Management efforts that focus only on local effects (e.g., species/environment interactions) are destined to be ineffective if community assembly is driven by regional scale properties.

One example of application of this approach is the ecologically-based invasive plant management on rangelands, which Krueger-Mangold et al. (2006) describe as incorporating strategies that encourage desirable plant communities and simultaneously disfavor invasive species. This "successional-based" strategy incorporates many of the elements of metacommunity approaches including local and regional processes, species functional traits, and propagule dispersal. Building resilient communities should comprise enhancing local conditions that favor native species and disfavor invasive species, limiting invasive species propagule production, and enhancing native species connectivity. Achieving this will be an inherently system and community-specific approach, and will require knowledge of species functional traits, local environmental conditions, and regional connectedness and processes.

We have predicted—and empirical evidence suggests (Krueger-Mangold et al., 2006)—that native dispersal can be a deterrent to invasions (**Figure 3**). Considering how this prediction can be applied to management, the clear theme that emerges is that managing to support native species may be as effective as attempting to directly reduce invasives. This idea is not new and several previous researchers have suggested that the management of natives may be the most effective way to manage invasions (e.g., Sheley et al., 1996; Krueger-Mangold et al., 2006). However, a nuance suggested by our prediction is that facilitating dispersal of natives should be a priority. This proposal could be viewed as the native equivalent of the invasion cliff posited by Davis (2009) above, with native success being proportional to propagule load. How can native dispersal be encouraged? One possible answer is habitat connectivity. Enhanced connectivity has long been associated with higher local diversity in both theoretical and empirical studies (e.g., Horn and MacArthur, 1972; Brown and Kodric-Brown, 1977; Tilman, 1994; Holyoak and Lawler, 1996; Hanski, 1998; Chesson, 2000; Amarasekare and Nisbet, 2001), and conservation efforts have found success in managing biodiversity through increasing connectivity, at least when connectivity management is successfully implemented (reviewed in Correa Ayram et al., 2016; Keeley et al., 2019). However, connectivity management should also be mindful of the effects of the interaction between connectivity and habitat heterogeneity in which high connectivity can lead to biotic homogenization, especially when environments are relatively homogeneous (Forbes and Chase, 2002; Strecker and Brittain, 2017). In addition, we also want to inject a note of caution. While managing for dispersal abilities of native species should be an effective means of mitigating invasive species' impacts, we do not advocate for human-enhanced dispersal of native species. Such activities could have a number of unintended consequences, including the unintentional movement of invasives. But perhaps more importantly, enhanced dispersal of natives has the potential to repeat the mistakes created by human involvement in invasive species, i.e., decoupling tradeoffs that naturally limit the distributions and abundances of species.

Nativity and Range-Expanding Species

An emerging issue in invasion biology is the rapid increase in species that expand their ranges as a result of human-induced environmental change (Essl et al., 2019). These species, termed "neonative" by Essl et al. (2019), are distinguished from other invasive species in that they expand their ranges without the aid of direct human agency, but do so as an indirect consequence of human induced environmental change. While the concept of neonativity has been criticized and declared a non-useful concept for a number of reasons, even its critics acknowledge that a large number of species of this type exist, and that many are problematic (Wilson, 2020). Vocabulary is often a sticking point in science, and the vocabulary of many concepts has been hotly debated, from community stability (Grimm and Wissel, 1997), to definitions of β-diversity (Anderson et al., 2011), to how to define an ecosystem (O'Neill, 2001). Invasion biology is no exception to this common mania (Richardson et al., 2000; Colautti and MacIsaac, 2004; Colautti and Richardson, 2009).

Defining invasive species will always be a necessity, particularly for regulation and management, but we suggest that a shift of focus from specific invasive species to communities of interest will move the conversation from identifying and defining invaders, to examining *effects* of invaders. While this perspective of invasives as just another species in a community may seem shortsighted and to downplay the importance of invaders, we contend that invaders are important for their effects on communities, not solely for their identities as invaders. It would also be unjust to suggest that metacommunity approaches can't or don't single out particular species for their effects in a metacommunity. One common prediction in many metacommunity models is that high rates of dispersal will allow competitively dominant species to reach all local communities in a metacommunity, resulting in biotic homogenization (Mouquet and Loreau, 2003; Mouquet et al., 2005), a prediction that has also been empirically verified in a number of studies (e.g., Forbes and Chase, 2002; Livingston et al., 2012). Thus, while a major focus of an investigation of an invaded metacommunity may be on the community as a whole, invaders can still be singled out and examined for their specific effects.

CONCLUSION

Invasion Biology has long been a field that sits at the intersection of basic and applied science and has been exemplary in the pursuit of converting theory and concept to practice. However, invasion is a community ecology problem, and community ecology has experienced a paradigm shift in recent years. Metacommunity theory and approaches have revolutionized the field of community ecology, but their adoption into the field of Invasion Biology has been slow. Here we have illustrated how some of the most fundamental concepts of Invasion Biology can be viewed through a metacommunity lens, demonstrated that this change in perspective can produce useful predictions regarding invasions, and illustrated how those concepts can be directly applied to management. Likewise, we encourage the metacommunity scientists to examine invasions as interesting and useful study systems to explore their theory and concepts. We stress that our treatment of invasion concepts is not exhaustive and serve more as illustration of potential than a comprehensive guide to the metacommunity ecology of invasions. Two pervasive themes that we repeatedly visit are the potential benefits of focusing on communities rather than on specific invaders, and the need for a multi-scale approach to Invasion Biology. Our hope is that this contribution will catalyze thought and provide a starting point for investigations that successfully wed Invasion Biology with metacommunity approaches.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary materials, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

BB and JB were involved in conceptual development, writing, and editing. Both authors contributed to the article and approved the submitted version.

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REFERENCES

Ackerly, D. D., and Cornwell, W. K. (2007). A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. *Ecol. Lett.* 10, 135–145. doi: 10.1111/j.1461-0248.2006.01006.x

Altermatt, F., and Fronhofer, E. A. (2018). Dispersal in dendritic networks: ecological consequences on the spatial distribution of population densities. *Freshw. Biol.* 63, 22–32. doi: 10.1111/fwb.12951

Amarasekare, P., and Nisbet, R. M. (2001). Spatial heterogeneity, source-sink dynamics, and the local coexistence of competing species. *Am. Nat.* 158, 572–584. doi: 10.1086/323586

Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., et al. (2011). Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecol. Lett.* 14, 19–28. doi: 10.1111/j.1461-0248.2010.01552.x

Andrade, R., Franklin, J., Larson, K. L., Swan, C. M., Lerman, S. B., Bateman, H. L., et al. (2020). Predicting the assembly of novel communities in urban ecosystems. *Landsc. Ecol.* doi: 10.1007/s10980-020-01142-1

Baiser, B., Buckley, H. L., Gotelli, N. J., and Ellison, A. M. (2013). Predicting food-web structure with metacommunity models. *Oikos* 122, 492–506. doi: 10.1111/j.1600-0706.2012.00005.x

Barney, J. N., Ho, M. W., and Atwater, D. Z. (2016). Propagule pressure cannot always overcome biotic resistance: the role of density-dependent establishment in four invasive species. *Weed Res.* 56, 208–218. doi: 10.1111/wre.12204

Barney, J. N., and Whitlow, T. H. (2008). A unifying framework for biological invasions: the state factor model. *Biol. Invasions* 10, 259–272. doi: 10.1007/s10530-007-9127-8

Beauchamp, V. B. (2014). *Wavyleaf Basketgrass: Help Stop It Now*! Virginia Native Plant Society.

Beaury, E. M., Finn, J. T., Corbin, J. D., Barr, V., and Bradley, B. A. (2020). Biotic resistance to invasion is ubiquitous across ecosystems of the United States. *Ecol. Lett.* 23, 476–482. doi: 10.1111/ele.13446

Bell, G. (2001). Neutral macroecology. *Science* 293, 2413–2418. doi: 10.1126/science.293.5539.2413

Berg, M., and Ellers, J. (2010). Trait plasticity in species interactions: a driving force of community dynamics. *Evol. Ecol.* 24, 617–629. doi: 10.1007/s10682-009-9347-8

Bertelsmeier, C., and Keller, L. (2018). Bridgehead effects and role of adaptive evolution in invasive populations. *Trends Ecol. Evol.* 33, 527–534. doi: 10.1016/j.tree.2018.04.014

Biswas, S. R., Mallik, A. U., Braithwaite, N. T., and Wagner, H. H. (2016). A conceptual framework for the spatial analysis of functional trait diversity. *Oikos* 125, 192–200. doi: 10.1111/oik.02277

Blanchet, F. G., Cazelles, K., and Gravel, D. (2020). Co-occurrence is not evidence of ecological interactions. *Ecol. Lett.* 23, 1050–1063. doi: 10.1111/ele.13525

Blossey, B., and Notzold, R. (1995). Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *J. Ecol.* 83, 887–889. doi: 10.2307/2261425

Borcard, D., Legendre, P., and Drapeau, P. (1992). Partialling out the spatial component of ecological variation. *Ecology* 73, 1045–1055. doi: 10.2307/1940179

Boyce, M. S. (1984). Restitution of r- and K-selection as a model of density-dependent natural selection. *Annu. Rev. Ecol. Syst.* 15, 427–447. doi: 10.1146/annurev.es.15.110184.002235

Brown, B. L., Sokol, E. R., Skelton, J., and Tornwall, B. (2017). Making sense of metacommunities: dispelling the mythology of a metacommunity typology. *Oecologia* 183, 643–652. doi: 10.1007/s00442-016-3792-1

Brown, B. L., and Swan, C. M. (2010). Dendritic network structure constrains metacommunity properties in riverine ecosystems. *J. Anim. Ecol.* 79, 571–580. doi: 10.1111/j.1365-2656.2010.01668.x

Brown, B. L., Wahl, C., and Swan, C. M. (2018). Experimentally disentangling the influence of dispersal and habitat filtering on benthic invertebrate community structure. *Freshw. Biol.* 63, 48–61. doi: 10.1111/fwb.12995

Brown, J. H., and Kodric-Brown, A. (1977). Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58, 445–449. doi: 10.2307/1935620

Büchi, L., and Vuilleumier, S. (2014). Coexistence of specialist and generalist species is shaped by dispersal and environmental factors. *Am. Nat.* 183, 612–624. doi: 10.1086/675756

Cadotte, M., Albert, C. H., and Walker, S. C. (2013). The ecology of differences: assessing community assembly with trait and evolutionary distances. *Ecol. Lett.* 16, 1234–1244. doi: 10.1111/ele.12161

Cadotte, M. W. (2006). Metacommunity influences on community richness at multiple spatial scales: a microcosm experiment. *Ecology* 87, 1008–1016. doi: 10.1890/0012-9658(2006)87[1008:MIOCRA]2.0.CO;2

Calcagno, V., Mouquet, N., Jarne, P., and David, P. (2006). Coexistence in a metacommunity: the competition-colonization trade-off is not dead. *Ecol. Lett.* 9, 897–907. doi: 10.1111/j.1461-0248.2006.00930.x

Cárdenas, L., Leclerc, J.-C., Bruning, P., Garrido, I., Détrée, C., Figueroa, A., et al. (2020). First mussel settlement observed in Antarctica reveals the potential for future invasions. *Sci. Rep.* 10:5552. doi: 10.1038/s41598-020-62340-0

Carrara, F., Altermatt, F., Rodriguez-Iturbe, I., and Rinaldo, A. (2012). Dendritic connectivity controls biodiversity patterns in experimental metacommunities. *Proc. Natl. Acad. Sci. U.S.A.* 109, 5761–5766. doi: 10.1073/pnas.1119651109

Catford, J. A., Jansson, R., and Nilsson, C. (2009). Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Divers. Distribut.* 15, 22–40. doi: 10.1111/j.1472-4642.2008.00521.x

Chao, A., Chiu, C.-H., and Hsieh, T. C. (2012). Proposing a resolution to debates on diversity partitioning. *Ecology* 93, 2037–2051. doi: 10.1890/11-1817.1

Chase, J. M. (2003). Community assembly: when should history matter? *Oecologia* 136, 489–498. doi: 10.1007/s00442-003-1311-7

Chase, J. M. (2007). Drought mediates the importance of stochastic community assembly. *Proc. Natl. Acad. Sci. U.S.A.* 104, 17430–17434. doi: 10.1073/pnas.0704350104

Chase, J. M. (2010). Stochastic community assembly causes higher biodiversity in more productive environments. *Science* 328, 1388–1391. doi: 10.1126/science.1187820

Chase, J. M., Amarasekare, P., Cottenie, K., Gonzalez, A., Holt, R. D., Holyoak, M., et al. (2005). "Competing theories for competitive metacommunities," in *Metacommunities: Spatial Dynamics and Ecological Communities,* eds M. Holyoak, M. A. Leibold, and R. D. Holt (Chicago, IL; London: University of Chicago Press), 335–354.

Chase, J. M., and Myers, J. A. (2011). Disentangling the importance of ecological niches from stochastic processes across scales. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 366, 2351–2363. doi: 10.1098/rstb.2011.0063

Chen, H., Qian, H., Spyreas, G., and Crossland, M. (2010). BIODIVERSITY RESEARCH: native-exotic species richness relationships across spatial scales and biotic homogenization in wetland plant communities of Illinois, USA. *Divers. Distribut.* 16, 737–743. doi: 10.1111/j.1472-4642.2010.00679.x

Chesson, P., and Huntly, N. (1997). The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *Am. Nat.* 150, 519–553. doi: 10.1086/286080

Chesson, P. L. (2000). Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.* 31, 343–366. doi: 10.1146/annurev.ecolsys.31.1.343

Chwedorzewska, K. J., Giełwanowska, I., Olech, M., Molina-Montenegro, M. A., Wódkiewicz, M., and Galera, H. (2015). *Poa annua* L. in the maritime antarctic: an overview. *Polar Rec.* 51, 637–643. doi: 10.1017/S0032247414000916

Colautti, R. I., Grigorovich, I. A., and MacIsaac, H. J. (2006). Propagule pressure: a null model for biological invasions. *Biol. Invasions* 8, 1023–1037. doi: 10.1007/s10530-005-3735-y

Colautti, R. I., and MacIsaac, H. J. (2004). A neutral terminology to define 'invasive' species. *Divers. Distribut.* 10, 135–141. doi: 10.1111/j.1366-9516.2004.00061.x

Colautti, R. I., and Richardson, D. M. (2009). Subjectivity and flexibility in invasion terminology: too much of a good thing? *Biol. Invasions* 11, 1225–1229. doi: 10.1007/s10530-008-9333-z

Copp, G. H., Garthwaite, R., and Gozlan, R. E. (2005). Risk identification and assessment of non-native freshwater fishes: a summary of concepts and perspectives on protocols for the UK. *J. Appl. Ichthyol.* 21, 371–373. doi: 10.1111/j.1439-0426.2005.00692.x

Correa Ayram, C. A., Mendoza, M. E., Etter, A., and Salicrup, D. R. P. (2016). Habitat connectivity in biodiversity conservation: a review of recent studies and applications. *Progr. Phys. Geogr.* 40, 7–37. doi: 10.1177/0309133315598713

Cote, J., Brodin, T., Fogarty, S., and Sih, A. (2017). Non-random dispersal mediates invader impacts on the invertebrate community. *J. Anim. Ecol.* 86, 1298–1307. doi: 10.1111/1365-2656.12734

Cottenie, K. (2005). Integrating environmental and spatial processes in ecological community dynamics. *Ecol. Lett.* 8, 1175–1182. doi: 10.1111/j.1461-0248.2005.00820.x

Cottenie, K., and de Meester, L. (2003). Connectivity and cladoceran species richness in a metacommunity of shallow lakes. *Freshw. Biol.* 48, 823–832. doi: 10.1046/j.1365-2427.2003.01050.x

Cottenie, K., and De Meester, L. (2004). Metacommunity structure: synergy of biotic interactions as selective agents and dispersal as fuel. *Ecology* 85, 114–119. doi: 10.1890/03-3004

Cottenie, K., Michels, E., Nuytten, N., and DeMeester, L. (2003). Zooplankton metacommunity structure: regional vs. local processes in highly interconnected ponds. *Ecology* 84, 991–1000. doi: 10.1890/0012-9658(2003)084[0991:ZMSRVL]2.0.CO;2

Crystal-Ornelas, R., and Lockwood, J. L. (2020). The 'known unknowns' of invasive species impact measurement. *Biol. Invasions* 22, 1513–1525. doi: 10.1007/s10530-020-02200-0

Dallas, T., Melbourne, B. A., and Hastings, A. (2019). When can competition and dispersal lead to checkerboard distributions? *J. Anim. Ecol.* 88, 269–276. doi: 10.1111/1365-2656.12913

Datry, T., Bonada, N., and Heino, J. (2016). Towards understanding the organisation of metacommunities in highly dynamic ecological systems. *Oikos* 125, 149–159. doi: 10.1111/oik.02922

Davidson, A. M., Jennions, M., and Nicotra, A. B. (2011). Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. *Ecol. Lett.* 14, 419–431. doi: 10.1111/j.1461-0248.2011.01596.x

Davis, M. A. (2009). *Invasion Biology*. New York, NY: Oxford University Press.

De Bie, T., De Meester, L., Brendonck, L., Martens, K., Goddeeris, B., Ercken, D., et al. (2012). Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. *Ecol. Lett.* 15, 740–747. doi: 10.1111/j.1461-0248.2012.01794.x

Diaz, S., and Cabido, M. (2001). Vive la différence: plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.* 16, 646–655. doi: 10.1016/S0169-5347(01)02283-2

Diniz-Filho, J. A. F., Siqueira, T., Padial, A. A., Rangel, T. F., Landeiro, V. L., and Bini, L. M. (2012). Spatial autocorrelation analysis allows disentangling the balance between neutral and niche processes in metacommunities. *Oikos* 121, 201–210. doi: 10.1111/j.1600-0706.2011.19563.x

Dray, S., and Legendre, P. (2008). Testing the species traits-environment relationships: the fourth-corner problem revisited. *Ecology* 89, 3400–3412. doi: 10.1890/08-0349.1

Drenovsky, R. E., Grewell, B. J., D'Antonio, C. M., Funk, J. L., James, J. J., Molinari, N., et al. (2012). A functional trait perspective on plant invasion. *Ann. Bot.* 110, 141–153. doi: 10.1093/aob/mcs100

Economo, E. P., and Keitt, T. H. (2008). Species diversity in neutral metacommunities: a network approach. *Ecology Letters* 10, 52–62. doi: 10.1111/j.1461-0248.2007.01126.x

Elton, C. S. (1958). *The Ecology of Invasions by Animals and Plants*. Methuen, MA; London: Chapman and Hall Ltd. doi: 10.1007/978-1-4899-7214-9

Enders, M., Havemann, F., Ruland, F., Bernard-Verdier, M., Catford, J. A., Gómez-Aparicio, L., et al. (2020). A conceptual map of invasion biology: integrating hypotheses into a consensus network. *Glob. Ecol. Biogeogr.* 29, 978–991. doi: 10.1111/geb.13082

Essl, F., Dullinger, S., Genovesi, P., Hulme, P. E., Jeschke, J. M., Katsanevakis, S., et al. (2019). A conceptual framework for range-expanding species that track human-induced environmental change. *BioScience*. 69, 908–919. doi: 10.1093/biosci/biz101

Falster, D. S., Brännström, Å., Westoby, M., and Dieckmann, U. (2017). Multitrait successional forest dynamics enable diverse competitive coexistence. *Proc. Natl. Acad. Sci. U.S.A.* 114, E2719–E2728. doi: 10.1073/pnas.1610206114

Forbes, A. E., and Chase, J. M. (2002). The role of habitat connectivity and landscape geometry in experimental zooplankton metacommunities. *Oikos* 96, 433–440. doi: 10.1034/j.1600-0706.2002.960305.x

Fridley, J. D. (2010). "Biodiversity as a bulwark against invasion: conceptual threads since elton," in *Fifty Years of Invasion Ecology,* ed D. M. Richardson (Oxford: Blackwell), 121–130. doi: 10.1002/9781444329988.ch10

Fridley, J. D., Stachowicz, J. J., Naeem, S., Sax, D. F., Seabloom, E. W., Smith, M. D., et al. (2007). The invasion paradox: reconciling pattern and process in species invasions. *Ecology* 88, 3–17. doi: 10.1890/0012-9658(2007)88[3:TIPRPA]2.0.CO;2

Frisch, D., Cottenie, K., Badosa, A., and Green, A. J. (2012). Strong spatial influence on colonization rates in a pioneer zooplankton metacommunity. *PLoS ONE* 7:e40205. doi: 10.1371/journal.pone.0040205

Funk, J. L., Cleland, E. E., Suding, K. N., and Zavaleta, E. S. (2008). Restoration through reassembly: plant traits and invasion resistance. *Trends Ecol. Evol.* 23, 695–703. doi: 10.1016/j.tree.2008.07.013

Funk, J. L., and Wolf, A. A. (2016). Testing the trait-based community framework: do functional traits predict competitive outcomes? *Ecology* 97, 2206–2211. doi: 10.1002/ecy.1484

Gallien, L., and Carboni, M. (2017). The community ecology of invasive species: where are we and what's next? *Ecography* 40, 335–352. doi: 10.1111/ecog.02446

Garland, T. Jr. (2014). Trade-offs. *Curr. Biol.* 24, R60–R61. doi: 10.1016/j.cub.2013.11.036

Gilroy, J. J., Avery, J. D., and Lockwood, J. L. (2017). Seeking international agreement on what it means to be "Native". *Conserv. Lett.* 10, 238–247. doi: 10.1111/conl.12246

Göthe, E., Angeler, D. G., and Sandin, L. (2013). Metacommunity structure in a small boreal stream network. *J. Anim. Ecol.* 82, 449–458. doi: 10.1111/1365-2656.12004

Grainger, T. N., and Gilbert, B. (2016). Dispersal and diversity in experimental metacommunities: linking theory and practice. *Oikos* 125, 1213–1223. doi: 10.1111/oik.03018

Gravel, D., Canard, E., Guichard, F., and Mouquet, N. (2011). Persistence increases with diversity and connectance in trophic metacommunities. *PLoS ONE* 6:e19374. doi: 10.1371/journal.pone.0019374

Grimm, V., and Wissel, C. (1997). Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia* 109, 323–334. doi: 10.1007/s004420050090

Grönroos, M., Heino, J., Siqueira, T., Landeiro, V. L., Kotanen, J., and Bini, L. M. (2013). Metacommunity structuring in stream networks: roles of dispersal mode, distance type, and regional environmental context. *Ecol. Evol.* 3, 4473–4487. doi: 10.1002/ece3.834

Grover, J. P. (1997). *Resouce Competition*. London: Chapman and Hall. doi: 10.1007/978-1-4615-6397-6

Gurevitch, J., Fox, G. A., Wardle, G., Inderjit, M., and Taub, D. (2011). Emergent insights from the synthesis of conceptual frameworks for biological invasions. *Ecol. Lett.* 14, 407–418. doi: 10.1111/j.1461-0248.2011.01594.x

Guzman, L. M., Germain, R. M., Forbes, C., Straus, S., O'Connor, M. I., Gravel, D., et al. (2019). Towards a multi-trophic extension of metacommunity ecology. *Ecol. Lett.* 22, 19–33. doi: 10.1111/ele.13162

Hanski, I. (1998). Metapopulation dynamics. *Nature* 396, 41–49. doi: 10.1038/23876

Hastings, A. (1980). Disturbance, coexistence, history, and competition for space. *Theor. Popul. Biol.* 18, 363–373. doi: 10.1016/0040-5809(80)90059-3

He, S., Soininen, J., Chen, K., and Wang, B. (2020). Environmental factors override dispersal-related factors in shaping diatom and macroinvertebrate communities within stream networks in China. *Front. Ecol. Evol.* 8:141. doi: 10.3389/fevo.2020.00141

Heino, J. (2011). A macroecological perspective of diversity patterns in the freshwater realm. *Freshw. Biol.* 56, 1703–1722. doi: 10.1111/j.1365-2427.2011.02610.x

Heino, J., Melo, A. S., Siqueira, T., Soininen, J., Valanko, S., and Bini, L. M. (2015). Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. *Freshw. Biol.* 60, 845–869. doi: 10.1111/fwb.12533

Heino, J., and Mykrä, H. (2008). Control of stream insect assemblages: roles of spatial configuration and local environmental factors. *Ecol. Entomol.* 33, 614–622. doi: 10.1111/j.1365-2311.2008.01012.x

Hillebrand, H., Bennett, D. M., and Cadotte, M. W. (2008). Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology* 89, 1510–1520. doi: 10.1890/07-1053.1

Holbrook, J. B. (2013). What is interdisciplinary communication? Reflections on the very idea of disciplinary integration. *Synthese* 190, 1865–1879. doi: 10.1007/s11229-012-0179-7

Holt, R. D. (1977). Predation, apparent competition and the structure of prey communities. *Theor. Popul. Biol.* 12, 197–229. doi: 10.1016/0040-5809(77)90042-9

Holt, R. D., Grover, J., and Tilman, D. (1994). Simple rules for interspecific dominance in systems with exploitative and apparent competition. *Am. Nat.* 144, 741–771. doi: 10.1086/285705

Holyoak, M., and Lawler, S. P. (1996). Persistence of an extinction-prone predator-prey interaction through metapopulation dynamics. *Ecology* 77, 1867–1879. doi: 10.2307/2265790

Holyoak, M., Leibold, M. A., and Holt, R. D. (2005). *Metacommunities: Spatial Dynamics and Ecological Communities, 1 Edn*. Chicago, IL and London: University of Chicago Press.

Horn, H. S., and MacArthur, R. H. (1972). Competition among fugitive species in a harlequin environment. *Ecology* 53, 749–752. doi: 10.2307/1934797

Howeth, J. G. (2017). Native species dispersal reduces community invasibility by increasing species richness and biotic resistance. *J. Anim. Ecol.* 86, 1380–1393. doi: 10.1111/1365-2656.12733

Howeth, J. G., Derry, A. M., and Reitzel, A. M. (2010). "Metacommunity biology as an eco-evolutionary framework for understanding exotic invasion in aquatic ecosystems," in *Eco-DAS VIII Symposium. American Society of Limnology and Oceanography* (American Society of Limnology and Oceanography), 93–109.

Hubbell, S. P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton, NJ: Princeton University Press.

Hui, C., and Richardson, D. M. (2017). "Chapter 8: Community Assembly and Succession," in *Invasion Dynamics* (Oxford: Oxford University Press), 191–221. doi: 10.1093/acprof:oso/9780198745334.003.0008

Hulme, P. E., Pyšek, P., Jarošík, V., Pergl, J., Schaffner, U., and Vilà, M. (2013). Bias and error in understanding plant invasion impacts. *Trends Ecol. Evol.* 28, 212–218. doi: 10.1016/j.tree.2012.10.010

Hunt, J. J. F. G., and Bonsall, M. B. (2009). The effects of colonization, extinction and competition on co-existence in metacommunities. *J. Anim. Ecol.* 78, 866–879. doi: 10.1111/j.1365-2656.2009.01532.x

Hutchinson, G. E. (1959). Homage to santa rosalia or why are there so many kinds of animals? *Am. Nat.* 63, 145–159. doi: 10.1086/282070

Iannone, B. V., Potter, K. M., Hamil, K.-A. D., Huang, W., Zhang, H., Guo, Q., et al. (2016). Evidence of biotic resistance to invasions in forests of the Eastern USA. *Landsc. Ecol.* 31, 85–99. doi: 10.1007/s10980-015-0280-7

Jamoneau, A., Chabrerie, O., Closset-Kopp, D., and Decocq, G. (2012). Fragmentation alters beta-diversity patterns of habitat specialists within forest metacommunities. *Ecography* 35, 124–133. doi: 10.1111/j.1600-0587.2011.06900.x

Jarić, I., and Cvijanović, G. (2012). The tens rule in invasion biology: measure of a true impact or our lack of knowledge and understanding? *Environ. Manage.* 50, 979–981. doi: 10.1007/s00267-012-9951-1

Jeschke, J., Gómez Aparicio, L., Haider, S., Heger, T., Lortie, C., Pyšek, P., et al. (2012). Support for major hypotheses in invasion biology is uneven and declining. *NeoBiota* 14, 1–20. doi: 10.3897/neobiota.14.3435

Johnson, A. L., and Swan, C. M. (2014). "Drivers of vegetation species diversity and composition in urban ecosystems," in *Urban Wildlife Conservation: Theory and Practice,* eds R. A. McCleery, C. E. Moorman, and M. N. Peterson (Boston: Springer), 75–90. doi: 10.1007/978-1-4899-7500-3_5

Johnson, A. L., Tauzer, E. C., and Swan, C. M. (2015). Human legacies differentially organize functional and phylogenetic diversity of urban herbaceous plant communities at multiple spatial scales. *Appl. Vegetation Sci.* 18, 513–527. doi: 10.1111/avsc.12155

Jost, L. (2007). Partitioning diversity into independent alpha and beta components. *Ecology* 88, 2427–2439. doi: 10.1890/06-1736.1

Keane, R. M., and Crawley, M. J. (2002). Exotic plant invasions and the enemy release hypothesis. *Trends Ecol. Evol.* 17, 164–170. doi: 10.1016/S0169-5347(02)02499-0

Keeley, A. T. H., Beier, P., Creech, T., Jones, K., Jongman, R. H. G., Stonecipher, G., et al. (2019). Thirty years of connectivity conservation planning: an assessment of factors influencing plan implementation. *Environ. Res. Lett.* 14:103001. doi: 10.1088/1748-9326/ab3234

Keller, R. P., Lodge, D. M., and Finnoff, D. C. (2007). Risk assessment for invasive species produces net bioeconomic benefits. *Proc. Natl. Acad. Sci. U.S.A.* 104, 203–207. doi: 10.1073/pnas.0605787104

Kilian, J. V., Klauda, R. J., Widman, S., Kashiwagi, M., Bourquin, R., Weglein, S., et al. (2012). An assessment of a bait industry and angler behavior as a vector of invasive species. *Biol. Invasions* 14, 1469–1481. doi: 10.1007/s10530-012-0173-5

Knapp, S., Dinsmore, L., Fissore, C., Hobbie, S. E., Jakobsdottir, I., Kattge, J., et al. (2012). Phylogenetic and functional characteristics of household yard floras and their changes along an urbanization gradient. *Ecology* 93, S83–S98. doi: 10.1890/11-0392.1

Kneitel, J. M., and Chase, J. M. (2004). Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecol. Lett.* 7, 69–80. doi: 10.1046/j.1461-0248.2003.00551.x

Krueger-Mangold, J. M., Sheley, R. L., and Svejcar, T. J. (2006). Toward ecologically-based invasive plant management on rangeland. *Weed Sci.* 54, 597–605. doi: 10.1614/WS-05-049R3.1

Latombe, G., Essl, F., and McGeoch, M. A. (2020). The effect of cross-boundary management on the trajectory to commonness in biological invasions. *NeoBiota* 62, 241–267. doi: 10.3897/neobiota.62.52708

Lawton, J. H. (1999). Are there general laws in ecology? *Oikos* 84, 177–192. doi: 10.2307/3546712

Legault, G., Bitters, M. E., Hastings, A., and Melbourne, B. A. (2020). Interspecific competition slows range expansion and shapes range boundaries. *Proc. Natl. Acad. Sci. U.S.A.* 117, 26854–26860. doi: 10.1073/pnas.2009701117

Legendre, P., Galzin, R., and Harmelin-Vivien, M. L. (1997). Relating behavior to habitat: solutions to the fourth-corner problem. *Ecology* 78, 547–562. doi: 10.2307/2266029

Leibold, M. A. (1996). A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. *Am. Nat.* 147, 784–812. doi: 10.1086/285879

Leibold, M. A., and Chase, J. M. (2018). *Metacommunity Ecology*. Princeton, NJ; Oxford: Princeton University Press. doi: 10.1515/9781400889068

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., et al. (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.* 7, 601–613. doi: 10.1111/j.1461-0248.2004.00608.x

Leibold, M. A., and Mikkelson, G. M. (2002). Coherence, species turnover, and boundary clumping: elements of meta-community structure. *Oikos* 97, 237–250. doi: 10.1034/j.1600-0706.2002.970210.x

Lenda, M., Knops, J. H., Skórka, P., Moroń, D., and Woyciechowski, M. (2018). Cascading effects of changes in land use on the invasion of the walnut juglans regia in forest ecosystems. *J. Ecol.* 106, 671–686. doi: 10.1111/1365-2745.12827

Levin, S. A. (1974). Dispersion and population interactions. *Am. Natural.* 108, 207–228.

Levine, J. M., Adler, P. B., and Yelenik, S. G. (2004). A meta-analysis of biotic resistance to exotic plant invasions. *Ecol. Lett.* 7, 975–989. doi: 10.1111/j.1461-0248.2004.00657.x

Levins, R., and Culver, D. (1971). Regional coexistence of species and competition between rare species. *Proc. Natl. Acad. Sci.U.S.A.* 68, 1246–1248. doi: 10.1073/pnas.68.6.1246

Lewin, R. (1986). Supply side ecology. *Science* 234, 25–27. doi: 10.1126/science.234.4772.25

Limberger, R., Pitt, A., Hahn, M. W., and Wickham, S. A. (2019). Spatial insurance in multi-trophic metacommunities. *Ecol. Lett.* 22, 1828–1837. doi: 10.1111/ele.13365

Liu, H., and Stiling, P. (2006). Testing the enemy release hypothesis: a review and meta-analysis. *Biol. Invasions* 8, 1535–1545. doi: 10.1007/s10530-005-5845-y

Livingston, G., Matias, M., Calcagno, V., Barbera, C., Combe, M., Leibold, M. A., et al. (2012). Competition–colonization dynamics in experimental bacterial metacommunities. *Nat. Commun.* 3:1234. doi: 10.1038/ncomms2239

Lockwood, J. L., Cassey, P., and Blackburn, T. (2005). The role of propagule pressure in explaining species invasions. *Trends Ecol. Evol.* 20, 223–228. doi: 10.1016/j.tree.2005.02.004

Lockwood, J. L., Cassey, P., and Blackburn, T. M. (2009). The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. *Div. Distr.* 15, 904–910.

Logue, J. B., Mouquet, N., Peter, H., and Hillebrand, H. (2011). Empirical approaches to metacommunities: a review and comparison with theory. *Trends Ecol. Evol.* 26, 482–491. doi: 10.1016/j.tree.2011.04.009

Lombaert, E., Guillemaud, T., Cornuet, J.-M., Malausa, T., Facon, B., and Estoup, A. (2010). Bridgehead effect in the worldwide invasion of the biocontrol harlequin ladybird. *PLoS ONE* 5:e9743. doi: 10.1371/journal.pone.0009743

Loreau, M., Mouquet, N., and Gonzalez, A. (2003). Biodiversity as spatial insurance in heterogeneous landscapes. *Proc. Natl. Acad. Sci. U.S.A.* 100, 12765–12770. doi: 10.1073/pnas.2235465100

Lowe, W. H., and McPeek, M. A. (2014). Is dispersal neutral? *Trends Ecol. Evol.* 29, 444–450. doi: 10.1016/j.tree.2014.05.009

MacArthur, R. (1972). *Geographical Ecology*. Princeton, NJ: Princeton University Press.

MacArthur, R. H. (1970). Species packing and competitive equilibria for many species. *Theor. Popul. Biol.* 1, 1–11. doi: 10.1016/0040-5809(70)90039-0

MacArthur, R. H., and Wilson, E. O. (1967). *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.

Matias, M. G., Mouquet, N., and Chase, J. M. (2013). Dispersal stochasticity mediates species richness in source–sink metacommunities. *Oikos* 122, 395–402. doi: 10.1111/j.1600-0706.2012.20479.x

Meijer, K., Schilthuizen, M., Beukeboom, L., and Smit, C. (2016). A review and meta-analysis of the enemy release hypothesis in plant-herbivorous insect systems. *PeerJ* 4:e2778. doi: 10.7717/peerj.2778

Melián, C. J., Krivan, V., Altermatt, F., Starý, P., Pellissier, L., and Laender, F. D. (2015). Dispersal dynamics in food webs. *Am. Nat.* 185, 157–168. doi: 10.1086/679505

Mitchell, C. E., and Power, A. G. (2003). Release of invasive plants from fungal and viral pathogens. *Nature* 421, 625–627. doi: 10.1038/nature01317

Moles, A. T., Gruber, M. A. M., and Bonser, S. P. (2008). A new framework for predicting invasive plant species. *J. Ecol.* 96, 13–17. doi: 10.1111/j.1365-2745.2007.01332.x

Moritz, C., Meynard, C. N., Devictor, V., Guizien, K., Labrune, C., Guarini, J. M., et al. (2013). Disentangling the role of connectivity, environmental filtering, and spatial structure on metacommunity dynamics. *Oikos* 122, 1401–1410. doi: 10.1111/j.1600-0706.2013.00377.x

Morlon, H., Chuyong, G., Condit, R., Hubbell, S., Kenfack, D., Thomas, D., et al. (2008). A general framework for the distance-decay of similarity in ecological communities. *Ecol. Lett.* 11, 904–917. doi: 10.1111/j.1461-0248.2008.01202.x

Mouquet, N., Hoopes, M. F., and Amarasekare, P. (2005). "The world is patchy and heterogeneous! Trade-off and source-sink dynamics in competitive metacommunities," in *Metacommunities: Spatial Dynamics and Ecological Communities,* eds M. Holyoak, M. A. Leibold, and R. D. Holt (Chicago, IL; London: University of Chicago Press), 237–262.

Mouquet, N., and Loreau, M. (2003). Community patterns in source-sink metacommunities. *Am. Nat.* 162, 544–557. doi: 10.1086/378857

Mwangi, P. N., Schmitz, M., Scherber, C., Roscher, C., Schumacher, J., Scherer-Lorenzen, M., et al. (2007). Niche pre-emption increases with species richness in experimental plant communities. *J. Ecol.* 95, 65–78. doi: 10.1111/j.1365-2745.2006.01189.x

Nekola, J. C., and White, P. S. (1999). The distance decay of similarity in biogeography and ecology. *J. Biogeogr.* 26, 867–878. doi: 10.1046/j.1365-2699.1999.00305.x

Niemiera, A. X., and Von Holle, B. (2009). *Invasive Plants–A Horticultural Perspective*. Virginia Cooperative Extension. doi: 10.1002/9780470767986.ch8

Norsworthy, J. K., Ward, S. M., Shaw, D. R., Llewellyn, R. S., Nichols, R. L., Webster, T. M., et al. (2012). Reducing the risks of herbicide resistance: best management practices and recommendations. *Weed Sci.* 60, 31–62. doi: 10.1614/WS-D-11-00155.1

Oficialdegui, F. J., Clavero, M., Sánchez, M. I., Green, A. J., Boyero, L., Michot, T. C., et al. (2019). Unravelling the global invasion routes of a worldwide invader, the red swamp crayfish (*Procambarus clarkii*). *Freshw. Biol.* 64, 1382–1400. doi: 10.1111/fwb.13312

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D. J., et al. (2020). *Vegan: Community Ecology Package*. R package version 2. 5–7.

O'Neill, B. J. (2016). Community disassembly in ephemeral ecosystems. *Ecology* 97, 3285–3292. doi: 10.1002/ecy.1604

O'Neill, R. V. (2001). Is it time to bury the ecosystem concept? (With full military honors, of course!). *Ecology* 82, 3275–3284. doi: 10.1890/0012-9658(2001)082[3275:IITTBT]2.0.CO;2

Patrick, C. J., and Brown, B. L. (2018). Species pool functional diversity plays a hidden role in generating β-diversity. *Am. Nat.* 191, E159–E170. doi: 10.1086/696978

Pearson, D. E., Ortega, Y. K., Eren, Ö., and Hierro, J. L. (2018). Community assembly theory as a framework for biological invasions. *Trends Ecol. Evol.* 33, 313–325. doi: 10.1016/j.tree.2018.03.002

Peng, S., Kinlock, N. L., Gurevitch, J., and Peng, S. (2019). Correlation of native and exotic species richness: a global meta-analysis finds no invasion paradox across scales. *Ecology* 100:e02552. doi: 10.1002/ecy.2552

Peres-Neto, P. R., Legendre, P., Dray, S., and Borcard, D. (2006). Variation partitioning of species data matrices: estimateion and comparision of fractions. *Ecology* 87, 2614–2625. doi: 10.1890/0012-9658(2006)87[2614:VPOSDM]2.0.CO;2

Peres-Neto, P. R., Leibold, M. A., and Dray, S. (2012). Assessing the effects of spatial contingency and environmental filtering on metacommunity phylogenetics. *Ecology* 93, S14–S30. doi: 10.1890/11-0494.1

Perez Rocha, M., Bini, L. M., Domisch, S., Tolonen, K. T., Jyrkänkallio-Mikkola, J., Soininen, J., et al. (2018). Local environment and space drive multiple facets of stream macroinvertebrate beta diversity. *J. Biogeogr.* 45, 2744–2754. doi: 10.1111/jbi.13457

Peterson, A. T. (2003). Predicting the geography of species' invasions via ecological niche modeling. *Q. Rev. Biol.* 78, 419–433. doi: 10.1086/378926

Pheloung, P. C., Williams, P. A., and Halloy, S. R. (1999). A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. *J. Environ. Manage.* 57, 239–251. doi: 10.1006/jema.1999.0297

Pianka, E. R. (1970). On r- and K-selection. *Am. Nat.* 104, 592–597. doi: 10.1086/282697

Preston, D. L., Henderson, J. S., and Johnson, P. T. J. (2012). Community ecology of invasions: direct and indirect effects of multiple invasive species on aquatic communities. *Ecology* 93, 1254–1261. doi: 10.1890/11-1821.1

Pyšek, P., and Richardson, D. M. (2007). "Traits associated with invasiveness in alien plants: where do we stand?," in *Biological Invasions,* ed W. Nentwig (Berlin; Heidelberg: Springer), 97–125. doi: 10.1007/978-3-540-36920-2_7

Pyšek, P., and Richardson, D. M. (2010). Invasive species, environmental change and management, and health. *Annu. Rev. Environ. Resour.* 35, 25–55. doi: 10.1146/annurev-environ-033009-095548

Reichard, S. H., and White, P. (2001). Horticulture as a pathway of invasive plant introductions in the united states: most invasive plants have been introduced for horticultural use by nurseries, botanical gardens, and individuals. *Bioscience* 51, 103–113. doi: 10.1641/0006-3568(2001)051[0103:HAAPOI]2.0.CO;2

Rejmanek, M., and Pitcairn, M. J. (2002). "When is eradication of exotic pest plants a realistic goal?," in *Turning the Tide: The Eradication of Invasive Species. the IUCN Species Survival Commission*, eds C. R. Veitch and M. N. Clout (Auckland: IUCN), 414.

Resetarits, W. J., and Silberbush, A. (2016). Local contagion and regional compression: habitat selection drives spatially explicit, multiscale dynamics of colonisation in experimental metacommunities. *Ecol. Lett.* 19, 191–200. doi: 10.1111/ele.12553

Riar, M. K., Carley, D. S., Zhang, C., Schroeder-Moreno, M. S., Jordan, D. L., Webster, T. M., et al. (2016). Environmental influences on growth and reproduction of invasive *Commelina benghalensis*. *Int. J. Agron.* 2016:5679249. doi: 10.1155/2016/5679249

Ricciardi, A., Blackburn, T. M., Carlton, J. T., Dick, J. T. A., Hulme, P. E., Iacarella, J. C., et al. (2017). Invasion science: a horizon scan of emerging challenges and opportunities. *Trends Ecol. Evol.* 32, 464–474. doi: 10.1016/j.tree.2017.03.007

Richardson, D. M. (2004). Plant invasion ecology — dispatches from the front line. *Divers. Distribut.* 10, 315–319. doi: 10.1111/j.1366-9516.2004.00129.x

Richardson, D. M., and Pyšek, P. (2006). Plant invasions: merging the concepts of species invasiveness and community invasibility. *Progr. Phys. Geogr.* 30, 409–431. doi: 10.1191/0309133306pp490pr

Richardson, D. M., Pyšek, P., Rejmánek, M., Barbour, M. G., Panetta, F. D., and West, C. J. (2000). Naturalization and invasion of alien plants: concepts and definitions. *Diversity Distributions* 6, 93–107. doi: 10.1046/j.1472-4642.2000.00083.x

Roy, H. E., Lawson Handley, L. J., Schönrogge, K., Poland, R. L., and Purse, B. V. (2011). Can the enemy release hypothesis explain the success of invasive alien predators and parasitoids? *BioControl* 56, 451–468. doi: 10.1007/s10526-011-9349-7

Sandel, B., and Corbin, J. D. (2010). Scale, disturbance and productivity control the native-exotic richness relationship. *Oikos* 119, 1281–1290. doi: 10.1111/j.1600-0706.2010.18230.x

Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., et al. (2017). No saturation in the accumulation of alien species worldwide. *Nat. Commun.* 8:14435.

Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., et al. (2018). Global rise in emerging alien species results from increased accessibility of new source pools. *Proc. Natl. Acad. Sci. U.S.A.* 115, E2264–E2273. doi: 10.1073/pnas.1719429115

Shea, K., and Chesson, P. (2002). Community ecology theory as a framework for biological invasions. *Trends Ecol. Evol.* 17, 170–176. doi: 10.1016/S0169-5347(02)02495-3

Sheley, R. L., Svejcar, T. J., and Maxwell, B. D. (1996). A theoretical framework for developing successional weed management strategies on rangeland. *Weed Technol.* 10, 766–773. doi: 10.1017/S0890037X00040793

Shmida, A., and Wilson, M. V. (1985). Biological determinants of species diversity. *J. Biogeogr.* 12, 1–20.

Siepielski, A. M., and McPeek, M. A. (2010). On the evidence for species coexistence: a critique of the coexistence program. *Ecology* 91, 3153–3164. doi: 10.1890/10-0154.1

Simberloff, D. (2009). The role of propagule pressure in biological invasions. *Annu. Rev. Ecol. Evol. Syst.* 40, 81–102. doi: 10.1146/annurev.ecolsys.110308.120304

Smith, A. L., Hodkinson, T. R., Villellas, J., Catford, J. A., Csergo, A. M., Blomberg, S. P., et al. (2020). Global gene flow releases invasive plants from environmental constraints on genetic diversity. *Proc. Natl. Acad. Sci. U.S.A.* 117, 4218–4227. doi: 10.1073/pnas.1915848117

Smith, M. D., Wilcox, J. C., Kelly, T., and Knapp, A. K. (2004). Dominance not richness determines invasibility of tallgrass prairie. *Oikos* 106, 253–262. doi: 10.1111/j.0030-1299.2004.13057.x

Sokol, E. R. (2016). *A Tutorial on Metacommunity Simulations (MCSim) for R*. Available online at: http://rpubs.com/sokole/159425 (accessed December 12, 2019)

Sokol, E. R. (2019). *MCSim: An R Package for Metacommunity Simulations*. Available online at: https://github.com/sokole/MCSim/releases/tag/v0.4.9

Sokol, E. R., Benfield, E. F., Belden, L. K., and Valett, H. M. (2011). The assembly of ecological communities inferred from taxonomic and functional composition. *Am. Nat.* 177, 630–644. doi: 10.1086/659625

Sokol, E. R., Brown, B. L., and Barrett, J. E. (2017). A simulation-based approach to understand how metacommunity characteristics influence emergent biodiversity patterns. *Oikos* 126, 723–737. doi: 10.1111/oik.03690

Sokol, E. R., Brown, B. L., Carey, C. C., Tornwall, B., Swan, C. M., and Barrett, J. E. (2015). Linking management to biodiversity in built ponds using metacommunity simulations. *Ecol. Modell.* 296, 36–45. doi: 10.1016/j.ecolmodel.2014.10.022

Sokol, E. R., Hoch, J. M., Gaiser, E., and Trexler, J. C. (2013). Metacommunity structure along resource and disturbance gradients in everglades wetlands. *Wetlands* 34, 135–146. doi: 10.1007/s13157-013-0413-1

Steiner, C. F., Stockwell, R. D., Kalaimani, V., and Aqel, Z. (2011). Dispersal promotes compensatory dynamics and stability in forced metacommunities. *Am. Nat.* 178, 159–170. doi: 10.1086/660835

Steiner, C. F., Stockwell, R. D., Kalaimani, V., and Aqel, Z. (2013). Population synchrony and stability in environmentally forced metacommunities. *Oikos* 122, 1195–1206. doi: 10.1111/j.1600-0706.2012.20936.x

Stohlgren, T. J., Jarnevich, C., Chong, G. W., and Evangelista, P. H. (2006). Scale and plant invasions: a theory of biotic acceptance. *Preslia* 78, 405–426.

Strecker, A. L., and Brittain, J. T. (2017). Increased habitat connectivity homogenizes freshwater communities: historical and landscape perspectives. *J. Appl. Ecol.* 54, 1343–1352. doi: 10.1111/1365-2664.12882

Swan, C. M., and Brown, B. L. (2017). Metacommunity theory meets restoration: isolation may mediate how ecological communities respond to stream restoration. *Ecol. Appl.* 27, 2209–2219. doi: 10.1002/eap.1602

Swearingen, J., Blattery, B., Reshetiloff, K., and Zwicker, S. (2014). *Plant Invaders of Mid-Atlantic Natural Areas, 4th Edn.* Washington, DC: National Park Service and U.S. Fish and Wildlife Service, 168.

Swenson, N. G., Erickson, D. L., Mi, X., Bourg, N. A., Forero-Montaña, J., Ge, X., et al. (2012). Phylogenetic and functional alpha and beta diversity in temperate and tropical tree communities. *Ecology* 93, S112–S125. doi: 10.1890/11-1180.1

Theoharides, K. A., and Dukes, J. S. (2007). Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. *N. Phytol.* 176, 256–273. doi: 10.1111/j.1469-8137.2007.02207.x

Thompson, P. L., Guzman, L. M., De Meester, L., Horváth, Z., Ptacnik, R., Vanschoenwinkel, B., et al. (2020). A process-based metacommunity framework linking local and regional scale community ecology. *Ecol. Lett.* 23, 1314–1329. doi: 10.1111/ele.13568

Tilman, D. (1982). *Resource Competition and Community Structure*. Princeton, NJ: Princeton University Press. doi: 10.1515/9780691209654

Tilman, D. (1994). Competition and biodiversity in spatially structured habitats. *Ecology* 75, 2–16. doi: 10.2307/1939377

Tilman, D. (2000). Causes, consequences and ethics of biodiversity. *Nature* 405, 208–211. doi: 10.1038/35012217

Tolonen, K. T., Cai, Y., Vilmi, A., Karjalainen, S. M., Sutela, T., and Heino, J. (2018). Environmental filtering and spatial effects on metacommunity organisation differ among littoral macroinvertebrate groups deconstructed by biological traits. *Aquatic. Ecol.* 52, 119–131. doi: 10.1007/s10452-018-9649-4

Tonkin, J. D., Heino, J., and Altermatt, F. (2018). Metacommunities in river networks: the importance of network structure and connectivity on patterns and processes. *Freshw. Biol.* 63, 1–5. doi: 10.1111/fwb.13045

Tornwall, B. M., Swan, C. M., and Brown, B. L. (2017). Manipulation of local environment produces different diversity outcomes depending on location within a river network. *Oecologia* 184, 663–674. doi: 10.1007/s00442-017-3891-7

Urban, M. C. (2004). Disturbance heterogeneity determines freshwater metacommunity structure. *Ecology* 85, 2971–2978. doi: 10.1890/03-0631

Van Kleunen, M., Dawson, W., Schlaepfer, D., Jeschke, J. M., and Fischer, M. (2010a). Are invaders different? A conceptual framework of comparative approaches for assessing determinants of invasiveness. *Ecol. Lett.* 13, 947–958. doi: 10.1111/j.1461-0248.2010.01503.x

Van Kleunen, M., Weber, E., and Fischer, M. (2010b). A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecol. Lett.* 13, 235–245. doi: 10.1111/j.1461-0248.2009.01418.x

Vanschoenwinkel, B., Buschke, F., and Brendonck, L. (2013). Disturbance regime alters the impact of dispersal on alpha and beta diversity in a natural metacommunity. *Ecology* 94, 2547–2557. doi: 10.1890/12-1576.1

Vilà, M., Espinar, J. L., Hejda, M., Hulme, P. E., Jarošík, V., Maron, J. L., et al. (2011). Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol. Lett.* 14, 702–708. doi: 10.1111/j.1461-0248.2011.01628.x

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., et al. (2007). Let the concept of trait be functional! *Oikos* 116, 882–892. doi: 10.1111/j.0030-1299.2007.15559.x

Warburton, E. M., Kohler, S. L., and Vonhof, M. J. (2016). Patterns of parasite community dissimilarity: the significant role of land use and lack of distance-decay in a bat–helminth system. *Oikos* 125, 374–385. doi: 10.1111/oik.02313

Werner, E. E., Yurewicz, K. L., Skelly, D. K., and Relyea, R. A. (2007). Turnover in an amphibian metacommunity: the role of local and regional factors. *Oikos* 116, 1713–1725. doi: 10.1111/j.0030-1299.2007.16039.x

Whittaker, R. H. (1962). Classification of natural communities. *Bot. Rev.* 28, 1–239.

Williamson, M. (1996). *Biological Invasions*. London: Chapman and Hall.

Wilson, J. R. U. (2020). Definitions can confuse: why the "Neonative" neologism is bad for conservation. *Bioscience* 70, 110–111. doi: 10.1093/biosci/biz159

Zavaleta, E. S., and Hulvey, K. B. (2007). Realistic variation in species composition affects grassland production, resource use and invasion resistance. *Plant Ecol.* 188, 39–51. doi: 10.1007/s11258-006-9146-z

Zhang, H., Qi, W., John, R., Wang, W., Song, F., and Zhou, S. (2015). Using functional trait diversity to evaluate the contribution of multiple ecological processes to community assembly during succession. *Ecography* 38, 1176–1186. doi: 10.1111/ecog.01123

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GLOSSARY

Alien Species

Species that have established a range outside of their historical ranges as a result of human transportation.

Biotic Acceptance

A paradigm suggesting that positive correlations between native species richness and invasive species richness occur because environmental conditions that are good for natives are also good for invasives. Often presented as a counter to the Biotic Resistance Hypothesis (Stohlgren et al., 2006).

Biotic Resistance

A paradigm suggesting that the susceptibility of a community to invasion is influenced by its biotic composition across trophic levels, and that higher levels of species richness generally deter invasion (Elton, 1958; Levine et al., 2004). There has remained equivocal evidence for the relationship between native and exotic richness.

Dispersal

Generalized term in metacommunity ecology that incorporates both movement and establishment of species. Viewed as the major "regional" process of metacommunity theory (Leibold et al., 2004).

Diversity Metrics (α, β, γ)

Common metrics used for describing metacommunities at multiple spatial scales. α = the diversity of a single local community or, when multiple local communities are being considered, the average diversity of localities. Frequently measured using either species richness or common diversity indices (e.g., Shannon, Simpson). γ = total diversity in a region, measured in the same way as α, but aggregated across all local communities in a region. β = turnover in composition between the local communities within a region. β-diversity can be measured in a number of different ways, including dissimilarity indices (e.g., Jaccard, Bray-Curtis). However, truly partitioning γ-diversity into independent α and β components (i.e., measures of β do not depend on α) is generally accomplished through $\alpha \times \beta = \gamma$ (Jost, 2007), though other valid partitionings also exist (Jost, 2007; Chao et al., 2012).

Enemy Release

Invasive species are often thought to have been introduced to new ranges that lack the suite of (often specialist) predators, diseases, etc. that limited size and population growth in their native range (Keane and Crawley, 2002).

Invasibility Criterion

According to ecological theory, the definitive criterion for co-existence of species in a community; states that to truly coexist with other species in a community, the species must be able to increase its abundance when it is rare (MacArthur, 1972; Chesson, 2000). This criterion distinguishes coexistence from co-occurrence of species in a community (Siepielski and McPeek, 2010). The name of the criterion derives from a scenario in which a species invades an extant community at low abundances.

Invasive Species

Non-native species to that location, often as a direct or indirect result of human action. Invasive species can cause a multitude of ecological, economic, and human health impacts and are distinguished from alien species in that they have demonstrable negative impacts on communities, ecosystems, or ecosystem services.

Local and Regional (in Metacommunity Terms)

Metacommunity concepts categorize the factors that control community assembly and composition into two parts: local and regional. Local effects are traditional niche-associated effects like environmental conditions and species interactions. Regional effects are those effects driven primarily by the dispersal of organisms between local communities of the metacommunity (Leibold et al., 2004).

Metacommunity Paradigms (Species Sorting, Patch Dynamics, Mass Effects, Neutrality)

Four paradigms are strongly associated with metacommunity theory. Species Sorting = classic niche-based paradigm in which community composition is controlled by local environmental conditions and species interactions (Whittaker, 1962). Patch Dynamics = paradigm in which composition of local communities is driven by a landscape patchwork of local extinction/colonization dynamics. A key aspect of Patch Dynamics is the assumed tradeoff between competitive ability and dispersal ability (Levins and Culver, 1971; Levin, 1974). Mass Effects = paradigm that recognizes that local effects are important determinants of community composition, but that the regional effect of high dispersal rates may swamp out the influence of local factors (Brown and Kodric-Brown, 1977; Shmida and Wilson, 1985). Neutrality = paradigm that considers the traits of species to be inconsequential in determining species composition of a community; composition is the product of random extinction and probabilistic colonization of species. Often considered to be a null model of metacommunity effects (Bell, 2001; Hubbell, 2001). An important recognition is that these four paradigms were historically developed independently, outside of the scope of metacommunity theory. As such, they are not mutually exclusive in terms of mechanisms or predictions, and do not represent the entire inference space of metacommunity theory (Brown et al., 2017).

Neonative

Species expanding their range as a result of anthropogenically-based environmental changes. A controversial neologism (Wilson, 2020) meant to capture the fuzzy category of often native species that are shifting ranges, complicating management and policy.

Propagule Pressure

The number and size of introduction events of a single species to a location. Often considered one of the most important and fundamental elements of biological invasions (Simberloff, 2009). The concept of propagule pressure is closely paralleled by "dispersal" in metacommunity theory.

Rescue Effects

In a metacommunity, when a species goes extinct at a locality, it can be "rescued" by recolonization from other local communities (Brown and Kodric-Brown, 1977).

Sorting Strength and Ecological Filters

Sorting strength is a measure of the influence local factors have on species composition of the local community. The name derives from the Species Sorting paradigm of metacommunity theory. Sorting strength is often conceived as a set of ecological filters (e.g., environmental conditions, local competition, or predation) that exclude species from a particular local community.

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Novel Insights to Be Gained From Applying Metacommunity Theory to Long-Term, Spatially Replicated Biodiversity Data

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Global loss of biodiversity and its associated ecosystem services is occurring at an alarming rate and is predicted to accelerate in the future. Metacommunity theory provides a framework to investigate multi-scale processes that drive change in biodiversity across space and time. Short-term ecological studies across space have progressed our understanding of biodiversity through a metacommunity lens, however, such snapshots in time have been limited in their ability to explain which processes, at which scales, generate observed spatial patterns. Temporal dynamics of metacommunities have been understudied, and large gaps in theory and empirical data have hindered progress in our understanding of underlying metacommunity processes that give rise to biodiversity patterns. Fortunately, we are at an important point in the history of ecology, where long-term studies with cross-scale spatial replication provide a means to gain a deeper understanding of the multiscale processes driving biodiversity patterns in time and space to inform metacommunity theory. The maturation of coordinated research and observation networks, such as the United States Long Term Ecological Research (LTER) program, provides an opportunity to advance explanation and prediction of biodiversity change with observational and experimental data at spatial and temporal scales greater than any single research group could accomplish. Synthesis of LTER network community datasets illustrates that long-term studies with spatial replication present an under-utilized resource for advancing spatio-temporal metacommunity research. We identify challenges towards synthesizing these data and present recommendations for addressing these challenges. We conclude with insights about how future monitoring efforts by coordinated research and observation networks could further the development of metacommunity theory and its applications aimed at improving conservation efforts.

Keywords: LTER, NCO, synthesis, metacommunity, biodiversity, spatio-temporal, long-term

INTRODUCTION

Biodiversity is a key asset for environmental sustainability via its role in maintaining ecosystem functions and services (Cardinale et al., 2012; Hooper et al., 2012; Díaz et al., 2019). However, over the past half-century, human activities have increased the rate of biodiversity loss more than at any other time in history (World Health Organization, 2005; United Nations, 2017). The term "biodiversity" has been used to describe variation at many different levels of biological organization, but here we focus on species diversity (i.e., data sets from which a researcher can calculate measures of species richness or evenness) (Cleland, 2011). In association with declining biodiversity, researchers have documented changes in species interactions (Tylianakis et al., 2008), distributions, and phenology across ecosystems (Parmesan and Yohe, 2003; Dudgeon et al., 2006; Parmesan, 2006; Martay et al., 2016). These changes, which are not ubiquitous across taxa and landscapes, are expected to accelerate in the future (Brook et al., 2008; Bellard et al., 2012; Urban, 2015), further affecting ecosystem structure and function (Seto et al., 2012; Grimm et al., 2013).

A key goal of biodiversity science in the Anthropocene is to anticipate threshold shifts in the distributions and abundances of organisms and the ecosystem services that they afford to society (United Nations, 2017). However, without explicit consideration of multiple spatial scales and the within- and among-species pool connections, conclusions about the processes driving patterns of biodiversity are incomplete. Community structure and processes are still very common research themes in ecology; however, the greatest increase in number of publications has been observed on themes such as scale, anthropogenic impacts, and climate change (McCallen et al., 2019). Metacommunity theory and its applications are essential to addressing scaling in terms of space (e.g., local vs. regional) and time (i.e., linked to organisms' generation times), especially in today's rapidly changing communities and ecosystems (Mouquet and Loreau, 2002; Fahrig, 2003; Fischer and Lindenmayer, 2007).

In the past two decades, short-term field studies have considerably advanced our understanding of metacommunities across space by demonstrating how dispersal traits and landscape heterogeneity can affect community assembly in predictable ways (Logue et al., 2011; Leibold and Chase, 2017; Wilcox et al., 2017). Such information can provide insight into the types of metacommunity dynamics that organize biodiversity in each ecosystem (e.g., Pulliam, 1988; De Bie et al., 2012). However, spatially explicit snapshot data are limited in their utility to identify the processes that underlie observed patterns (Leibold et al., 2004; Brown et al., 2017; Sokol et al., 2017). Because ecological studies are often limited to the short-term (Hughes et al., 2017), considerable variability often remains unexplained in examinations of observational data. Assemblage composition and habitat availability may vary through time because of disturbance, seasonality, multi-year climatic variation (e.g., El Niño Southern Oscillation), and shifts of propagules in and out of dormancy (Holyoak et al., 2020). Many investigators acknowledge the limitation of not having temporal data (Frishkoff et al., 2014), particularly in dynamic systems such as streams (Datry et al., 2016; Sarremejane et al., 2017; Tonkin et al., 2018). Not only can the environment change through time (e.g., habitat availability, environmental heterogeneity, and connectivity), but so too can the intrinsic processes regulating local biotic interactions (e.g., priority effects, intransitive competition) and dispersal from the relevant regional species pool (Chase, 2003; Fukami, 2015; Zarnetske et al., 2017). That is, temporal changes in biodiversity can occur regardless of environmental change.

With short-term spatially replicated metacommunity data, it can be difficult to distinguish between (1) exogenous environmental drivers of compositional changes and (2) endogenous community dynamics that may result from deterministic processes (e.g., multiple stable equilibria, endpoint assembly cycles, frequency-dependent coexistence in continuous space) on metacommunity composition. For instance, intransitive competition (i.e., "rock-paper-scissors" competition scenario) can result in endpoint assembly cycles (EACs) in which communities are decoupled from the influence of local environmental factors (Law and Morton, 1993, 1996; Steiner and Leibold, 2004). However, repeated observations in both space and time are necessary to demonstrate EAC dynamics. Specifically, the data would need to demonstrate that (1) all species involved in intransitive competitive dynamics persist regionally, (2) that the species involved cannot coexist locally, and (3) that low to moderate levels of dispersal among patches in the metacommunity allow for the EACs to play out. Therefore, both temporal and spatial replication are needed to test multiple hypotheses that explain how biodiversity is changing in such spatially complex landscapes (Leibold and Chase, 2017).

In the context of metacommunity assembly, given the problem of inferring spatio-temporal processes from spatial patterns alone, there have been multiple calls for long-term, spatial data collection to advance metacommunity research (Adler et al., 2005; Cottenie, 2005; Leibold and Chase, 2017; Holyoak et al., 2020). Financial and logistical constraints in field studies often hamper a comprehensive exploration of biodiversity trends across temporal and spatial scales. However, the various types of coordinated research networks [e.g., the United States Long Term Ecological Research (LTER) program, the International-LTER

(ILTER), the global Nutrient Network, NutNet[1], the Smithsonian ForestGEO Network], and observatory networks [e.g., the United States Global Lake Ecological Observatory Network (GLEON), the National Critical Zone Observatory (CZO), and the United States National Ecological Observatory Network (NEON; Bourgeron et al., 2018)], provide a growing resource of long-term data that can be leveraged in synthesis science. Most of these coordinated research and observation networks, hereafter referred to as observation networks, have been working for over 10 years (e.g., the United States LTER will be 40 years old in 2020, the ILTER is 27 years old, GLEON is 16 years old, CZO is 12 years old, and the Long Term Agricultural Research network is 9 years old), while NEON recently completed construction of all 81 field sites and is slated to collect data for the next 30 years (**Table 1**).

With the maturation of long term data sets from such observation networks, the field of ecology is approaching an exciting point where there is the opportunity to empirically explore spatial and temporal representativeness of species within and among sites across ecosystems. Ultimately, a deeper understanding of the representativeness of species in space and time will lead to a better understanding of how scale influences metacommunity organization and biodiversity dynamics, which is key to making more general theoretical insights that transcend beyond the nuances of individual study systems. Here we provide evidence from a synthesis effort of LTER data showing that some LTER sites have the spatial replication within sites over time needed to capture asymptotic species-time-area-relationships (*sensu* Adler et al., 2005). The results of this synthesis suggest that these datasets could provide an untapped resource for metacommunity studies. When long-term studies include spatial contexts through multiple sites (within the regional species pool), they enable a more complete assessment of biodiversity change relative to long-term studies at a single site and allow for researchers to explore how sampling design might influence insights into metacommunities (**Box 1**). Spatio-temporal biodiversity patterns can take decades or longer to be described and explained (Magurran et al., 2010), partly owing to high temporal variability in community dynamics or lags in the processes, such as extinction debt, that structure biodiversity (Tilman et al., 1994; Kuussaari et al., 2009). More synthesis of data from long-term observation networks has the potential to uncover additional long-term, spatially replicated data that will aid in exploring the problem in identifying the spatio-temporal mechanisms underlying metacommunity assembly manifested in spatial biodiversity patterns.

Another key aspect of some observation networks (e.g., LTER, LTAR) is the existence of manipulative experiments that may also aid in teasing apart pattern from process in metacommunities. Observational studies considering metacommunity dynamics across space and time can still result in limited inferences about the dynamics of a metacommunity in the future. Most ecological systems may exist in different states wherein species compositions and abundances vary considerably, for example, with gradual shifts between states during succession or abrupt transitions when tipping points are reached (Suding and Hobbs,

TABLE 1 | Summary of coordinated research networks with community data useful for metacommunity analyses.

Network	Organism(s)	Ecosystem(s)	Data publicly available (if yes, link provided)
Long Term Ecological Research Network	Plants, animals, microbes	Forest (tropical and temperate), grassland, desert, tundra, marine, freshwater	Yes https://portal.edirepository.org/nis/home.jsp
National Ecological Observation Network	Plants, animals, microbes	Forest (tropical and temperate), grassland, desert, tundra, freshwater	Yes https://data.neonscience.org/
International Long Term Ecological Research Network	Plants, animals, microbes	Forest (tropical and temperate), grassland, desert, tundra, marine, freshwater	Yes https://deims.org/
Nutrient Network	Plants, animals, microbes	Grassland, tundra	Yes https://nutnet.org/data
Global Lake Ecological Observatory Network	Plants, animals, microbes	Freshwater	Yes https://gleon.org/data
Long Term Agricultural Research Network	Plants, animals, microbes	Grasslands, croplands, pasture lands	Yes https://ltar.ars.usda.gov/data-listing/
Smithsonian ForestGEO	Plants	Forest (tropical and temperate)	Mixed https://forestgeo.si.edu/explore-data

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[1] http://www.nutnet.org/

BOX 1 | Uncovering the regional species pool.

One of the most challenging aspects of any metacommunity study is adequately characterizing the regional species pool of interest because it is context-dependent and the "region" is defined by the researcher. When samples are taken in multiple localities at a single point in time, we often assume that the species found across all localities capture the whole regional species pool. However, we know that not all species that could occur at study sites are observed in a single temporal snapshot because stochastic colonization/extinction events and/or transient dynamics might be occurring during the study (reviewed by Holyoak et al., 2020). For example, species experiencing diapause or having low detection probability might be missed or demographic stochasticity may eliminate one or more species in an isolated year (**Figure 1**). It takes time to sample the regional species pool, but spatially replicated sampling schemes can (1) increase the total number of species encountered and (2) decrease the time it takes to discover them. Additionally, succession and environmental change may add to the pool of species that can potentially occur in the study sites over time, as can the arrival of invasive species (**Figure 2**; Pickett, 1989; Li et al., 2020). Although the number of species observed at a site may be approximately the same across years, substantial compositional temporal turnover of species may take place (Tonkin et al., 2017).

Long-term, spatially replicated data collection allows for the data to suggest the relevant spatial extent to study for characterizing the regional species pool for a given question. For example, researchers can see whether spatial or temporal samples saturate first and which sites continue to reveal more species diversity with greater sampling extent. Then, by looking at the temporal curves in a spatial context, researchers can better understand the most dynamic or undersampled regions of the landscape. This may help identify local sites that are on the periphery of the metacommunity that may be less influenced by spatio-temporal variation and/or dispersal (i.e., locally saturated sites whose composition is nested inside of the composition of other sites); and sites that are important integrators of spatio-temporal processes or important dispersal connections (i.e., sites with highly variable composition where repeated sampling continues to reveal new species and different composition). In a similar vein, Erõs and Schmera (2010) combined field survey data on fish in a temporally and spatially dynamic stream system with simulation experiments to explore how spatial and temporal scales and their interaction influence species accumulation, which can lead to different inferences about metacommunity organization (e.g., the role of spatial versus environmental effects; Sály and Erõs, 2016).

However, it is also important to note the limitations of species-time-area-relationships in evaluating sample representativeness over space and time within the context of understanding spatio-temporal metacommunity dynamics. For instance, species-time-area-relationship curves do not reveal insights about the temporal variability in changes in the abundance of organisms within and between sites, which is central to understanding mechanisms of metacommunity assembly [e.g., mass effects, species recovery from a historic disturbance (Scheffer, 2010)]. A new method for distinguishing changes in species richness across space due to separate effects of species abundance distribution, density, and the spatial configuration of individuals on a landscape presented by McGlinn et al. (2020) presents a promising path forward for more informed assessments of species-area-relationships, but incorporation of the temporal component into such new methods remains lacking. Regardless, we recommend that monitoring programs include the longitude and latitude of each sample plot if they want to be amenable to this new method, which requires plot locality information.

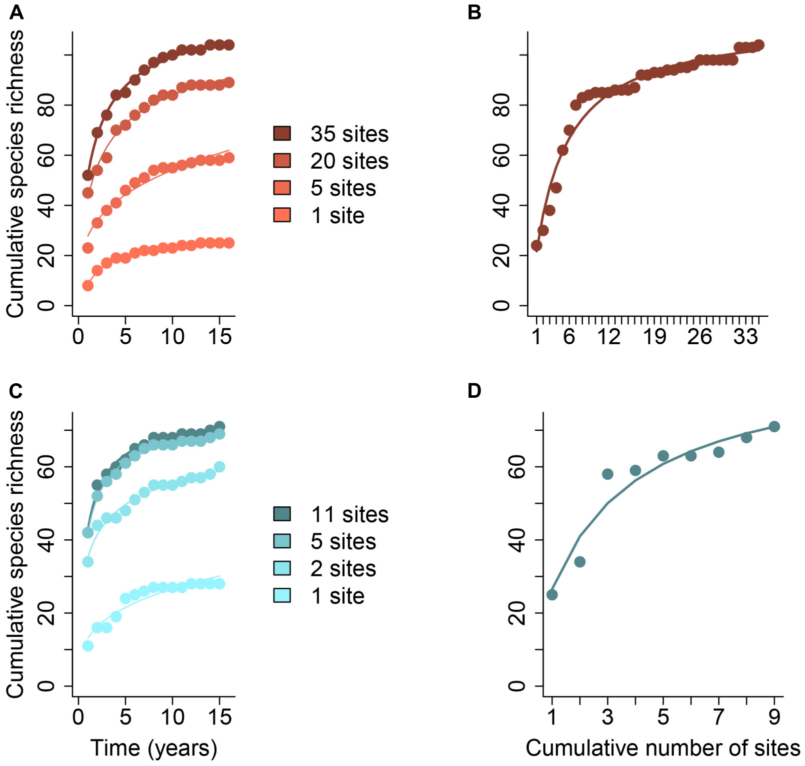

FIGURE 1 | Species accumulation curves over time (years) and space with increasing numbers of study sites, indicated with different colors. Species accumulation curves through time **(A,C)** and space **(B,D)** are shown for birds from the Central Arizona – Phoenix United States LTER (2001–2016, Bateman et al., 2017) **(A,B)** and for sessile invertebrates from the Santa Barbara Channel United States LTER (2004–2016, Reed, 2018) **(C,D)**. The total number of species increases with the number of study sites, and the steepness of the curve also tends to increase with the number of study sites. Curves were fit according to the Arrhenius, Lomolino, and Michaelis-Menten models described in Dengler (2009) using the R package vegan (Oksanen et al., 2017). The most parsimonious model (lowest AIC) is shown for each subset of sites. Data and R code for generating this figure can be found in the **Supplementary Data Sheets 2–4**.

(Continued)

BOX 1 | Continued

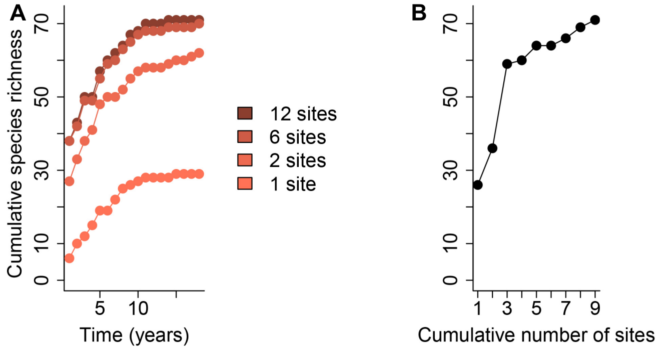

FIGURE 2 | Changes in a regional species pool over time. The species accumulation curve for a collection of sites may not level off over time due to the successional nature of communities, species invasions, or environmental change. **(A)** shows the species accumulation curve over 21 years for plants growing in the pumice plain habitat on Mt. St. Helens, United States (1989–2009; del Moral, 2010), a community undergoing succession following volcanic eruption. **(B)** shows the species accumulation curve over space for the same sites. Data and R code for generating this figure can be found in the **Supplementary Data Sheets 1, 4**.

2009). Even with extensive time series, it may be difficult to know where organisms within communities and metacommunities lie on a given temporal trajectory relative to a previous disturbance or an impending state change (Bestelmeyer et al., 2011). By contrast, field experiments with manipulations that influence aspects of metacommunity dynamics present the opportunity to test theoretical metacommunity frameworks to learn where theory aligns with observations (Logue et al., 2011), thus allowing for more robust predictions.

Long-term field manipulations are a key component of most United States LTER Network and other long-term ecological research programs because they can experimentally test how biodiversity responds to ecological processes occurring over extended periods (Turner et al., 2003). For example, by simulating the loss of eastern hemlock (*Tsuga canadensis*) due to the invasive wooly adelgid (*Adelges tsugae*) and measuring ant biodiversity for 13 years, researchers at the Harvard Forest LTER found that this experimental disturbance reduced the importance of species sorting for community composition (Sackett et al., 2011; Record et al., 2018). Long-term manipulations can also reveal how biodiversity responds to repeated environmental fluctuations, yielding knowledge that cannot be obtained with short-term experiments. By simulating annual kelp forest loss from ocean storms for 9 years, researchers at the Santa Barbara Coastal LTER demonstrated strong shifts in marine biodiversity that were contrary to findings from an earlier 2-year study (Castorani et al., 2018).

The Cedar Creek Biodiversity Experiment is a long-term manipulation of soil nitrogen availability and plant diversity that critically demonstrated the importance of biodiversity for ecosystem functioning (Tilman et al., 2012). This experiment has also allowed United States LTER researchers to answer additional questions related to community assembly and metacommunity ecology. For example, to assess the extent to which plant communities were dispersal-limited, seed mixtures were added into plots of a native grassland (Tilman, 1997). Increased seed additions led to greater local species richness, providing evidence that some species are dispersal limited (Tilman, 1997). Seed addition experiments have also shown that local species interactions, such as resource competition, are important for structuring local plant communities (Fargione et al., 2003). These results, when placed in the broader context of metacommunity ecology, show how both local and regional processes can influence biodiversity.

Long-term ecological research programs situated within a network of sites are critically important for understanding trends in biodiversity, especially when historical contexts are known and infrastructure enables long-term field experiments. Data sets published by observation networks often contain abundant and co-located biotic and abiotic data to investigate patterns of biodiversity through the lens of metacommunity theory. For example, spatio-temporal metacommunity dynamics can be investigated across numerous ecosystems and taxa by means of NEON's frequent and coordinated biotic and abiotic sampling within plots or stream reaches nested within sites across 20 climatic domains (Keller et al., 2008). Such networks provide economies of scale for infrastructure for long-term and networked sites, dedicated human resources for data collection, and taxonomic expertise (Bourgeron et al., 2018). Based on insights we made while curating LTER data for metacommunity analyses, we identify challenges towards synthesizing these data and present recommendations for addressing these challenges. We also provide guidance for long-term monitoring programs based on our insights.

CHALLENGES TO ADVANCING METACOMMUNITY SCIENCE AND PATHS FORWARD

Challenge One – Scale Mismatch Among Data Sets in Synthesis Efforts

To address broad questions about the generality of the metacommunity framework in ecology, it is necessary to broadly test the theory across ecosystems and organisms. This presents a challenge with respect to mismatches in temporal and spatial scaling across data sets (Lamy et al., 2018). Observatory networks can employ various scales of temporal resolution – days, weeks, seasons, years, or even decades and plot sizes (e.g., Keller et al., 2008). Cross-ecosystem syntheses of biodiversity often compare data that has been aggregated or standardized to a common temporal or spatial grain (e.g., annual observation frequencies; Collins et al., 2018). However, trends or shifts in biodiversity can be affected by species' generation times (Kuussaari et al., 2009), phenological patterns, and the frequency and duration of dispersal events (e.g., Tilman, 1997) and environmental fluctuations (e.g., Free et al., 2013), which do not always align with common ways of standardizing space and time across data sets (e.g., annual sampling schedules).

In light of these challenges, research questions focused on understanding the underlying processes that structure metacommunity assembly (i.e., species interactions, environmental filtering, dispersal limitation) must be aware of heterogeneity in sampling effort and spatial grain (i.e., plot size) across studies, which biodiversity estimates and variability among samples are sensitive to [Chase and Knight (2013), Spake et al. (2020)]. Spake et al. (2020) suggest that in formal meta-analyses scale dependence in effect sizes may be assessed using meta-regressions exploring relationships between either spatial (i.e., plot size) or temporal (i.e., sampling interval) grain and effect sizes across studies. They also illustrate with simulated community data how effect sizes calculated with the log response ratio metric applied to biodiversity estimates (i.e., species richness) were more accurate than those calculated with the common Hedge's *g* metric. In instances, when effect sizes applied to biodiversity estimates are highly scale dependent, the use of a scale-independent metric (e.g., Hurlbert's Probability of Interspecific Encounter) is preferred (Chase and Knight, 2013). Given the challenges of synthesizing biodiversity data with varying grains of sampling in space and time, we have two recommendations for monitoring programs. First, ensure that raw data are published with ample metadata, so that synthesis researchers can extract relevant information on grains of sampling (Spake et al., 2020). Second, we recommend that programs coordinate efforts to agree upon standardized sampling protocols for particular taxa to promote synthesis (see more specifics on such coordination in the Challenge Three subsection below).

Challenge Two – Rare Species

In a non-stationary world, rare species will be crucial for predicting future states of novel ecosystems (Lyons et al., 2005; Jain et al., 2014). However, trends and patterns observed for rare taxa can be challenging to interpret because they arise from a combination of observation error and stochastic colonization dynamics (Hanski et al., 2004; McGill et al., 2007). Capturing rare species dynamics is an important step in quantifying the regional species pool, which is an essential component of studies that embrace spatial dimensions and/or dispersal. Only with long-term temporal data from multiple sites can one understand the presence or absence of rare taxa because transient or local dynamics can influence how community assembly proceeds (Brown et al., 1995; Pandit et al., 2009; Siqueira et al., 2012). Local and regional species composition patterns universally contain a few dominant species, while most taxa are rare and show stochastic local colonization and extinction dynamics (Hanski et al., 2004; McGill et al., 2007). Although dominant species can contribute disproportionately to ecosystem function (Degrassi et al., 2019), rare species can also contribute meaningfully to ecosystem functions and services through novel additions to functional diversity and functional redundancy in a community (Lyons et al., 2005; Jain et al., 2014; Leitao et al., 2016). Despite the low abundances of rare species, it is critical to better understand how they contribute to community trait diversity and resilience, as environmental change may favor their increase in abundance and influence future ecosystem functioning (Tilman and Downing, 1994; Lyons et al., 2005; MacDougall et al., 2013; Jain et al., 2014).

Based on insights from our LTER data synthesis, we suggest observation networks balance temporal and spatial replication to better characterize the regional species pool, including rare taxa (**Box 1**). For instance, a higher frequency of observations is necessary to capture seasonally distinct communities or seasonally rare taxa (Tonkin et al., 2017). Another approach would be to implement adaptive cluster sampling to capture rare species, where the study area is spatially partitioned into a grid and the intensity of survey effort is intensified around grid cells with higher counts of particular rare species (Brown et al., 2013). Also, working groups should develop strategies for monitoring and interpreting future trends of the rare taxa that might predict invasion or threshold responses in future climate scenarios.

Challenge Three – Economies of Scale

It can often be difficult to assess whether long-term data are collected at optimal temporal resolutions and spatial extents to capture all relevant community assembly dynamics (e.g., dispersal kernel shape, demographic rates) or structural characteristics (e.g., spatial heterogeneity of suitable habitat, species occurrence, biomass). Increasing the spatial extent of data collection around existing long-term study sites will enable researchers and managers to compile the information needed for understanding trends in biodiversity and will allow for better characterization of regional species pools informed by data. Resources are often not available in any individual research program to capture both the necessary spatial and temporal resolution. There is a growing need for both spatial and temporal replication in biodiversity data, which requires a plan for coordination among single-PI projects and multiple long-term observatories in a network of networks to provide economies of scale within the research community.

We recommend that scientific societies provide a hub for coordination among and between single-PI and large-scale observation networks to help identify opportunities where single-PI and observation network projects can fill complementary knowledge gaps. For instance, the National Science Foundation's Macrosystems Biology program and NEON-Enabled Science solicitations provide an opportunity for short duration (3 years) studies that leverage NEON infrastructure. We also recommend that researchers use cross-project collaborative opportunities (e.g., Research Coordination Network working groups, United States LTER All Scientist Meeting working groups) to establish data collection priorities and standards for advancing metacommunity research.

Data collection priorities could inform monitoring frequency and spatial replication based on organismal life histories (e.g., time until reproduction, dispersal abilities) and current knowledge gaps (Wolfe et al., 1987). Adopting pre-existing, standardized sampling and data archiving protocols that are consistent among sites will also enable researchers and policy makers to scale-up local studies to global scale research initiatives (e.g., Group on Earth Observations – Biodiversity Observation Network's essential biodiversity variables; Haase et al., 2018). Recent proposals for integrating measures of biodiversity and ecosystem integrity across observatory networks may advance synergy within and among these networks (Haase et al., 2018). In addition to observation networks, spatially replicated studies in long-term databases, such as BioTime (Dornelas et al., 2018), offer additional data sources.

Data standards can also aid synthesis efforts. Furthermore, data to be used for multi-site analyses are best archived in harmonized datasets (with consistent structure and format). Examples include the GLEON DataONE Repository for synchronized hydrological sensor data[2] and the ecocomDP standard data pattern for community data[3] that members of our group have developed with the Environmental Data Initiative (EDI)[4] for implementation in their data portal, which publishes data products from the United States LTER and NSF Macrosystems Biology programs. A key outcome of the LTER synthesis group that we are a part of has been to harmonize LTER community ecology data sets into the ecocomDP standard data pattern to promote future use of LTER data in metacommunity studies. A key first step in using LTER time series to address hypotheses in metacommunity ecology is the identification of appropriate data sets. The analysis ready data provided by ecocomDP provides additional metadata for improved discovery with information on taxonomic resolutions, and nesting of sampling designs over space and time – key pieces of information for identifying the suitability of a data set for a metacommunity study. Currently, seventy community ecology data sets generated by the LTER network have been formatted into the ecocomDP standard data pattern and there are ∼100 more data sets in the queue for processing. Completed data sets are discoverable by going to the EDI Data Repository[5] and searching for the term "ecocomDP." Ultimately, these types of harmonized data sets will allow for greater advances in metacommunity studies because efforts to clean and format data leading up to analyses do not have to be repeatedly performed by individual researchers and there is the additional benefit that results from studies can then also be more reproducible (Reichman et al., 2011).

Challenge 4 – Statistical Integration of Long-Term, Spatially Replicated Data With Theory

Although we are at a point where some observation networks have amassed long-term, spatially replicated community data sets with saturating species-time-area relationships, the statistical integration of these data with theoretical concepts remains a key challenge. There have long been calls for moving beyond the classic metacommunity conceptual archetypes (i.e., mass effects, patch dynamics, species sorting, neutral theory) to better account for temporal dynamics, but theoretical and statistical approaches remain incomplete (Leibold and Chase, 2017). For instance, ecosystem stability over large spatial scales can be addressed in a metacommunity framework with long-term, spatially replicated data (Wang and Loreau, 2014, 2016). However, such analyses often consider aggregate metrics of ecosystems (e.g., biomass) rather than species diversity and composition, which may be of greater interest to federal agencies or non-governmental organizations, as these often uphold policy based on species diversity rather than aggregate metrics (i.e., the Endangered Species Act).

Greater strides in metacommunity science will be made as long-term, spatially replicated observation network data enter a loop, wherein the data impart information into the development of models and theory, and models and theory inform future data collection (Dietze, 2017). A promising path forward involves incorporating novel approaches to quantify metacommunity dynamics [e.g., joint species distribution models (Ovaskainen et al., 2019), open-source simulation tools (Sokol et al., 2017), process-based models (Keyel et al., 2016; Thompson et al., 2020)] into such cyclical rapid data assimilation and model/theory refinement. For instance, recent work by Thompson et al. (2020) revisits the metacommunity concept with a process-based framework that integrates local and regional dynamics of ecological communities with three main underlying dimensions (i.e., density independent responses to abiotic conditions, density-dependent biotic interactions, and dispersal) that link to the classic metacommunity conceptual archetypes. Near-term forecasting of process-based metacommunity models based on this reconceived metacommunity framework could help to identify which species traits best capture variation within and between species that influence density dependence to inform future monitoring and data collection efforts.

PROSPECTUS

Given the alarming rate at which biodiversity and associated ecosystem services are being lost (Ceballos et al., 2015; Johnson et al., 2017), understanding changes in biodiversity in both space and time is fundamental for science-informed conservation. While the metacommunity framework has the potential to uncover mechanisms explaining biodiversity patterns to inform conservation, the lack of spatio-temporal data has hindered researchers' ability to disentangle environmental drivers from biotic niche-based processes generated within the

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[2] http://gleon.org/data/repositories

[3] https://github.com/EDIorg/ecocomDP

[4] https://environmentaldatainitiative.org

[5] https://portal.edirepository.org/nis/home.jsp

community. Incorporating a long-term temporal dimension into field-based metacommunity research is key to understanding the mechanisms generating observed patterns in biodiversity. However, resources for field studies are limited and temporal replication often comes at the expense of spatial replication and taxonomic resolution (e.g., Keller et al., 2008). Large, collaborative observation networks provide the opportunity to inform metacommunity theory with empirical data at spatial and temporal scales greater than any single researcher could accomplish on their own. To better understand how metacommunity dynamics operate in reality, the infrastructure of manipulative field experiments at sites within these networks allows ecologists to test challenging questions posed by metacommunity theory at real-world scales. Looking forward, such large-scale efforts can be better leveraged (Bourgeron et al., 2018) to address issues of scale mismatches in data synthesis, rare species, economies of scale, and the integration of data with theory. By coordinating biodiversity research efforts, ecologists will better understand how and why species persist across space and time, and how biodiversity patterns emerge across a diverse range of ecosystems and over long temporal scales.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

SR, NV, and ES led the writing and editing of the manuscript. ES, NW, and CS secured funding from the LTER to support the working group. All authors contributed to the conceptualization, review, data collection, and editing of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.612794/full#supplementary-material

Supplementary Data Sheet 1 | The plant data from Mt. St. Helens in **Figure 2** of **Box 1**.

Supplementary Data Sheet 2 | The bird data from the Central Arizona Phoenix LTER in **Figure 1** of **Box 1**.

Supplementary Data Sheet 3 | The sessile invertebrate data from the Santa Barbara Channel LTER in **Figure 1** of **Box 1**.

Supplementary Data Sheet 4 | The R code for generating the figures in **Box 1**.

REFERENCES

Adler, P. B., White, E. P., Lauenroth, W. K., Kaufman, D. M., Rassweiler, A., and Rusak, J. A. (2005). Evidence for a general species–time–area relationship. *Ecology* 86, 2032–2039. doi: 10.1890/05-0067

Bateman, H., Childers, D., Katti, M., Shochat, E., and Warren, P. (2017). *Point-Count Bird Censusing: Long-Term Monitoring of Bird Abundance and Diversity in Central Arizona-Phoenix, Ongoing Since 2000. Environmental Data Initiative*. Available online at: https://doi.org/10.6073/pasta/201add557165740926aab6e056db6988 (accessed December 15, 2020).

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., and Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecol. Lett.* 15, 365–377. doi: 10.1111/j.1461-0248.2011.01736.x

Bestelmeyer, B. T., Ellison, A. M., Fraser, W. R., Gorman, K. B., Holbrook, S. J., Laney, C. M., et al. (2011). Analysis of abrupt transitions in ecological systems. *Ecosphere* 2:art129. doi: 10.1890/ES11-00216.1

Bourgeron, P., Kliskey, A., Alessa, L., Loescher, H., Krauze, K., Virapongse, A., et al. (2018). Understanding large-scale, complex, human–environmental processes: a framework for social–ecological observatories. *Front. Ecol. Environ.* 16, S52–S66. doi: 10.1002/fee.1797

Brook, B. W., Sodhi, N. S., and Bradshaw, C. J. (2008). Synergies among extinction drivers under global change. *Trends Ecol. Evol.* 23, 453–460. doi: 10.1016/j.tree.2008.03.011

Brown, B. L., Sokol, E. R., Skelton, J., and Tornwall, B. (2017). Making sense of metacommunities: dispelling the mythology of a metacommunity typology. *Oecologia* 183, 643–652. doi: 10.1007/s00442-016-3792-1

Brown, J. A., Salehi, M., Moradi, M., Panahbehagh, B., and Smith, D. R. (2013). Adpative survey designs for sampling rare and clustered populations. Math. Comput. Simul. 93, 108–116. doi: 10.1016/j.matcom.2012.09.008

Brown, J. H., Mehlman, D. W., and Stevens, G. C. (1995). Spatial variation in abundance. *Ecology* 76, 2028–2043. doi: 10.2307/1941678

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., et al. (2012). Biodiversity loss and its impact on humanity. *Nature* 486, 59–67. doi: 10.1038/nature11148

Castorani, M. C., Reed, D. C., and Miller, R. J. (2018). Loss of foundation species: disturbance frequency outweighs severity in structuring kelp forest communities. *Ecology* 99, 2442–2454. doi: 10.1002/ecy.2485

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., and Palmer, T. M. (2015). Accelerated modern human–induced species losses: entering the sixth mass extinction. *Sci. Adv.* 1:e1400253. doi: 10.1126/sciadv.1400253

Chase, J. M. (2003). Community assembly: when should history matter? *Oecologia* 136, 489–498. doi: 10.1007/s00442-003-1311-7

Chase, J. M., and Knight, T. M. (2013). Scale-dependent effect sizes of ecological drivers on biodiversity: why standardised sampling is not enough. *Ecol. Lett.* 16:17–26. doi: 10.1111/ele.12112

Cleland, E. E. (2011). Biodiversity and ecosystem stability. *Nat. Educ. Knowledge* 3:14.

Collins, S. L., Avolio, M. L., Gries, C., Hallett, L. M., Koerner, S. E., Pierre, K J. La, et al. (2018). Temporal heterogeneity increases with spatial heterogeneity in ecological communities. *Ecology* 99, 858–865. doi: 10.1002/ecy.2154

Cottenie, K. (2005). Integrating environmental and spatial processes in ecological community dynamics. *Ecol. Lett.* 8, 1175–1182. doi: 10.1111/j.1461-0248.2005.00820.x

Datry, T., Melo, A. S., Moya, N., Zubieta, J., De la Barra, E., and Oberdorff, T. (2016). Metacommunity patterns across three Neotropical catchments with varying environmental harshness. *Freshw. Biol.* 61, 277–292. doi: 10.1111/fwb.12702

De Bie, T., De Meester, L., Brendonck, L., Martens, K., Goddeeris, B., Ercken, D., et al. (2012). Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. *Ecol. Lett.* 15, 740–747. doi: 10.1111/j.1461-0248.2012.01794.x

Degrassi, A. L., Brantley, S., Levine, C. R., Mohan, J., Record, S., Tomback, D. F., et al. (2019). Loss of foundation species revisited: conceptual framework with lessons learned from eastern hemlock and whitebark pine. *Ecosphere* 10:e02917.

Dengler, J. (2009). Which function describes the species–area relationship best? A review and empirical evaluation. *J. Biogeogr.* 36, 728–744. doi: 10.1111/j.1365-2699.2008.02038.x

Díaz, S., Settele, J., Brondízio, E., Ngo, H., Guèze, M., Agard, J., et al. (2019). Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the intergovernmental science-policy platform on biodiversity and ecosystem services. *Popul. Dev. Rev.* 45, 680–681. doi: 10.1111/padr.12283

Dietze, M. C. (2017). *Ecological Forecasting*. Princeton, NJ: Princeton University Press.

Dornelas, M., Antão, L. H., Moyes, F., Bates, A. E., Magurran, A. E., Adam, D., et al. (2018). BioTIME: a database of biodiversity time series for the Anthropocene. *Glob. Ecol. Biogeogr.* 27, 760–786. doi: 10.1111/geb.12729

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z.-I., Knowler, D. J., Lévêque, C., et al. (2006). Freshwater biodiversity: importance, threats, status and conservation challenges. *Biol. Rev.* 81, 163–182.

Erõs, T., and Schmera, D. (2010). Spatio-temporal scaling of bioidiversity and the species-time relationship in a stream fish assemblage. *Freshw. Biol.* 55:2391–2400. doi: 10.1111/j.1365-2427.2010.02438.x

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.* 34, 487–515.

Fargione, J., Brown, C. S., and Tilman, D. (2003). Community assembly and invasion: an experimental test of neutral versus niche processes. *Proc. Natl. Acad. Sci. U.S.A.* 100, 8916–8920. doi: 10.1073/pnas.1033107100

Fischer, J., and Lindenmayer, D. B. (2007). Landscape modification and habitat fragmentation: a synthesis. *Glob. Ecol. Biogeogr.* 16, 265–280. doi: 10.1111/j.1466-8238.2007.00287.x

Free, C. L., Baxter, G. S., Dickman, C. R., and Leung, L. K. P. (2013). Resource pulses in desert river habitats: productivity-biodiversity hotspots, or mirages? *PLoS One* 8:e72690. doi: 10.1371/journal.pone.0072690

Frishkoff, L. O., Karp, D. S., M'Gonigle, L. K., Mendenhall, C. D., Zook, J., Kremen, C., et al. (2014). Loss of avian phylogenetic diversity in neotropical agricultural systems. *Science* 345, 1343–1346. doi: 10.1126/science.1254610

Fukami, T. (2015). Historical contingency in community assembly: integrating niches, species pools, and priority effects. *Annu. Rev. Ecol. Evol. Syst.* 46, 1–23. doi: 10.1146/annurev-ecolsys-110411-160340

Grimm, N. B., Chapin, F. S., Bierwagen, B., Gonzalez, P., Groffman, P. M., Luo, Y., et al. (2013). The impacts of climate change on ecosystem structure and function. *Front. Ecol. Environ.* 11, 474–482. doi: 10.1890/120282

Haase, P., Tonkin, J. D., Stoll, S., Burkhard, B., Frenzel, M. I, Geijzendorffer, R., et al. (2018). The next generation of site-based long-term ecological monitoring: linking essential biodiversity variables and ecosystem integrity. *Sci. Total Environ.* 613, 1376–1384. doi: 10.1016/j.scitotenv.2017.08.111

Hanski, I. A., Gaggiotti, O. E., and Gaggiotti, O. F. (eds) (2004). *Ecology, Genetics and Evolution of Metapopulations*. Cambridge, MA: Academic Press.

Holyoak, M., Caspi, T., and Redosh, L.W. (2020). Integrating disturbance, seasonality, multi-year temporal dynamics, and dormancy into the dynamics and conservation of metacommunities. *Front. Ecol. Evol.* 8:571130. doi: 10.3389/fevo.2020.571130

Hooper, D. U., Adair, E. C., Cardinale, B. J., Byrnes, J. E., Hungate, B. A., Matulich, K. L., et al. (2012). A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486, 105. doi: 10.1038/nature11118

Hughes, B. B., Beas-Luna, R., Barner, A. K., Brewitt, K., Brumbaugh, D. R., Cerny-Chipman, E. B., et al. (2017). Long-term studies contribute disproportionately to ecology and policy. *Bioscience* 67, 271–281. doi: 10.1093/biosci/biw185

Jain, M., Flynn, D. F., Prager, C. M., Hart, G. M., DeVan, C. M., Ahrestani, F. S., et al. (2014). The importance of rare species: a trait-based assessment of rare species contributions to functional diversity and possible ecosystem function in tall-grass prairies. *Ecol. Evol.* 4, 104–112. doi: 10.1002/ece3.915

Johnson, C. N., Balmford, A., Brook, B. W., Buettel, J. C., Galetti, M., Guangchun, L., et al. (2017). Biodiversity losses and conservation responses in the Anthropocene. *Science* 356, 270–275. doi: 10.1126/science.aam9317

Keller, M., Schimel, D. S., Hargrove, W. W., and Hoffman, F. M. (2008). A continental strategy for the National Ecological Observatory Network. *Front. Ecol. Environ.* 6, 282–284. doi: 10.1890/1540-9295(2008)6[282:acsftn]2.0.co;2

Keyel, A. C., Gerstenlauer, J. L., and Wiegand, K. (2016). SpatialDemography: a spatially explicit, stage-structured, metacommunity model. *Ecography* 39, 1129–1137. doi: 10.1111/ecog.02295

Kuussaari, M., Bommarco, R., Heikkinen, R. K., Helm, A., Krauss, J., Lindborg, R., et al. (2009). Extinction debt: a challenge for biodiversity conservation. *Trends Ecol. Evol.* 24, 564–571.

Lamy, T., Reed, D. C., Rassweiler, A., Siegel, D. A., Kui, L., Bell, T. W., et al. (2018). Scale-specific drivers of kelp forest communities. *Oecologia* 186, 217–233. doi: 10.1007/s00442-017-3994-1

Law, R., and Morton, R. D. (1993). Alternative permanent states of ecological communities. *Ecology* 74, 1347–1361. doi: 10.2307/1940065

Law, R., and Morton, R. D. (1996). Permanence and the assembly of ecological communities. *Ecology* 77, 762–775. doi: 10.2307/2265500

Leibold, M. A., and Chase, J. M. (2017). *Metacommunity Ecology*. Princeton, NJ: Princeton University Press.

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., et al. (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.* 7, 601–613. doi: 10.1111/j.1461-0248.2004.00608.x

Leitao, R. P., Zuanon, J., Villéger, S., Williams, S. E., Baraloto, C., Fortunel, C., et al. (2016). Rare species contribute disproportionately to the functional structure of species assemblages. *Proc. R. Soc. B* 283:20160084. doi: 10.1098/rspb.2016.0084

Li, D., Olden, J. L., Lockwood, J. L., Record, S., McKinney, M. L., and Baiser, B. (2020). Changes in taxonomic and phylogenetic diversity in the Anthropocene. *Proc. R. Soc. B Biol. Sci.* 287:20200777. doi: 10.1098/rspb.2020.0777

Logue, J. B., Mouquet, N., Peter, H., Hillebrand, H., and Metacommunity Working Group (2011). Empirical approaches to metacommunities: a review and comparison with theory. *Trends Ecol. Evol.* 26, 482–491. doi: 10.1016/j.tree.2011.04.009

Lyons, K. G., Brigham, C. A., Traut, B. H., and Schwartz, M. W. (2005). Rare species and ecosystem functioning. *Conserv. Biol.* 19, 1019–1024. doi: 10.1111/j.1523-1739.2005.00106.x

MacDougall, A. S., McCann, K. S., Gellner, G., and Turkington, R. (2013). Diversity loss with persistent human disturbance increases vulnerability to ecosystem collapse. *Nature* 494, 86–89. doi: 10.1038/nature11869

Magurran, A. E., Baillie, S. R., Buckland, S. T., Dick, J. M., Elston, D. A., Scott, E. M., et al. (2010). Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. *Trends Ecol. Evol.* 25, 574–582. doi: 10.1016/j.tree.2010.06.016

Martay, B., Monteith, D. T., Brewer, M. J., Brereton, T., Shortall, C. R., and Pearce-Higgins, J. W. (2016). An indicator highlights seasonal variation in the response of Lepidoptera communities to warming. *Ecol. Indic.* 68, 126–133. doi: 10.1016/j.ecolind.2016.01.057

McCallen, E., Knott, J., Nunez−Mir, G., Taylor, B., Jo, I., and Fei, S. (2019). Trends in ecology: shifts in ecological research themes over the past four decades. *Front. Ecol. Environ.* 17, 109–116. doi: 10.1002/fee.1993

McGill, B. J., Etienne, R. S., Gray, J. S., Alonso, D., Anderson, M. J., Benecha, H. K., et al. (2007). Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecol. Lett.* 10, 995–1015. doi: 10.1111/j.1461-0248.2007.01094.x

McGlinn, D. J., Xiao, X., May, F., Gotelli, N. J., Engel, T., Blowes, S. A., et al. (2020). Measurement of Biodiversity (MoB): a method to separate the scale-dependent effects of species abundance distribution, density, and aggregation on diversity change. *Methods Ecol. Evol.* 10, 258–269. doi: 10.1111/2041-210x.13102 del Moral, R. (2010). Thirty years of permanent vegetation plots, Mount St. Helens, Washington, USA. *Ecology* 91, 2185–2185. doi: 10.1890/09-2357.1

Mouquet, N., and Loreau, M. (2002). Coexistence in metacommunities: the regional similarity hypothesis. *Am. Nat.* 159, 420–426. doi: 10.1086/338996

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., et al. (2017). *Vegan: Community Ecology Package. R Package Version 2.4-3*. Vienna: R Foundation for Statistical Computing.

Ovaskainen, O., Rybicki, J., and Abrego, N. (2019). What can observational data reveal about metacommunity processes? *Ecography* 42, 1877–1886. doi: 10.1111/ecog.04444

Pandit, S. N., Kolasa, J., and Cottenie, K. (2009). Contrasts between habitat generalists and specialists: an empirical extension to the basic metacommunity framework. *Ecology* 90, 2253–2262. doi: 10.1890/08-0851.1

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* 37, 637–669. doi: 10.1146/annurev.ecolsys.37.091305.110100

Parmesan, C., and Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37–42. doi: 10.1038/nature01286

Pickett, S. T. (1989). "Space-for-time substitution as an alternative to long-term studies," in *Long-Term Studies in Ecology*, ed. G. E. Likens (New York, NY: Springer), 10–135.

Pulliam, H. R. (1988). Sources, sinks, and population regulation. *Am. Nat.* 132, 652–661. doi: 10.1086/284880

Record, S., McCabe, T., Baiser, B., and Ellison, A. M. (2018). Identifying foundation species in North American forests using long-term data on ant assemblage structure. *Ecosphere* 9, 02139.

Reed, D. C. (2018). *SBC LTER: Reef: Annual Time Series of Biomass for Kelp Forest Species, Ongoing Since 2000. Environmental Data Initiative*. Available online at: https://doi.org/10.6073/pasta/23965abf42954f345cfd6642fe3c4810 (accessed December 15, 2020).

Reichman, O. J., Jones, M. B., and Schildhauer, M. P. (2011). Challenges and opportunities of open data in ecology. *Science* 331, 703–705. doi: 10.1126/science.1197962

Sackett, T. E., Record, S., Bewick, S., Baiser, B. H., Sanders, N. J., and Ellison, A. M. (2011). Response of macroarthropod assemblages to the loss of hemlock (*Tsuga canadensis*), a foundation species. *Ecosphere* 2:art74. doi: 10.1890/es11-00155.1

Sály, P., and Erõs, T. (2016). Effect of field sampling design on variation partitioning in a dendritic stream network. *Ecol. Complex.* 28, 187–199. doi: 10.1016/j.ecocom.2016.05.002

Sarremejane, R., Cañedo-Argüelles, M., Prat, N., Mykrä, H., Muotka, T., and Bonada, N. (2017). Do metacommunities vary through time? Intermittent rivers as model systems. *J. Biogeogr.* 44, 2752–2763. doi: 10.1111/jbi.13077

Spake, R., Mori, A. S., Beckmann, M., Martin, P. A., Duguid, M. C., and Doncaster, C. P. (2020). Implications of scale dependence for cross-study syntheses of biodiversity differences. *Ecol. Lett.* (in press). doi: 10.1111/ele.13641

Scheffer, M. (2010). Complex systems: foreseeing tipping points. *Nature* 467, 411. doi: 10.1038/467411a

Seto, K. C., Güneralp, B., and Hutyra, L. R. (2012). Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proc. Natl. Acad. Sci. U.S.A.* 109, 16083–16088. doi: 10.1073/pnas.1211658109

Siqueira, T., Bini, L. M., Roque, F. O., Marques Couceiro, S. R., Trivinho-Strixino, S., and Cottenie, K. (2012). Common and rare species respond to similar niche processes in macroinvertebrate metacommunities. *Ecography* 35, 183–192. doi: 10.1111/j.1600-0587.2011.06875.x

Sokol, E. R., Brown, B. L., and Barrett, J. E. (2017). A simulation-based approach to understand how metacommunity characteristics influence emergent biodiversity patterns. *Oikos* 126, 723–737. doi: 10.1111/oik.03690

Steiner, C. F., and Leibold, M. A. (2004). Cyclic assembly trajectories and scale-dependent productivity–diversity relationships. *Ecology* 85, 107–113. doi: 10.1890/03-3010

Suding, K. N., and Hobbs, R. J. (2009). Threshold models in restoration and conservation: a developing framework. *Trends Ecol. Evol.* 24, 271–279. doi: 10.1016/j.tree.2008.11.012

Thompson, P. L., Guzman, L. M., De Meester, L., Horváth, Z., Ptacnik, R., Vanschoenwinkel, B., et al. (2020). A process-based metacommunity framework linking local and regional scale community ecology. *Ecol. Lett.* 23, 1314–1329. doi: 10.1111/ele.13568

Tilman, D. (1997). Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* 78, 81–92. doi: 10.1890/0012-9658(1997)078[0081:cirlag]2.0.co;2

Tilman, D., and Downing, J. A. (1994). Biodiversity and stability in grasslands. *Nature* 367, 363. doi: 10.1038/367363a0

Tilman, D., May, R. M., Lehman, C. L., and Nowak, M. A. (1994). Habitat destruction and the extinction debt. *Nature* 371, 65–66. doi: 10.1038/371065a0

Tilman, D., Reich, P. B., and Isbell, F. (2012). Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. *Proc. Natl. Acad. Sci. U.S.A.* 109, 10394–10397. doi: 10.1073/pnas.1208240109

Tonkin, J. D., Bogan, M. T., Bonada, N., Rios-Touma, B., and Lytle, D. A. (2017). Seasonality and predictability shape temporal species diversity. *Ecology* 98, 1201–1216. doi: 10.1002/ecy.1761

Tonkin, J. D., Death, R. G., Muotka, T., Astorga, A., and Lytle, D. A. (2018). Do latitudinal gradients exist in New Zealand stream invertebrate metacommunities? *PeerJ.* 6:e4898. doi: 10.7717/peerj.4898

Turner, M. G., Collins, S. L., Lugo, A. L., Magnuson, J. J., Rupp, T. S., and Swanson, F. J. (2003). Disturbance dynamics and ecological response: the contribution of long-term ecological research. *AIBS Bull.* 53, 46–56. doi: 10.1641/0006-3568(2003)053[0046:ddaert]2.0.co;2

Tylianakis, J. M., Didham, R. K., Bascompte, J., and Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.* 11, 1351–1363. doi: 10.1111/j.1461-0248.2008.01250.x

United Nations (2017). *The Sustainable Development Report Goals*. New York, NY: United Nations.

Urban, M. C. (2015). Accelerating extinction risk from climate change. *Science* 348, 571–573. doi: 10.1126/science.aaa4984

Wang, S., and Loreau, M. (2014). Ecosystem stability in space: α, β and γ variability. *Ecol. Lett.* 17, 891–901. doi: 10.1111/ele.12292

Wang, S., and Loreau, M. (2016). Biodiversity and ecosystem stability across scales in metacommunities. *Ecol. Lett.* 19, 510–518. doi: 10.1111/ele.12582

Wilcox, K. R., Tredennick, A. T., Koerner, S. E., Grman, E., Hallett, L. M., Avolio, M. L., et al. (2017). Asynchrony among local communities stabilises ecosystem function of metacommunities. *Ecol. Lett.* 20, 1534–1545. doi: 10.1111/ele.12861

Wolfe, D. A., Champ, M. A., Flemer, D. A., and Mearns, A. J. (1987). Long-term biological data sets: their role in research, monitoring, and management of estuarine and coastal marine systems. *Estuaries* 10:181. doi: 10.2307/1351847

World Health Organization (2005). *Millennium Ecosystem Assessment: Ecosystems and Human Well-Being*. Geneva: World Health Organization.

Zarnetske, P. L., Baiser, B., Strecker, A., Record, S., Belmaker, J., and Tuanmu, M.-N. (2017). The interplay between landscape structure and biotic interactions. *Curr. Lands. Ecol. Rep.* 2:12–29. doi: 10.1007/s40823-017-0021-5.

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