

Cross-Taxon Congruence of Taxonomic and Functional Beta-Diversity Facets Across Spatial and Temporal Scales

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An intensively debated issue in ecology is whether the variations in the biodiversity patterns of different biological groups are congruent in space and time. In addition, ecologists have recognized the necessity of accounting for both taxonomic and functional facets when analysing spatial and temporal congruence patterns. This study aimed to determine how the cross-taxon congruence of taxonomic and functional beta diversity varies across space and time, using data from four floodplains at a continental scale. Our general hypothesis was that the congruence between aquatic biological groups, either taxonomic or functional, would decrease with the "between-group" functional distance. Also, we examined how congruence patterns varied across spatial and temporal scales by focusing on how the cross-taxon relationships differ among Brazilian floodplains and between dry/ wet periods. Our study comprised information on eight biological groups from the four largest Brazilian river-floodplain systems, and cross-taxon congruence was assessed using Procrustes analysis. Our results show how detailed analyses can reveal different patterns of cross-taxon congruence, and partially support the hypothesis that the strength of cross-taxon congruence is negatively related to between-group functional distance.

Keywords: turnover, richness difference, aquatic communities, freshwater, spatial concordance

INTRODUCTION

Biodiversity decline has been attributed to several anthropogenic impacts, including habitat loss and fragmentation, introduction of alien species, and climate change (Cardinale et al., 2012). Thus, a key goal of ecologists is to evaluate how these impacts threaten biodiversity and, ultimately, ecosystem function and human wellbeing (Cardinale et al., 2012; Brose and Hillebrand, 2016). However, reaching this goal is often hampered by biodiversity knowledge shortfalls (e.g., Whittaker et al., 2005; Hortal et al., 2015). Given the accelerated pace of anthropogenic impacts and the paucity of financial and personnel resources (especially in areas of high biodiversity), ecologists often rely on biodiversity shortcuts by using proxies (Rosser, 2017).

Among the different biodiversity shortcuts, surrogates are often used in biomonitoring and conservation planning research (Rodrigues and Brooks, 2007). The use of surrogates is based on the assumption that diversity patterns of different taxa covary in space, a phenomenon called cross-taxon congruence or community concordance (Lovell et al., 2007; Westgate et al., 2014). Under budget shortage, the congruence-based approach may be useful to identify surrogates that portray fundamental aspects of biodiversity, providing a cost-effective biomonitoring program (Padial et al., 2012). However, the reliability of crosstaxon congruence strongly depends on the strength of the correlation among different groups of organisms (Heino, 2010).

The ecological processes affecting cross-taxon congruence are still poorly understood and, at least, three non-exclusive mechanisms operating at different spatial scales are thought to drive cross-taxon congruence (Lovell et al., 2007). The first one assumes the two biological groups may respond similarly to environmental gradients and temporal environmental variability (Padial et al., 2012). Secondly, congruence may emerge from common biogeographical history, whereby the resident biological groups underwent similar dispersal constraints and/or evolutionary trajectories (Burrascano et al., 2018). The third mechanism involves the role of biotic interactions independently of environmental and spatial factors. In this case, the diversity of a group of organisms can be positively correlated with the diversity of their resources (Vasconcelos et al., 2019) or negatively related with the diversity of predators and competitors (Banos et al., 2020).

The spatial covariation among taxa may also be mediated by trait similarity. For instance, as dispersal abilities are constrained by body size, similarity in this trait can be a predictor of crosstaxon congruence (Velghe and Gregory-Eaves, 2013; Hájek et al., 2014). Besides, dispersal abilities may decrease with body size affecting community composition and likely cross-taxon congruence (De Bie et al., 2012; Lansac-Tôha et al., 2021a). For example, organisms that are passively dispersed by wind, such as algae and ciliates, would drift further than fish, when considering a single hydrological basin (Incagnone et al., 2015). Body size can impose fundamental constraints on other life history traits, such as trophic level, reproductive rate, life span, and metabolic rate (Fenchel, 1974). Then, high congruence among taxa with similar body size may emerge because of the functional similarity among biological groups.

River-floodplains are environmentally heterogeneous systems, which typically harbor a high diversity of species (Diniz et al., 2021). Nevertheless, despite their importance for regulating flood regimes, biomass and nutrient cycling, floodplains as other freshwater ecosystems are understudied. In floodplains the annual hydrological regime is a key factor influencing their structure and functioning and flood pulses are of the utmost importance as they promote biotic and abiotic exchange between the river and its surrounding landscape (Junk et al., 1989). Floods also tend to produce the so-called "homogenization" phenomenon, reducing the spatial variability of biological (beta diversity) and environmental factors (Thomaz et al., 2007). In contrast, during droughts, many aquatic habitats are isolated from each other, and local communities are strongly and differently influenced by local factors such as resource fluctuation, competition and predation, which tend to increase beta diversity (Quirino et al., 2019).

Here we aimed to determine whether the cross-taxon congruence in taxonomic and functional beta diversity varies across space and time, using a comprehensive field dataset that encompasses a continental geographical extent. Our surveys combine information on eight biological groups from floodplain lakes that show high variation in species diversity and functional traits. We test the general hypothesis that the congruence between biological groups will decrease with increasing trait dissimilarity. Moreover, we anticipated that strengths in cross-taxon congruence will depend on temporal dynamics and spatial scale (Vieira et al., 2015; Lários et al., 2017). To accomplish this task, we used a sequential scale-out perspective focusing on the strength of cross-taxon congruence. First, the analyses were carried out for each floodplain and period (dry and wet) separately. Second, the analyses were repeated using spatio-temporal data from each floodplain separately. Third, for each period, we analysed the data from all floodplains. The data from the first strategy are similar (in structure) to those obtained in regional studies (e.g., within a specific floodplain) which were conducted once only. Similarly, the data from the second strategy are akin to those obtained in regional studies whose sampling designs considered the temporal variation. Finally, the last strategy emulates a study whose dataset was obtained once and at a broad spatial scale. We expect to highlight the importance of context dependence in using biological surrogates in ecological assessments.

MATERIALS AND METHODS

Study Area

We surveyed four Neotropical floodplain systems (Amazônia, Araguaia, Pantanal, and Paraná; **Figure 1**) over a spatial extent of 2,300 km ($3^{\circ}-23^{\circ}$ S). The Amazônia ($3^{\circ}02' - 3^{\circ}34'$ S and $59^{\circ}38' - 60^{\circ}50'$ W) and the Araguaia ($12^{\circ}49' - 13^{\circ}25'$ S and $50^{\circ}36' - 50^{\circ}43'$ W) floodplains are located in northern and central Brazil, respectively, while the South Matogrossense Pantanal ($18^{\circ}46' - 19^{\circ}34'$ S and $53^{\circ}013' - 53^{\circ}038'$ W) floodplains are located south of the study area. In terms of human impacts, there is a



FIGURE 1 | Map of the study area showing the surveyed freshwater lakes from the Amazônia (red symbols), Araguaia (green symbols), Pantanal (orange symbol and Paraná (blue symbols) floodplains.

gradient ranging from the Amazônia floodplain, which has relatively pristine forests and tributaries, through the Pantanal and Araguaia, with moderate to intense human activities, to the Paraná floodplain, which is located in the most economically developed region of Brazil (Rocha et al., 2017).

The Amazônia and Araguaia floodplains have an equatorial climate characterized by average temperatures ranging from 25 to 29°C and high average annual precipitation (1,300 to 2,000 mm) (Irion et al., 1997). Conversely, the Pantanal and Paraná floodplains have tropical and subtropical climates, respectively, with comparatively lower average temperatures (between 16 and 28°C) and annual precipitation rates (ca. 1,400 mm) (Stevaux, 1994). These floodplains have very marked and distinct

hydrological periods (Stevaux, 1994; Irion et al., 1997; Agostinho et al., 2004), excepting the Paraná River floodplain, which is strongly influenced by an upstream cascade of reservoirs, thus reducing the amplitude and duration of the flood pulses (Agostinho et al., 2004). For more details on these four floodplains and their features, see Lansac-Tôha et al. (2021a, 2021b).

Sampling Periods

Two sampling campaigns were carried out during dry and wet water periods in each of the four floodplains. In the dry period, we sampled 66 lakes connected to the main rivers or their tributaries. Sampling was done in September 2011 in

TABLE 1 | Comparisons of the major cross-biological group functional traits.

Biological Group	Average Body Size (cm)	Cellular Organization	Reproductive Type	Dispersal Mode	Nutrition
Ciliates	0.008406	unicellular	binary fission	passive	heterotrophic
Testate amoebae	0.009773	unicellular	binary fission	passive	heterotrophic
Rotifers	0.03033	multicellular	parthenogenesis	passive	heterotrophic
Microcrustaceans	0.059988	multicellular	parthenogenesis/sexual	passive	heterotrophic
Ostracods	0.087824	multicellular	parthenogenesis/sexual	passive	heterotrophic
Fish	18.35	multicellular	sexual	active	heterotrophic
Macrophytes	50	multicellular	mostly parthenogenesis	passive	autotrophic

the Paraná floodplain (20 lakes), in October 2011 in Amazônia (16 lakes), in November 2011 in Araguaia (18 lakes), and in March 2012 in the Pantanal floodplain (12 lakes). During the wet period, samples were collected in August 2011 in the Pantanal (18 lakes), in February 2012 in Paraná (20 lakes), in March 2012 in Araguaia (18 lakes),



FIGURE 2 Summary of the analytical approach. (A) the combinations of the three nested subsets, how the taxonomic and functional datasets are organized, and the calculation of each beta diversity component. (B) the steps to obtain the cross-taxon congruence values. First, we performed a Principal Coordinates Analysis (PCoA) on each dissimilarity matrix and then the Procrustes correlations between each pair of ordinations, separately for taxonomic and functional data. (C) A Mantel test was carried out between pairs of congruence and functional dissimilarity between biological groups.



and in May 2012 in Amazônia (15 lakes), totalling 71 lakes in this period (**Figure 1**).

Biological Communities

We analyzed data from eight biological groups, including phytoplankton, ciliates, testate amoebae, rotifers, planktonic microcrustaceans (cladocerans and copepods), ostracods, fish and macrophytes, in all four floodplains during dry and wet periods. All these groups are commonly used in studies of aquatic communities, distribution patterns, beta diversity and crosstaxon congruence. The sampling methods and laboratory analysis for each group can be found in detail in Lansac-Tôha et al. (2021a). Sampling, counting and identification of species of each biological group were performed by the same team. Sampling permit was issued by the Brazilian Environmental Ministry (Instituto Chico Mendes de Conservação da Biodiversidade - ICMBio, authorization from the System and Information on Biodiversity -SISBIO; protocol #29.652).

Functional Traits

We gathered information about the functional traits of the eight biological groups aforementioned. The literature sources used for functional classification and the relationship between each trait and its corresponding ecosystem function can be found in **Supplementary Table S1**. To investigate the effect of

functional differences on the cross-taxon congruence, we estimated the functional distances among biological groups. For this purpose, we considered biological characteristics that are commonly known to interfere with the distribution patterns of organisms, such as body size (De Bie et al., 2012), cellular organization (uni or multicellular) (Hillebrand et al., 2001), reproductive type (binary fission, parthenogenesis, sexual or mixed) (Browne and MacDonald, 1982), dispersal mode (passive or active) (Lansac-Tôha et al., 2019) and nutrition (heterotrophic or autotrophic) (Barton et al., 2013) (**Table 1**).

Data Analysis

Before the analysis, we splitted our data in three different ways: the first dataset included separate data for each floodplain (Amazônia, Araguaia, Pantanal, and Paraná) and each period (dry and wet), generating eight subsets; the second dataset also considered each floodplain separately but included both periods, generating four subsets; and the third dataset included all floodplains, but separate periods (two subsets). All data handling and statistical analyses were performed in the R environment (R Core Team, 2021) and each procedure is described below.

First, we computed taxonomic site-by-site dissimilarity matrices for each biological group and subsets by applying the



Sørensen index on presence-absence and the Bray-Curtis index on abundance data (except for aquatic macrophytes, for which we collected presence/absence data only) (Peres-Neto and Jackson, 2001; Legendre, 2014). Following Podani and Schmera (2011), the total taxonomic beta diversity (β_{total}^T) was decomposed into replacement (β_{repl}^T) , richness (β_{Rdiff}^T) or abundance difference (β_{ABdiff}^T) components, using the *beta* function from R-package "BAT" (Cardoso et al., 2015). Before calculating and decomposing the total functional beta diversity (β_{total}^F) into its components $(\beta_{repl}^F, \beta_{Rdiff}^F)$, and $\beta_{ABdiff}^F)$, functional traits were used to calculate dissimilarities for each biological group based on Gower's index, using the function gowdis from package "FD" (Laliberté et al., 2014). Then, these eight species-by-species functional dissimilarity matrices were subjected to a hierarchical clustering using the function hclust from package "stats". Finally, the functional trees were used in the same beta function to calculate and decompose the functional beta diversity. After all these procedures, we produced dissimilarity matrices representing the following combinations [floodplain * period 8) + floodplain 4) + period (2)] * presence-absence/ abundance 2) * taxonomic/functional 2) * beta-diversity component 3) * biological group 8) (Figure 2A). Because only presence/absence data was available for macrophytes, we produced and analysed 1,260 matrices out of the 1,344 expected from the full combination above.

We first summarized each dissimilarity matrix using the two first axes of a Principal Coordinates Analysis (PCoA). This analysis was carried out using the function cmdscale from the "stats" R-package. Then, we assessed cross-taxon congruence using Procrustes analysis on the PCoA scores (Jackson, 1995; Peres-Neto and Jackson, 2001). We opted for Procrustes instead of other usual congruence-based methods (e.g., Mantel) because it is more robust in dealing with large environmental gradients (Peres-Neto and Jackson, 2001). In the Procrustes analysis, the mismatch between two ordination configurations (Jackson, 1995) is given by the badness-of-fit statistic (m^2) . We transformed the m^2 into a goodness-of-fit Procrustes r statistic, where r = $\sqrt{1-m^2}$ (Peres-Neto and Jackson, 2001). The Procrustes r ranges from 0 (no congruence) to 1 (perfect congruence). We restricted the evaluation of congruences among biological groups to the same facet (i.e., taxonomic and functional). In all cases, Procrustes analysis was performed with respect to the same data types (presence-absence or abundance) and the same subsets, using the function protest from R-package "vegan" (Oksanen et al., 2018) (Figure 2B).

Finally, to assess the relationship between the congruence strengths (as given by Procrustes r) and functional distances among biological groups, we used the Mantel test implemented in the function *mantel* from R-package "vegan". Mantel tests considered the Gower-based functional dissimilarities among



biological groups and the pairwise congruences among biological groups. Under our hypothesis, we expect a negative correlation between cross-taxon congruence and functional distance (Figure 2C).

RESULTS

Cross-Taxon Congruence Patterns Across Spatial and Temporal Scales

All dissimilarities calculated for each biological group for taxonomic and functional facets, considering the three scaleout perspective, are given in the **Supplementary Material S2**. Overall, cross-taxon congruence was low (<0.65) for all beta diversity components regardless of the diversity facet. Congruence was higher for the β_{repl} component (presence/ absence data) and the β_{ABdiff} component (abundance data), although variations were observed with spatial scale.

At floodplain scale, when hydrological periods were analysed individually, the cross-taxon congruence based on presenceabsence data showed little variation between dry and wet periods (**Figure 3**). When the data of two hydrological periods were combined, the lowest values of congruence were, in general, found in the Upper Paraná River floodplain. At the continental scale, we found clear differences between taxonomic and functional facets, with higher congruence for the taxonomic facet, especially for β_{total}^{T} and β_{repl}^{T} (**Figure 3**). The differences between hydrological periods were minor. For abundance data, congruence decreased at the continental scale (**Figure 4**). The southern floodplains (Paraná and Pantanal) showed higher congruences within periods, but the pattern was reversed when periods were combined. That is, congruence values (based on β_{total} and β_{ABdiff}) decreased from the Amazônia to the Paraná floodplains. It is noteworthy that for the β_{ABdiff} component, the congruences for both taxonomic and functional facets were similar at all scales (**Figure 4**). The raw congruence values of all pairs of combinations between biological groups based on presence-absence and abundance data, for all datasets, are provided in **Supplementary Figures S1–S8**.

Relationships Between Congruence and Functional Resemblance Across Biological Groups

Higher functional distances were found between phytoplankton and fish, ciliates and macrophytes, and testate amoebae and macrophytes. In contrast, lower distances were found between ciliates and testate amoebae, microcrustaceans and ostracods, ciliates and phytoplankton, and rotifers and microcrustaceans (**Figure 5**).

Mantel test showed that the expected negative relationship between functional dissimilarity and congruence appeared mainly at large spatial scale and mainly for the β_{total} and β_{repl} components of beta diversity (**Figures 6**, 7). Although some positive relationships emerged at the floodplain scale, the average values of the Mantel test were negative, especially for



abundance data ($\beta_{total} = -0.58$ and $\beta_{repl} = -0.70$ for abundance and $\beta_{total} = -0.37$ and $\beta_{repl} = -0.48$, for presence-absence data).

DISCUSSION

Cross-taxon congruence can indicate a common response to environmental variation and be caused by strong biotic interactions (Lansac-Tôha et al., 2021b). However, our results show that the spatial scale, the type of data, and the degree of anthropogenic impact can affect cross-taxon congruence. Besides, we found low levels of congruence independently of the biodiversity facet. Therefore, our results imply that using wellknown taxonomic groups as surrogates of the changes in composition and diversity of other floodplain communities can have several limitations.

Cross-Taxon Congruence at Floodplain Scale

We found low levels (r < 0.55) of cross-taxon congruence at the floodplain scale. In river-floodplain systems, the low connectivity among habitats during the dry period produces high

environmental heterogeneity and constraints dispersal. contributing to an increase in the relative importance of the environment (Dias et al., 2016). Under this rationale, one could expect a higher strength of cross-taxon congruence during the dry periods because the wide environmental gradients would cause large changes in species composition of different taxa (Padial et al., 2012). However, our results did not support this prediction as the strengths of cross-taxon congruence were similar between the hydrological periods. Thus, our results at the floodplain scale are in line with those obtained in other small-scale studies (Padial et al., 2012; Westgate et al., 2014; de Morais et al., 2018). In short, levels of cross-taxon congruence are unlikely to be higher in a specific hydrological period.

Seasonal variation in water level is known to result in large changes in composition and abundance (Bozelli et al., 2015). The magnitude of the temporal turnover in aquatic communities likely depends on the sampling interval relative to the length of the generation cycle of a given community (Van Allen et al., 2017). For instance, microbial and macroinvertebrate communities can show complete turnover in minutes (Fenchel, 1974) and days to months (Allan, 1976), respectively. Indeed, owing to the large environmental changes caused by the hydrological variation, we found increased crosstaxon congruence levels when both hydrological periods were



analyzed together (for each floodplain). Such increase was evident when the analyses were based on abundance data, exhibiting a gradient from North to South. This pattern likely resulted from similar seasonal changes in the abundance of multiple groups (Thomaz et al., 2007). Interestingly, the low levels of cross-taxon congruence in the Upper Paraná River floodplain do not invalidate our inference about the importance of hydrological variation in promoting congruence. This is so because the hydrological regime in this floodplain is strongly regulated by upstream dams, reducing the duration and intensity of floods (Agostinho et al., 2004). Thus, cross-taxon congruence might tend to decline in the absence of a major force (i.e., hydrological variation) determining simultaneously the dynamics of different communities between seasons.

Cross-Taxon Congruence at Continental Scale

At large spatial extents, both biogeographic processes and higher environmental heterogeneity are thought to promote cross-taxon congruence (e.g., Rooney and Azeria, 2015; Burrascano et al., 2018). Indeed, studies have shown that cross-taxon congruence in species richness tends to increase with spatial scale (e.g., Wolters et al., 2006; Qian and Kissling, 2010; Burrascano et al., 2018). Thus, the low levels of cross-taxon congruence at the broader spatial scale in our study (i.e., when all floodplains were analyzed together), especially for β_{Rdiff} , was surprising. Although environmental heterogeneity increases with the spatial extent, the magnitude of beta diversity differs among organisms. For instance, the composition of small-sized and passively dispersing organisms changed slowly (β total ranging from 0.52 to 0.75) when compared to large body-sized and actively dispersing organisms (fish β total = 0.90). Therefore, the distribution patterns of organisms may differ depending on their intrinsic characteristics, which may lead to a weaker cross-taxon congruence at broad spatial scales.

Relationship Between Cross-Taxon Congruence and Functional Distance

A negative relationship between functional dissimilarity and congruence is expected when ecologically dissimilar species have different niche requirements. For example, studies have shown that cross-taxon congruence is strongest between biological groups with similar body sizes (Velghe and Gregory-Eaves, 2013; Hájek et al., 2014). Our study demonstrated that the relationship between functional dissimilarity and congruence can vary with the spatial scale (i.e., positive at a small spatial scale and negative at a large spatial scale). At a small spatial scale, both direct and indirect biotic interactions might result in a positive relationship between functional dissimilarity and congruence (Lansac-Tôha et al., 2021b). For example, in the Amazonia floodplain, during the dry period, fish and phytoplankton had the highest congruence for β repl (Figure 5; Supplementary Figure S1). Planktivorous fish are known to produce strong effects on the structure and dynamics of the zooplankton community through predation-driven control (Lazzaro et al., 2003). These changes can achieve the lowest trophic levels, through an effect known as "trophic cascade" (Carpenter et al., 1985). In this sense, reductions in zooplankton abundance, especially microcrustacean, may weaken the predation pressure on phytoplankton, triggering changes in their abundances (Attayde and Hansson, 2001).

CONCLUSION

Our findings highlight that the consistent low levels of crosstaxon congruence indicate a low prospect for the reliable use of surrogates in floodplain systems (Padial et al., 2012; Lários et al., 2017). Thus, inferences about the effects of anthropic activities in these systems (e.g., sand mining, water diversion, damming) should be restricted to the biological groups effectively monitored. Similarly, one should not expect that conservation actions planned for a specific biological group (e.g., fish, water birds) would necessarily be beneficial or optimal for other groups. Thus, our study adds to the growing body of evidence that surrogates should be used with caution (de Morais et al., 2018).

Enhancing the efficiency of monitoring programs can be more cost-effective if only one or a few biological groups can predict distribution patterns of other biological groups. However, the strength of community congruence in our study was weak and rarely exceeded 0.7, which is often recommended for a single biological group to predict the spatial patterns of others (Lovell et al., 2007; Heino, 2010). Furthermore, even when the degree of congruence between two biological groups was high at a certain scale, the same pattern was not always repeated at other spatial or temporal scales, making it difficult to unequivocally suggest any specific indicator taxon amongst the groups studied here.

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.

ETHICS STATEMENT

The animal study was reviewed and approved by the Sampling permit was issued by the Brazilian Environmental Ministry (Instituto Chico Mendes de Conservação da Biodiversidade -ICMBio, authorization from the System and Information on Biodiversity -SISBIO; protocol #29.652).

AUTHOR CONTRIBUTIONS

FM-LT: Conceptualization, Methodology, Formal analysis, Data curation, Writing-original draft, Writing-review and editing, Visualization. JHe: Conceptualization, Methodology, Writing-review editing, Supervision. LB: and Conceptualization, Methodology, Writing-review and editing. MB: Conceptualization, Methodology, Formal analysis, Writing-review editing. Conceptualization, and OP: Methodology, Writing-review and editing, Visualization. BQ: Data Curation, Writing-review and editing, Visualization. AP: Data Curation, Writing-review and editing. BM: Data Curation, Writing-review and editing. FF: Writing-review and editing, Visualization. FO: Data Curation, Writing-review and editing. BM: Data Curation, Writing-review and editing. FB: Data Curation, Writing-review and editing. MS: Data Curation, Writing-review and editing. MD-F: Data Curation, Writing-review editing. RC: Data Curation, and Writing-review and editing. RD: Data Curation, Writing-review and editing. CB: Resources, Data Curation, Writing-review and editing. JHi: Investigation, Resources, Data Curation, Writing-review and editing, RM: Investigation, Resources, Data Curation, Writing-review and editing. EB: Resources, Writing-review and editing, CP: Resources, Data Curation, Writing-review and editing, LR: Investigation, Resources, Data Curation, Writing-review and editing. SJ: Investigation, Resources, Data Curation, Writing-review and editing. KM: Conceptualization, Investigation, Writing-review editing. FA-LT: Conceptualization, and Resources. Writing-review and editing, Project administration, Funding acquisition. LV: Conceptualization, Resources, Writing-review and editing, Supervision.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2022.903074/ full#supplementary-material

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