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Editorial: The role of rivers in the origins, evolution, adaptation, and distribution of biodiversity

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Editorial on the Research Topic
The role of rivers in the origins, evolution, adaptation, and distribution of biodiversity

Rivers represent ubiquitous landscape features and affect biodiversity in fundamental ways. Not only do they provide the medium necessary to sustain aquatic life, but they also influence the structure and biodiversity of both riparian and non-riparian habitats. Therefore, rivers can potentially affect the origins, evolution, adaptation, and distribution of both aquatic and terrestrial biota. The goal of this Research Topic was to provide a forum to discuss recent advances in the study of the role of rivers in the ecology and evolution of biodiversity. Specifically, we aimed to highlight the current and historical role of rivers in the evolutionary process and reveal different ways by which rivers affect biodiversity. In this editorial, we will review (i) the role of rivers in the origin and evolution of species; (ii) how river reorganization can affect species diversity; (iii) the effect of riverine habitats as environmental filters; and (iv) the importance of community-based management for biodiversity conservation.

Rivers and the origin and evolution of terrestrial species

The association of rivers with the speciation process in non-aquatic species can be traced back to Wallace's explorations in the Amazon, where he documented that several species of primates had closely related, yet morphologically different, populations across some major rivers (Wallace, 1852). These observations were subsequently interpreted as evidence of the vicariant force of rivers in the speciation process, a model that became known as the *Riverine Barrier Hypothesis* (Sick, 1967; Capparella, 1988, 1991). Although there are many examples of rivers acting as biogeographical barriers

throughout the world, it is in the Amazon that this phenomenon is more widespread and best documented. Nonetheless, it took over a century to fully appreciate the role of Amazonian rivers in defining species' distributions (Haffer, 1969, 1974; Hershkovitz, 1977; Cracraft, 1985). Increasingly detailed range maps have allowed biologists to investigate the role of rivers as biogeographical barriers for entire communities (Ayres and Clutton-Brock, 1992; Gascon et al., 2000; Hayes and Sewlal, 2004) and to formulate evolutionary hypotheses to account for congruent river-bounded distributions (Cracraft and Prum, 1988; Silva and Oren, 1996; Bates et al., 1998).

By the end of the 20th century, molecular studies started to link phenotypic and genotypic variation across riverine barriers (Capparella, 1988, 1991), inspiring legions of scholars who investigated the role of rivers in dividing evolutionary lineages (Marks et al., 2002; Aleixo, 2004; Ribas et al., 2012). These were followed by multi-taxon studies that began to reveal commonalities, but also some unique taxon-specific distribution patterns, including barrier effects of relatively minor Amazonian rivers (Naka et al., 2012; Boubli et al., 2015) and disparate times of divergence among co-distributed taxa (Naka and Brumfield, 2018). With the advent of next generation sequencing, multi-locus studies are shedding light into patterns of gene flow and introgression across rivers, particularly around river headwaters, where rivers are much narrower and potentially cease to represent meaningful biogeographic barriers (Pulido-Santacruz et al., 2018).

Despite major advances in the field, most of these studies were restricted to the Amazon basin and to either birds or primates. Recent studies, however, show that the dissecting power of rivers are not restricted to this region (Harcourt and Wood, 2011). Molecular studies have shown the role of rivers such as the Congo (Anthony et al., 2007), the Mississippi (Jackson and Austin, 2010), and the Paraná (Kopuchian et al., 2020) as potential current and historic biogeographic barriers. Similarly, in the last decade, studies evaluating the role of rivers as biogeographical barriers in non-avian and non-primate groups started to appear in the literature, including studies on lizards (Avila-Pires et al., 2012), frogs (Fouquet et al., 2012, 2015; Godinho and da Silva, 2018), invertebrates (Guilherme et al., 2022), and plants (Nazareno et al., 2017, 2019).

In this Research Topic, five articles include new data that broaden our understanding on the role of rivers in the speciation process, filling important taxonomic, geographical, and theoretical gaps. Three studies provide contrasting views on the role of Amazonian rivers in structuring different mammal and avian lineages. Whereas Silva et al. found that the distribution of Amazonian Phyllostomidae bats was not defined by rivers, Mourthé et al. found that rivers were key in structuring Amazonian primate diversity, finding a significant effect of annual discharge and river sinuosity on primate beta-diversity. Working on birds, Dornas et al. investigated the role of two eastern Amazonian rivers as barriers, in a region with few prior biogeographical studies. Using a comparative approach, these authors found that 14 avian lineages responded differently to these riverine barriers. These contrasting results suggest that (i) ecological traits and dispersal ability may predict the importance of rivers as biogeographical barriers, and (ii) different lineages may have different histories and be affected by rivers in different ways along their evolutionary history.

Using molecular data, two studies explored the role of rivers in the evolutionary history of the herpetofauna, including an Amazonian heliothermic lizard (*Kentropyx calcarata*) and a treefrog (*Dendropsophus elegans*) in the Atlantic Forest of Brazil. Cronemberger et al. evaluated the genetic structure of *K. calcarata* in the light of different evolutionary scenarios and found that although Amazonian rivers likely acted as barriers to dispersal, they were not the sole drivers of diversification. Pirani et al., on the other hand, describe the genomic divergence and phenotypic admixture of *D. elegans*, showing the effect of the Rio Doce as a biogeographical barrier. These results add to the growing body of information pointing this river in the Atlantic Forest as a major barrier, as shown in the past for small non-volant mammals (Costa, 2003), a species of gecko (Pellegrino et al., 2005) and a species of bird (Cabanne et al., 2008).

Quite surprisingly, until now we lacked basic knowledge on how riverine barriers affect species dispersal. Conducting a series of dispersal experiments in real-life conditions, Naka et al. evaluated how hundreds of individuals of dozens of bird species cope with the challenge of crossing a river gap in the Amazon basin. Using a methodology previously used in Panama by Moore et al. (2008), this study showed that nearly a third of the individuals tested failed at crossing even 100 m of open water. Their results revealed that ultimately, dispersal limitations are directly related to the flying apparatus of birds. Species with more rounded wings performed worse in the experiments than those species with more elongated ones. Surprisingly, ecological traits, such as habitat preference and river island specialization had little predictive power in the outcome of the experiments. These results open new perspectives on experimental studies to evaluate the dissecting power of rivers on biodiversity.

Riverine landscape evolution and diversification

Until very recently, most riverine studies viewed rivers as fixed vicariant forces. However, rivers do change through time. Drainage network reorganization can have pervasive effects on species distributions. One specific way by which rivers reorganize, is by a process known as river capture, where topographic changes may alter river networks (Bishop, 1995). The effect of these changes on biodiversity became known as the *River Capture Hypothesis* (Albert et al., 2018) and has shown great potential in the understanding of species distributions, particularly in fish. Recent studies have shown that river

network rearrangements can also promote speciation in lowland Amazonian birds (Musher et al., 2022).

In this Research Topic, two studies investigate this phenomenon at two different scales. Val et al. conducted a comprehensive meta-analysis to test the *River Capture Hypothesis* using nearly 15,000 species of obligate freshwater fishes in more than 3,000 river basins. Their results indicate that fish species richness can be explained by landscape evolution models, including the *River Capture*, *Mega Capture*, and the *Intermediate Capture Rate Hypotheses*, supporting the conclusion that landscape changes represent a meaningful mechanistic driver of net diversification in riverine and riparian organisms. At a smaller scale, Sá Leitão et al. used genomic data to investigate if river reorganization could explain the genetic differentiation and structure of two Amazonian dwarf cichlids. Their results are consistent with the *River Capture Hypothesis* and offer a mechanistic link between the isolation and differentiation of fish populations and the drainage evolution of the basin, suggesting that the geological history of the region may be responsible for promoting species diversification.

Rivers as environmental filters

The ecological characteristics of rivers also affect the distribution of species, not only by restricting their movements, but also by providing differential habitats along its margins. Recent studies from northern Amazonia, have shown that water sediments are key to explaining bird species composition (Laranjeiras et al., 2019, 2021) and that avian communities respond promptly to changes in riverine habitats and climatic variables along ecological gradients (Naka et al., 2020). In this Research Topic, two articles show how habitat heterogeneity can drive compositional differences among both avian and butterfly species assemblages. Sinha et al. showed the influence of both biotic and abiotic factors in defining compositional differences among avian local species assemblages in the Himalayas. Using standardized avian surveys, they found that riparian bird communities in the drier and more seasonal Western Himalayas were poorer and more clustered phylogenetically and functionally than those communities in the Eastern Himalayas, pointing out the influence of habitat and climatic factors on patterns of avian beta diversity. Back in the Amazon, Rabelo et al. show that seasonal flooding of Amazonian forests strongly determines the composition of butterfly assemblages. In this case, small topographic variation can create distinct flooding gradients that directly affect species abundance and community composition. These results add to the growing body of work demonstrating that environmental filtering plays a crucial role in structuring biotic communities. Together, these results suggest that habitat heterogeneity can create the conditions that maintain distinct communities and even provide ecological gradients along which populations can diverge and possibly speciate.

This is, in fact, what Hay et al. found in their genomic study of the adaptive evolution of an Amazonian Characin fish. These authors found that variation in water characteristics was a key factor contributing to adaptive divergence. Specifically, variation in genes involved in acid-sensitive ion transport and light-sensitive photoreceptor pathways were strongly associated with water pH and turbidity variability. These results offer a hint at how river characteristics can drive genomic changes through natural selection, impacting the distribution of biodiversity in riverine habitats.

Conservation of riverine systems

Overfishing and overhunting represent significant threats to riverine biodiversity. While natural reserves are key for protecting riverine environments and their biodiversity, governments often fail in providing secure conservation. In fact, many protected areas in the tropics are themselves vulnerable to human activities (Laurance et al., 2012). Recent studies have shown that community-based conservation management can integrate both socio-economic needs with conservation goals in tropical ecosystems (Campos-Silva et al., 2018), providing benefits to entire biotas (Campos-Silva et al., 2021).

In this Research Topic, Andrade et al. analyze historical time series of protection of four different species of turtles in the Brazilian Amazon. Using data from 1974 to 2019, they estimate that over a million nests and more than 30,000,000 hatchings were protected by both government and community-based protection initiatives. They compare the effect of both kinds of protection, and showed that in some cases, government-based protection resulted in higher support capacity in the production of nests and hatchlings, but in other cases, communities were more efficient in protecting both nests and hatchlings. As such, they conclude that community-based protection and monitoring programs are an important component of conservation and should be incorporated by the government's environmental agencies for turtle management in the Amazon.

Final considerations

Despite the importance of riverine systems to both human wellbeing and biodiversity conservation, tropical rivers, which harbor an exceptional and disproportionate high number of species, are under assault (Latrubesse et al., 2017). Main threats include their use for energy production (i.e., hydroelectrical dams) and canalization to control their courses and allow navigation (Anderson et al., 2018). At the same time, climate change is disrupting natural patterns of rainfall and flooding worldwide (Barichivich et al., 2018), further modifying natural riverine ecosystems.

Although we have come a long way since Wallace's visit to the Amazon in the 19th century, our discovery of biological patterns is often outpaced by habitat destruction. Therefore, it is key to both increase protection of tropical rivers and accelerate and expand the kind of studies that are presented in this Research Topic. Understanding the complexity of riverine systems often requires great amounts of human and financial resources and we urge scientists to both deepen their Research Topics and use novel strategies to engage both local communities and the general public in the conservation of tropical rivers.

The increasing number of whole genome sequences available for an ever-growing number of taxa, allows us to better understand the past and present role of rivers as vicariate agents, as well as to understand current and past patterns of gene flow across barriers. On the other hand, ecological studies are broadening our understanding of rivers as environmental filters. Such advances can now be better contextualized by the outstanding advances in the understanding of the geologic, climatic, and geomorphological changes in riverine landscapes (Sawakuchi et al., 2022).

Unfortunately, the rate of destruction of many of these pristine systems is greater than the rate of new scientific discoveries. Particular attention should be given to rivers and their potential for evolutionary change in organisms when designing new protected area networks. We hope this Research Topic not only adds to the science of riverine biology, but also highlights the many opportunities that lay down the road, and at the same time call the attention to the urgent need of conserving the world's rivers, both for human wellbeing and biodiversity conservation.

Author contributions

LN did the leading writing. All authors contributed with ideas and reviews.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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