Review:

Amazonian avian biogeography: broadscale patterns, microevolutionary processes, and habitat specific models revealed by multidisciplinary approaches

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ABSTRACT

Our understanding of Amazonian biogeography is quickly increasing, catalyzed by the growing use of genomic datasets, improved knowledge of species distributions, and the accumulation of new data on the geological and climatic history of the region. The high number of species in Amazonia and their intricate patterns of geographic distribution triggered the development of many diversification hypotheses that shaped historical biogeography as a discipline. Here, we present a historical overview of avian biogeographic studies in Amazonia, their recent advances, outstanding questions, and future directions. We focus on how new approaches have led to novel understandings of the distribution patterns and diversification processes that underpin avian diversity. We show how genomic tools are being used to establish new hypotheses about the drivers of diversification and highlight the importance of recent studies of birds in previously overlooked environments, such as floodplains and open vegetation enclaves. We emphasize the importance of gene flow, species traits, and habitat affinities in studying diversification processes to fully acknowledge the complexity of Amazonian ecosystems and their history. We then discuss the current gaps in Amazonian taxonomic and biogeographic knowledge, with a focus on the issues that we believe hinder our understanding of the field. Amazonia has been facing increasing levels of forest loss due to agricultural expansion, infrastructure development, mining, climate change, and illegal activities catalyzed by weak governance. To halt biodiversity loss, it is crucial to increase our knowledge of the natural history and biogeography of Amazonian species. We suggest increasing incentives for research and training at institutions based in the region, as well as the establishment of partnerships with governments, local communities, NGOs, and international institutions to bring diverse communities together to address crucial questions.

KEYWORDS

Spatial diversification, habitat heterogeneity, gene flow, genomics, species distribution, historical biogeography, Amazonia, birds

LAY SUMMARY

- Amazonia is a natural laboratory for ornithological research and has played a central role in our understanding of how species originate.
- Biogeographic studies have been vital in efforts to describe patterns of species richness.
- Recent studies have greatly expanded our knowledge of the effects of landscape dynamics on speciation processes.
- Genomic datasets, improved knowledge of species distributions, and the accumulation of new information on the geological and climatic history of the region are considerably changing our view on how Amazonian biodiversity was formed.
- In this review, we present a historical overview of avian biogeographic studies in Amazonia, describe recent advances, address outstanding questions, and explore exciting new directions and future approaches.

"Even though Amazonia is presented as a single, large, green ellipse in most world maps, it is actually a heterogeneous place, with each region and habitat type holding a distinct set of species." (Ribas 2023)

INTRODUCTION

Amazonia contains the world's largest and most speciose contiguous tropical rainforest, hosting well over 1,778 species of birds Vale et al. 2008, with many that are yet to be recognized (Tavares et al. 2011, Pulido-Santacruz et al. 2018, Cracraft et al. 2020). It is therefore unsurprising that Amazonia has been a focal point for ornithological research and played a central role in the development of many areas of biodiversity research (e.g., Historical Biogeography, Phylogeography, and Tropical Ecology). Amazonia is an evolutionary hotspot of Neotropical biodiversity, as its high rates of speciation and low rates of extinction have enabled the region to accumulate species and serve as a source of diversity for surrounding biomes (Smith et al. 2017, Antonelli et al. 2018, Musher et al. 2019). Its influence extends far beyond Neotropical biotas, playing an outsized role in global carbon and hydrological cycles and therefore in climate change mitigation (Tian et al. 2000, Azevedo et al. 2020). Amazonia's leading global role in hosting biodiversity and delivering ecosystem services is being undermined by the combined impacts of land-use change and climate change - creating a pressing need for further research to provide information for enhancing governance and conservation strategies (Feng et al. 2021, Albert et al. 2023).

Biogeography has been vital in efforts to describe patterns of species richness in Amazonia (Guayasamin et al. 2021). Recent comparative studies have made large strides toward answering key questions regarding the effects of landscape evolution in the speciation process; however, the results are still contentious (Smith et al. 2014, Weir et al. 2015, Harvey et al. 2017, Naka and Brumfield 2018, Silva et al. 2019, Thom et al. 2020, Musher et al. 2022). Understanding how the interplay of different ecological and evolutionary forces has produced

Amazonia's contemporary avifauna is a decidedly nontrivial task (Bush 1994, Naka and Pil 2020, Tobias et al. 2020). During the last decade, the growing use of genomic-scale datasets combined with denser spatial sampling, improved statistical models, and finer resolution of paleogeographic reconstructions has dramatically improved our understanding of the role that different processes play in both generating species and promoting intraspecific genetic differentiation (Cronemberger et al. 2020, Harvey et al. 2020, Thom et al. 2020, Del-Rio et al. 2022, Luna et al. 2022). Such studies have been crucial for building a detailed picture not only of the history and possible fates of the Amazonian avifauna but also of the environments in which they co-evolved, directly contributing to policymaking and conservation planning (Ribas et al. 2022).

The last decade has also brought novel geological and climatological insights into the history of the Amazonian landscape (Cheng et al. 2013, Arruda et al. 2018, Bicudo et al. 2019, Mason et al. 2019, Pupim et al. 2019, Ruokolainen et al. 2019, Sawakuchi et al. 2022, Kern et al. 2023, Sacek et al. 2023). Amazonia has been geologically, hydrologically, and climatically dynamic, even over relatively short timescales (e.g., over 1,000s of years), affecting drainage systems and vegetation distribution throughout the region. If the distribution of distinct environments and landscapes is dynamic over time (Hoorn et al. 2010, Pupim et al. 2019), it is also increasingly apparent that species diversification patterns are more dynamic and intricate than previously assumed (Musher et al. 2022, Thom et al. 2022a). Although early and seminal biogeographic studies were heavily influenced by a vicariance framework (Haffer 1969, Nelson 1978, Cracraft and Prum 1988), recent research has introduced a more nuanced view of the role of geographic barriers, which involves organismal dispersal, ecological interactions, functional traits, and gene flow.

Amazonia has traditionally been viewed as a single entity, with most biogeographical studies focusing on *terra-firme* (upland, non-flooded) forest species. However, the basin is composed of a mosaic of distinct habitats and associated avian communities, with significant environmental and vegetational heterogeneity, longitudinal diversity gradients, and distinct areas of endemism often, but not exclusively, bounded by major rivers (Cohn-Haft et al. 2007, Tuomisto et al. 2019). Recent studies have considerably improved our collective understanding of the evolutionary history of species occurring in distinct environments. New biogeographic research is expanding in remit beyond the *terra-firme* avifauna, shedding light on the evolution of other Amazonian ecosystems (Thom et al. 2018, Capurucho et al. 2020b, Ritter et al. 2020, Luna et al. 2021, 2022; Sawakuchi et al. 2022), and inferring the effects of functional traits on diversification patterns (Burney and Brumfield 2009, Claramunt et al. 2012, Harvey et al. 2017).

In this review, we summarize the main distribution patterns and diversification processes shaping the bird communities of major Amazonian ecosystems, describe how Amazonian bird biogeography has grown in recent years, and discuss major advances and outstanding questions. The main questions that we address include: (1) What are the drivers of speciation and genetic diversity? (2) How has landscape evolution, including geomorphological and climatic history, influenced diversification? (3) To what extent are functional traits and habitat affinities associated with the distinct diversification patterns? (4) In what ways has genomic data brought new and exciting questions to the surface? And, (5), how can our developing knowledge about Amazonian biogeographic history become more collaborative and provide information that helps maintain ecological and evolutionary processes in the face of increasing anthropogenic impacts?

THE HISTORICAL BIOGEOGRAPHY OF BIRD COMMUNITIES ASSOCIATED WITH DISTINCT AMAZONIAN ENVIRONMENTS

Many alternative hypotheses have been proposed to explain the diversification of Amazonian organisms, and at one point, these were considered mutually exclusive explanations for the origin of the regional species pools. Amazonian diversification hypotheses have been thoroughly reviewed elsewhere (Haffer 2008; Leite and Rogers 2013) and are based on paleoenvironmental events and landscape features and their association with species' distribution patterns (Haffer 1969, Cracraft and Prum 1988). Despite the strong concordance in the geographic distributions of Amazonian birds, molecular studies have failed to agree on the generality of any single hypothesis (Ribas et al. 2012, Naka and Brumfield 2018, Silva et al. 2019). The lack of a general agreement could be due to distinct reasons, including: (1) tree-based biogeographic studies that typically ignore microevolutionary and genomic processes (e.g., gene flow; (Thom et al. 2018, 2022a); (2) coarse resolution and limited genetic, geological, and climatic information; and (3) considerable temporal and spatial overlap between the predictions of alternative hypotheses (Leite and Rogers 2013, Papadopoulou and Knowles 2016). These shortcomings severely limit our ability to test specific processes, given that most diversification hypotheses are actually not mutually exclusive. Moreover, Amazonia is composed of many distinct habitats (e.g., *várzea* and white-sand ecosystems) and microhabitats that segregate horizontally (e.g., bamboo stands and treefall gaps) and vertically (e.g., canopy and understory), each homing distinct bird communities. Species occurring in these environments have been impacted by landscape evolution in diverse ways, according to variation in their ecological attributes, dispersal capacity, and generation times (Hayes and Sewlal 2004, Burney and Brumfield 2009, Harvey et al. 2017, Capurucho et al. 2020a, Johnson et al. 2023). To understand

Amazonian biogeography, it is thus necessary to explore diversification histories across the habitat spectrum and account for species' ecologies. Recent genomic studies have pushed the field towards testing more complex diversification scenarios that account for life history differences between species (Harvey et al. 2017, Barbosa et al. 2022, Johnson et al. 2023). Below, we briefly discuss recent findings for major Amazonian habitat types and highlight new perspectives for studying Amazonian biogeography in the context of habitat heterogeneity.

Upland *Terra-Firme* Forest Habitats

Species occupying *terra-firme* forests (forests that are not seasonally inundated by the large rivers) are the most well-studied group in Amazonia, and their diversity and distributional patterns have served as the basis for most diversification hypotheses tested to date (Sick 1967, Haffer 1969, Ribas et al. 2012). The mode in which lineages diversified and/or colonized Amazonia was likely variable, and multiple hypotheses postulate a continuous exchange with neighboring biomes over deep evolutionary scales (e.g., Museum hypothesis; Fjeldså et al. 1999, Fjeldsa et al. 2012). Lowland tropical forests were likely present in northern South America long before the establishment of the modern Amazonian Basin (Burnham and Johnson 2004; Hoorn et al. 2010), the Andean uplift, and the origin of savanna habitats (Simon et al. 2009). Although faunal exchange with surrounding regions (Batalha-Filho et al. 2013) played an important role in community assembly, we constrain our discussion to in situ speciation processes that are likely the major contributors to the contemporary levels of species richness.

The ever-changing network of Amazonian rivers (Albert et al. 2018b, Pupim et al. 2019, Ruokolainen et al. 2019, Rossetti et al. 2021) has long been known to represent key barriers to dispersal for many birds and primates (Wallace 1854, Sick 1967). Large rivers demarcate the range edges of the distributions of many taxa, as well as the boundaries between distinct genetic and vocal types that likely also represent undescribed forms. This turnover leads to distinct avian communities within interfluves, known as areas of endemism (Cracraft 1985, Isler et al. 2007, Borges and Da Silva 2012, Ribas et al. 2012, Fernandes 2013, Thom and Aleixo 2015, Quaresma et al. 2022). Indeed, indigenous people living in Amazonia have long known the importance of rivers in limiting the distribution of organisms and would routinely traverse rivers in search of specific animal resources (Wallace 1854, Ribas 2023). Thus, the effects of rivers can be seen at multiple scales, from populations to entire ecological communities (Maximiano et al. 2020). Key questions about the biogeographic importance of rivers do remain difficult to test, however. For example, are wide rivers secondary barriers to dispersal for species that arose due to other causes or partial barriers where hybrid zones come to rest? Or how do rivers promote speciation despite some gene flow across them? Although some of these scenarios have been explored with simulations (Santorelli Junior et al. 2022), robust tests with empirical data are still scarce (Naka and Brumfield 2018).

For decades, researchers debated whether the genesis of the contemporary river network was responsible for the differentiation of bird lineages on opposite river margins (e.g., the Riverine Hypothesis) through vicariance (Nores 1999, Aleixo 2004, Ribas et al. 2012), or whether rivers act as secondary barriers between lineages that have evolved due to other causes (Haffer 1997, Naka and Brumfield 2018). The latter scenario could be linked, for example, to forest contractions during glacial periods (Haffer 1969; Vanzolini 1970). A key assumption regarding the singular vicariant effect of large rivers is that divergence times between co-distributed species isolated by a river should be concordant with the establishment of the barrier. To address this hypothesis, studies have tested for synchronous diversification events across major river barriers (Smith et al. 2014c, Naka and Brumfield 2018, Silva et al. 2019). Their results have not corroborated overlapping divergence times for most species tested; instead, estimates between pairs of taxa on opposite margins varied considerably and were associated with species traits such as dispersal capacity or forest stratum preference (Burney and Brumfield 2009, Smith et al. 2014c). Alternative hypotheses associated with the secondary effects of large rivers have also been rejected, as comparative phylogeographic studies have not found spatially consistent signatures of recent changes in effective population sizes that could be related to major vegetational changes during the Quaternary (Silva et al. 2019). Instead, a potential synergistic effect of landscape evolution, climate change, and species ecology in driving isolation and dispersion has been suggested (Silva et al. 2019). This view postulates that the dynamic nature of rivers in Amazonia is one of the primary forces of population differentiation that, coupled with environmental changes and the inherent life histories of species, leads to idiosyncratic genetic diversity and diversification patterns (Burney and Brumfield 2009, Claramunt et al. 2012, Smith et al. 2014c, Crouch et al. 2019, Silva et al. 2019).

An emerging idea proposes that the large Amazonian tributaries may currently function as secondary barriers delimiting the distribution of taxa that were isolated by past riverine channels (Musher et al. 2022). As rivers change their course or loose their barrier effect, species may expand their distributions until they become bounded by rivers that are currently large and stable. This ephemerality of riverine barriers has been one of the reasons why it has been challenging to establish causality for rivers as barriers for avian speciation (Weir et al. 2015, Mason et al. 2019, Pupim et al. 2019, Ruokolainen et al. 2019). During the past hundreds of thousands of years, large Amazonian tributaries have been highly dynamic, experiencing massive river capture and avulsion events (Rossetti 2014, Albert et al. 2021). This suggests that the current location of rivers and their effectiveness as barriers might not be representative of paleolandscapes (Peñalba et al. 2019, Ribas et al. 2022), especially in western Amazonia, where the low topographic relief facilitates more rapid river rearrangement due to erosional hydrodynamics. Whereas sediment-rich rivers draining the western lowlands, such as the Solimões, Juruá, Japurá, and Marañon rivers, can frequently rearrange through avulsions (see the *Floodplain forests habitats* section), sediment-poor rivers draining the eastern Amazonian shields are more stable, and river course alterations tend to be driven by infrequent tectonic events, e.g., Bishop (1995), Rossetti (2014), but see Musher et al. (2022).

Importantly, the rate at which river rearrangements occur should also influence rates of regional diversification through effects on speciation, extinction, and dispersal (Albert et al. 2018a). River rearrangements may influence rates of speciation and extinction by subdividing species' ranges, and they promote dispersal by removing barriers from the landscape, thus enabling the expansion of distributions with the colonization of new regions. When river rearrangements occur at a high rate, they might prevent the differentiation of upland forest species by allowing gene flow between populations formerly isolated on opposite banks. However, in specific situations, rearrangements might both increase speciation rates and reduce the probability of extinction through intermittent gene flow (Albert et al. 2018a, Musher et al. 2022). This process could also give origin to unique introgressed lineages resulting from the combination of previously isolated and divergent gene-pools (Barrera-Guzmán et al. 2018, Musher et al. 2022). Moreover, river rearrangements are expected to lead to inconsistencies in the timing of species' divergences and spatial relationships. A recent study on central Amazonian birds revealed a wide array of patterns in the geographic distribution of populations affected by river rearrangements, including variable levels of gene flow (Musher et al. 2022). This study also indicated more dynamic lineage histories in southwestern Amazonia, where frequent drainage rearrangements occurred, than in the southeast, where rivers flow on top of the more geologically stable Brazilian Shield (see also Fig. 6 in Silva et al. 2019).

Although the dating of diversification events across barriers has been extremely variable for *terra-firme* forest birds, there is emerging evidence for the spatio-temporal sequence of those events. For instance, the oldest splits within the basin are often found between lineages or clades occurring on opposite sides of the main channel of the Amazon River, with subsequent splits separating the westernmost lineages, followed by more recent diversification events towards the southeastern portion of the basin (Silva et al. 2019). This is a common pattern, however, by no means encompasses all the variation observed in *terra-firme* forest birds, and there are many lineages with contrasting histories. Accounting for all of this variation has been a major challenge in developing a unified narrative for the evolution of the Amazonian avifauna.

Genomic studies have provided much finer resolution to key aspects associated with riverine dynamics by accounting for microevolutionary processes (e.g., genetic introgression) that can impact phylogenetic and phylogeographic approaches (Weir et al. 2015, Del-Rio et al. 2022, Thom et al. 2022a, Musher et al. 2022). We suggest that future studies focus on the following open questions: (1) how and how often do *terra-firme* populations diverge with gene flow? (2) Are there common spatial patterns of gene flow between lineages across the basin? (3) Do we find increased evidence of synchronous divergence across rivers by accounting for gene flow and species traits? (4) How do individuals disperse across rivers, and how might this impact longitudinal gradients of avian diversity in Amazonia? (5) To what extent are biogeographic histories idiosyncratic, and to what extent are they shared? The ongoing focus on *terra-firme* species using large-scale genomic datasets derived from reduced representation or whole-genome sequencing for multiple co-occurring species will provide tools to elucidate these and many other open questions in Amazonian biogeography.

Floodplain Forest Habitats

The Amazonian floodplains cover more than 300,000 km^2, and approximately 15% of the non-aquatic Amazonian bird species are specialists of habitats formed by the seasonal flooding pulse (Remsen and Parker 1983). The evolutionary processes that drove diversification of floodplain specialist birds are only now beginning to be characterized, and patterns of genetic structure are still being described (Choueri et al. 2017, Thom et al. 2020, Barbosa et al. 2021, Luna et al. 2021, Silva et al. 2021).

Across the Amazonian floodplains, bird species segregate along a myriad of environments that are associated with riverine geomorphological and hydrological conditions (Remsen and Parker 1983; Laranjeiras et al. 2019). White-water rivers that have their headwaters in the Andes give origin to highly dynamic environments, the *várzeas*. These rivers carry high amounts of sediment that continually reshape the floodplains. Black and clear water rivers, on the other hand, carry low amounts of sediment and drain old cratons (e.g., the Brazilian and Guiana shields), producing the more stable *igapó* environments. Even within the same river, floodplain environments vary depending on how far they are from the main channel. Habitats farther away from open running water tend to be more stable, while river-edge habitats and islands are highly impacted by sediment deposition and erosion (Junk et al. 2011). These differences lead to a marked variation in microhabitats that have distinct levels of dynamicity and spatial distribution. While more stable environments tend to have continuous and widespread distributions, early successional river-edge environments are spatially fragmented and more prevalent in white-water rivers. Bird species occupying floodplain environments have variable levels of association with this vast array of successional habitats (e.g., *Conirostrum margaritae* and *Cecropia* patches; *Myrmochanes hemileucus* and *Tessaria* scrubs), from widespread generalists to river-island specialists (Remsen and Parker 1983, Rosenberg 1990). Recent studies have shown that species occurring in more dynamic and ephemeral habitats (i.e., early successional habitats) have less genetic diversity, more dynamic population sizes through time, and less genetic structure in space compared to taxa occupying more stable environments (Barbosa et al. 2021, Luna et al. 2022, Johnson et al. 2023). Although this remarkable variation in habitat affinity offers a great opportunity to explore the ecological aspects leading to population differentiation, studies accounting for habitat preference within the floodplains are scarce or limited in the number of species or samples per species, which limits generalizations.

Floodplain species have been neglected in biogeographic studies for a long period (but see Aleixo 2006 and Cadena et al. 2011), potentially for distinct reasons. First, the diversity of species found along the floodplains is considerably lower than in the non-flooded forests. Second, traditionally recognized floodplain species tend to be widespread over Amazonia, have less phenotypic variation (Cohn-Haft et al. 2007) and shallower genetic structure across space (Harvey et al. 2017, Johnson et al. 2023). Lastly, historical sampling efforts were systematically focused on *terra-firme* forests, despite watersheds being used to access Amazonian interfluves. The lack of spatial sampling precluded a more comprehensive understanding of floodplain species distributions and geographic variation in phenotypic traits. This is even more pronounced when we consider modern specimens with associated tissue samples that can be used in molecular studies. Tissue sample availability for many species was patchy or absent in most parts of the basin, especially in eastern Amazonia. However, recent efforts to sample floodplain ecosystems are changing this scenario (Cohn-Haft et al. 2007, Moncrieff et al. 2019, 2021; Del-Rio et al. 2021). Many recent expeditions led by the Instituto Nacional de Pesquisas da Amazônia (INPA; Cohn-Haft et al. 2007, Borges et al. 2019) and Museu Paraense Emilio Goeldi (MPEG) have greatly facilitated genomic studies of floodplain birds. These studies, relying on a more complete geographic sampling, have changed our understanding of the histories of lineages in these environments (Choueri et al. 2017, Thom et al. 2018, 2020, 2022b; Barbosa et al. 2021, Luna et al. 2022, Johnson et al. 2023).

The earliest phylogeographic studies on floodplain forest lineages reported low levels of genetic diversity among widespread species with no signal of population differentiation, corroborating the expectations described above (Aleixo 2006, Cadena et al. 2011). These results suggested that the linear configuration of floodplain environments facilitates high levels of gene flow, and that species occupying seasonally flooded environments were likely selected for high vagility given the dynamism of these environments (Remsen and Parker 1983). More recent phylogeographic studies, however, have shown that the central portion of the Amazonian floodplains, between the Negro and Madeira river mouths, is a suture zone for floodplain forest species, characterized by transitions between taxa isolated within major tributaries (Choueri et al. 2017, Thom et al. 2018, 2020b, Luna et al. 2021, 2022, Silva et al. 2021). These results confirmed previous biogeographic assessments based on species distributions that reported a rapid change in community composition along the central Amazonian floodplains (Cohn-Haft et al., 2007), between the mouths of the Negro and Madeira rivers. While some species are absent in this region, leading to disjunct populations on major Amazonian rivers, others form extensive hybrid zones that may be associated with secondary contact due to riverine historical dynamics (Thom et al. 2018, 2020; Silva et al. 2021). This pattern has been more prevalent in river-edge and island specialists that occur in environments perhaps more sensitive to changes in river sedimentation dynamics. The substantial levels of genetic structure and complex patterns of differentiation have been attributed to climatic oscillations shaping the distribution of flooded habitats through time (Thom et al. 2018, 2020, 2022b; Silva et al. 2021, Luna et al. 2021, 2022; Barbosa et al. 2021).

A key aspect linking the diversification of floodplain forest species to riverine dynamics over time is historical changes in effective population sizes. Studies have reported recent and synchronous population size expansions for multiple lineages across Amazonia, with more intense oscillations in populations occurring in habitats that are more susceptible to historical riverine dynamics (Thom et al. 2020, Luna et al. 2021, Sawakuchi et al. 2022). Another prominent pattern linking diversification histories to riverine dynamics is the isolation of floodplain forest bird populations by ria lakes (Thom et al. 2020, Luna et al. 2022), which are formed by the Amazon river's damming effect on its tributaries (Irion et al. 2009, Thom et al. 2020, Luna et al. 2022). In sediment-poor rivers such as the Negro and Tapajós, sediment deposition occurs upstream of ria lakes, forming large archipelagos with stable and abundant floodplain habitats, while along the ria lakes seasonally flooded habitats are scarce or unavailable. The extent of ria lakes within Amazonia changed considerably over time, controlled by historical variation in the discharge of interacting rivers and sea level fluctuations (Sawakuchi et al. 2022). The large gaps in the distribution of floodplain environments (up to 150 km in the Tapajos River) match the range limits of multiple taxa that have recent but well-differentiated allopatric populations up and down stream of ria lakes (Thom et al. 2020, Luna et al. 2022).

Amazonian floodplains are a natural laboratory for studying the effects of a dynamic landscape and habitat specialization on patterns of population differentiation and persistence through time; however, there are many open questions to be explored. An important component to be tested in the future is the potential high rate of floodplain population extinction. Most species restricted to floodplain environments are characterized by long branches in their phylogenies, diverging from taxa occurring in other parts of the Neotropical region several million years ago (Aleixo 2002, Harvey et al. 2020). This characteristic contrasts with the lower levels, or absence, of population genetic structure across the entire basin and reduced genetic diversity when compared to *terra-firme* forest species (these patterns are also found in species characteristic of white-sand ecosystems; see below). Testing for higher extinction rates in this group of species is a non-trivial task, but exploring associations between fluctuations in historical effective population sizes, habitat preference, and phylogenetic branch lengths might help clarify the processes leading to this common pattern. The effects of interspecific competition in driving levels of habitat specificity and eventually patterns of population differentiation and genetic diversity is another poorly explored component within the floodplains. Playback experiments have shown differential levels of aggression between closely related species occurring along a successional gradient in Amazonia (Robinson and Terborgh 1995), which could potentially explain why some species are restricted to or occur in much higher abundance in marginal habitats (e.g., river islands) while analogous environments are available on the margins. The occupation of dynamic habitats is a significant predictor of levels of population differentiation (Johnson et al. 2023), and understanding the contribution of competition in habitat segregation between species is vital to test the importance of multiple ecological components in species diversification.

Lowland Open Vegetation Habitats

The main open vegetation habitats found in Amazonia (Fig. 1) can be broadly divided into white-sand ecosystems (WSE) (Capurucho et al. 2020b) and savanna relicts (Bates et al. 2003, Werneck 2011, Carvalho and Mustin 2017). These two ecosystems look relatively similar in vegetation physiognomy and share some species, yet their biogeographic patterns can be quite different. The Amazonian savannas are occupied by bird lineages that occur in the central (Cerrado) and/or northern South American savannas (Silva 1995). Bird species adapted to open vegetation habitats are commonly found in both Amazonian savannas and WSE, while community composition in these patchy habitats is dependent on biogeographic context (Aleixo and Poletto 2007, Alonso et al. 2013, Borges et al. 2016a, b). Typical savanna taxa usually exhibit weak or a lack of genetic structure within and between Amazonian and other South American savannas, despite being isolated by large tracts of forested environments (Bates et al. 2003, Ritter et al. 2020, Els et al. 2021, Lima-Rezende et al. 2022). On the other hand, WSE harbors many bird lineages that are restricted or nearly restricted to these Amazonian habitats (Borges et al. 2016b), but that also present relatively shallow population structure. Considering the fragmented nature of WSE and Amazonian savannas, the shallow genetic structure found among bird populations in different fragments and across Amazonia is surprising (Bates et al. 2003, Capurucho et al. 2013, Matos et al. 2016, Ritter et al. 2020, 2021; Els et al. 2021). However, there are exceptions to this pattern. For example, *Galbula leucogastra,* a characteristic WSE bird, shows strongly structured lineages isolated by the major Amazonian rivers (Ferreira et al. 2018), highlighting that a more thorough investigation of organismal traits affecting population structure in WSE is worth exploring. The shallow structure within WSE species contrasts with the old evolutionary origins of many of these birds, as the speciation events are estimated to have occurred before the Pleistocene (Capurucho et al. 2020b), in a similar fashion to what was described for floodplain species (see above). Authors have associated these patterns (old origins, but shallow genetic structure) with the historical dynamics of WSE linked to climatic oscillations and drainage shifts (Hayakawa and Rossetti 2015, Rossetti et al. 2016, 2018; Zular et al. 2019), causing local extinctions and recolonizations (Capurucho et al. 2013, Ritter et al. 2020). As a recent review discusses biogeographic and ecological patterns of WSE (Capurucho et al. 2020b), we refer readers interested in this topic to that publication.

Pleistocene climatic changes and the recent dynamics of WSE distribution, in part controlled by these same climatic changes, caused variation in population sizes in many WSE bird lineages (Capurucho et al. 2013, Matos et al. 2016, Ritter et al. 2020). These studies have shown that, at the beginning of the last glacial cycle (~120,000 ya), population sizes of WSE birds were smaller and have since grown, especially after the last glacial maximum (~20,000ya) (Capurucho et al. 2013, Matos et al. 2016, Ritter et al. 2020). A recent genomic and comparative approach showed that demographic change patterns are clustered in both space and time, as most expanding populations occur north of the Amazon river and expansions date to the last 100,000 years, showing that populations responded in concert to environmental changes (Capurucho et al. 2023). Outstanding questions remain as to how connectivity among WSE patches across Amazonia is achieved and whether gene flow among populations is ongoing or was driven by past climatic and landscape changes. Despite the congruence in demographic histories, patterns of genetic structure, relationships among populations, the ranges of WSE species are substantially different, thus an evaluation of traits driving these patterns would also be an interesting research focus.

GENOMIC AND BIG DATA REVOLUTION

Amazonian bird biogeography has vastly benefited from large-scale datasets propelled by a combination of new genomic approaches, better spatial sampling of species, increased resolution of occurrence data, and improved phylogenetic reconstructions. High-throughput sequencing technologies have become much cheaper and more accessible within the past decade or so, allowing researchers to implement these approaches for non-model organisms. Phylogenomic datasets have provided better resolution to disentangle the effects of multiple landscape and environmental processes on species' demographic histories by improving accuracy in parameter estimations (e.g., effective population size, gene flow, divergence times), allowing for testing the synchrony of diversification events (Thom et al. 2020, Luna et al. 2022), and enhancing the power of model-based approaches (Thom et al. 2018). The continuous improvement in spatial sampling and occurrence data of Amazonian birds has greatly contributed to this new generation of studies by expanding our understanding of secondary contact and hybridization between taxa (Weir et al. 2015, Pulido-Santacruz et al. 2018, Del-Rio et al. 2022) and highlighting the biogeographic importance of small rivers (Borges and Da Silva 2012, Whitney et al. 2013, Musher et al. 2022). Below, we discuss important discoveries in Amazonian avian biogeography derived from the big data revolution.

Macroecology and Phylogenetic Structure of Amazonian Bird Communities

Haffer (1969) developed the refuge hypothesis based on the limits and overlap of bird species' geographic ranges. Almost two decades later, Cracraft (1985) delineated avian areas of endemism using species distribution data. The areas of endemism drawn for Amazonia are still a robust description of beta diversity patterns in *terra-firme* bird species (Braga et al. 2022). Access to bird geographic range maps, occurrence data, and phylogenetic trees has allowed researchers to apply complex macroecological and biogeographic analyses (e.g., Oliveira et al. 2017, Antonelli et al. 2018, Crouch et al. 2019). However, studies applying these analyses have yielded opposing results among them, and in disagreement with previously described patterns, evidencing the complexity of the region's species accumulation through time and the importance of well-curated datasets (Oliveira et al. 2017). Regarding the latter, there are well-known issues that affect our knowledge about the diversity of Amazonian birds, including inaccurate range maps (Vale et al. 2017), taxonomic uncertainties, sampling biases (Hughes et al. 2021), poorly curated or vetted species lists (Lees et al. 2014), and many taxa missing from large phylogenies and/or unreliable reconstructions of lineage histories (Jetz et al. 2012). Although many of the recent publications show interesting results, they are also prone to having one or a few of these issues influence their results. For example, it is important to consider that studies using large scale datasets based on range maps and large-scale phylogenies (e.g., Antonelli et al. 2018, Crouch et al. 2019) may be subject to errors resulting from missing data, inaccurate projections of species distributions, and out-of-date taxonomies.

Studies evaluating community turnover based on species distributions and occurrences have shown opposing results. Based on extensive field data at both margins of one Amazonian river (Tapajós), Maximiano et al (2020) found that the river is important in delimiting turnover among bird communities. However, Fluck et al (2020), using published range data for Amazonian birds (Birdlife), found that climate and geographic distance are more important than rivers for determining beta diversity of passerine birds (Fluck et al. 2020). Despite showing that rivers are strong dispersal barriers for birds, Oliveira et al. (2017) argued that, based on their recently developed biogeographic analyses, bird occurrence data does not support currently recognized Areas of Endemism (Cracraft 1985, da Silva et al. 2005, Borges and Silva 2012).

However, in both Fluck et al (2020) and Oliveira et al. (2017), the basic data used relies on secondary information obtained from large and poorly curated databases, or on published distribution ranges of Amazonian birds that do not incorporate precise taxonomic information. In addition, Oliveira et al.'s expectations that all taxa, including those adapted to distinct ecosystems, should respond similarly to the same barriers seem implausible, as has been shown throughout this review.

By assessing the contribution of in-situ diversification and dispersal to community structure patterns based on phylogenetic diversity metrics, a recent study evidenced new biogeographic predictors of biodiversity across Amazonia (Crouch et al. 2019). Sedimentary regions of recent geological origin, like the Andean slopes and areas along the Amazon river, have underdispersed bird communities, while the old cratons have overdispersed communities (Crouch et al. 2019). Amazonia has also contributed to community assembly in different Neotropical ecoregions (Batalha-Filho et al. 2014, Tello et al. 2014, Thom and Aleixo 2015, Antonelli et al. 2018, Musher et al. 2019). Therefore, in addition to generating intricate and diverse biogeographic patterns, Amazonia has also been identified as a primary source ("providers of lineages" *sensu* Antonelli et al. 2018) of avian lineages that subsequently colonized other parts of the Neotropics (Antonelli et al. 2018, Musher et al. 2019).

Hybridization and Gene Flow

Geographic isolation driven by biogeographic barriers plays a crucial role in speciation within Amazonia; however, as discussed above, barriers are dynamic over time and some species are more vagile and likely to overcome those barriers. Temporal variation in barrier permeability can lead to secondary contact between previously isolated populations. The outcomes of secondary contact might range from sympatry among reproductively isolated species (Musher et al. 2022) to the formation of extensive hybrid zones and lineage fusion (Thom et al. 2018, Del-Rio et al. 2022, Musher et al. 2022). The extent and magnitude of the effects of introgression have been long acknowledged in population-level studies; however, its impacts on Amazonian biogeography are only starting to be appreciated (Smith et al. 2014, Harvey and Brumfield 2015, Weir et al. 2015, Thom et al. 2018, 2020; Musher et al. 2022). Most diversification models for Amazonian biota were based on phylogeographic patterns that did not account for reticulated evolution, usually due to limited datasets (e.g., mtDNA) obtained with Sanger DNA sequencing technologies (Fig. 2). Although mtDNA data is still useful for uncovering major genetic structure and biogeographic breaks, it has limited information for estimating patterns of gene flow. Genetic introgression, especially between non-sister taxa, can result in variable levels of differentiation across the genome, impacting phylogenetic models that assume bifurcating cladogenesis, biasing tree-based biogeographic inferences, and the estimation of demographic parameters (Leaché et al. 2014, Thom et al. 2018, 2020; Ji et al. 2022). Recent genomic approaches in Amazonia have revealed that gene flow might be a widespread process within recently diverged lineages, including the formation of hybrid zones (Weir et al. 2015, Thom et al. 2018, Pulido-Santacruz et al. 2020, Del-Rio et al. 2022), hybrid speciation events (Barrera-Guzmán et al. 2018, Musher et al. 2022), mitochondrial capture (Ferreira et al. 2018), and pre- and postzygotic isolation with gene flow (Pulido-Santacruz et al. 2018, Musher et al. 2022). These results reinforce the importance of incorporating introgression into biogeographic inferences and suggest that many more instances of genetic introgression may be uncovered as more lineages are studied.

Interpreting diversification histories and patterns of genetic structure without accounting for gene flow may be particularly challenging for taxa bounded by large rivers due to the intrinsic properties of these barriers. The Amazon Basin is composed of multiple large tributaries that run in parallel, causing taxa to be surrounded by two or more closely related lineages that occur on opposing river margins. If introgression occurs across rivers between non-sister taxa, this will result in reticulated patterns of diversification. As discussed above, multiple processes might lead to a higher incidence of gene flow between taxa isolated by rivers (i.e., *terra-firme* taxa), including variation in species dispersal abilities (Naka et al. 2022), headwater effects (Weir et al. 2015), and riverine dynamics (Musher et al. 2022). Postzygotic genetic incompatibilities also play an important role in speciation processes within Amazonia, limiting lineage fusions after secondary contact (Pulido-Santacruz et al. 2018, Cronemberger et al. 2020). For instance, genetic incompatibilities were reported in a wide hybrid zone between *Rhegmatorhina* species, where cytonuclear incompatibilities might be associated with the geographic displacement of the genetic break between the mitochondrial and nuclear DNA (Del-Rio et al. 2022).

Introgression also plays an important role in patterns of genetic diversity of floodplain forest species and is widespread among the taxa studied to date (Thom et al. 2018, 2020; Luna et al. 2021, 2022). The high prevalence of gene flow between differentiated populations can probably be explained by the high dynamism and ephemerality of some floodplain environments over time (e.g., river islands), with higher rates of gene flow between populations occurring in ever-changing *várzea* forest systems (Thom et al. 2020, Luna et al. 2022, Johnson et al. 2023). Extensive hybrid zones have been described along Amazonian floodplains and may offer a great opportunity to explore the evolution of reproductive isolation in this system (Thom et al. 2018).

Isolation-by-distance (Wright 1943), a pattern of increasing genetic divergence with increasing geographic distance, is also a prevalent mechanism along the floodplains that can confound the estimation of genetic structure and gene flow and deserves further attention in Amazonian biogeographic studies (Thomaz et al. 2016, Bradburd et al. 2018, Buainain et al. 2020, Luna et al. 2021, Thom et al. 2022b).

The high incidence of gene flow reported above shows that complex diversification processes are more common than previously expected and that the field should embrace the reticulated nature of at least part of Amazonian biodiversity. Genomic datasets were key in uncovering reticulated patterns, and further development in molecular biology and analytical approaches might expand our knowledge. Tracking the presence of gene flow among multiple populations is now a relatively simple task with genomic data, but testing the processes underlying introgression remains challenging. As previously stated, these mechanisms are not mutually exclusive, and they may all be active at the same time. Demographic modeling using coalescent methods is an effective tool for gaining important insights into these complex diversification histories. It can aid in testing alternative topologies that account for gene flow, as well as determining whether introgression has occurred continuously since divergence (Isolation-migration model) or after secondary contact between populations (Musher et al. 2020; Thom et al. 2020; Thom et al. 2018; Raposo do Amaral et al. 2021). These approaches, however, are limited by spatial implicit models constrained by assumptions (e.g., panmixia within populations and non-overlapping generations) and are typically designed to capture the signal in the data associated with only one of these events. Ultra-parameterized models with multiple pulses of gene flow combined with historical changes in effective population sizes, for example, are frequently unidentifiable and may produce spurious results even when using whole genome data.

Recent methodological approaches might ameliorate this problem by taking advantage of spatially explicit simulations (Provost et al. 2021), ancestral recombination graphs (Hubisz et al. 2020) and accounting for intrinsic genomic properties (Martin et al. 2019, Thom et al. 2022a). The implementation of more realistic models in comparative approaches that account for species' traits, and habitat preferences will be essential in establishing a more complete picture of how a dynamic landscape shaped species diversification in Amazonia.

CURRENT CHALLENGES

Although studies from the last few decades have advanced our understanding of Amazonian historical biogeography, many gaps still exist (Fig. 2). There are multiple studies that extensively discuss the effects of knowledge gaps in biodiversity research (e.g., Hortal et al. 2015, Lees et al. 2020, Soares et al. 2022, Carvalho et al. 2023); therefore, we are going to briefly discuss issues that we believe can negatively impact Amazonian biogeographic studies, in particular the Linnean and Wallacean shortfalls *sensu* Hortal et al. (2015).

Taxonomy is one of the main challenges in advancing biogeographic knowledge of Amazonian birds. The majority of Amazonian avian taxonomy was proposed in the 19th and early 20th centuries, when species or subspecies status was determined on the basis of typically subjective morphological features or inferred reproductive isolation, often based on very few specimens. Importantly, in the first half of the 20th century, there was a lumping phase based on the polytypic species concept (Gill 2014). As a result, many evolutionarily independent lineages currently exist as subspecies or undescribed taxa within arbitrarily defined polytypic species. More recently, our knowledge about species distributions, genetic differentiation, and morphological variation has expanded manifold, but taxonomy has not always kept pace with the new information (Aleixo 2023). Consequently, the diversity of birds in the Neotropics, and especially in the Amazonian lowlands, is expected to be significantly underestimated. Due to differing species concepts, biologists often disagree about the species status of many taxa, which in turn affects the number of recognized species by different taxonomic entities (de Queiroz 2005) and subsequently conservation planning (Peterson and Navarro-Sigüenza 2016, McClure et al. 2020, Simkins et al. 2020, Lees et al. 2022). For birds, the biological species concept has dominated the taxonomic landscape and impeded the recognition of well-supported, allopatric, and differentiated lineages as species. For example, using the phylogenetic species concept, Barrowclough et al. (2016) estimated that overall global bird diversity would eventually almost double. Biogeographic studies within Amazonia have shown that many species are composed of independent evolutionary lineages, similar to those proposed by Barrowclough et al. (2016), and would merit species-level recognition (for an extreme example, see Berv et al. 2021). Recognition of these monophyletic and allopatric lineages as species progresses slowly as new evidence is presented to ornithological committees and their taxonomic bodies (Barrowclough et al. 2016; Lees et al. 2020). A faster recognition of many of these monophyletic, distinct, and allopatric lineages as species would lead to an improved description of bird diversity and be extremely valuable for biological conservation and management in Amazonia (Gill 2014).

Our understanding of the geographic range limits of many Amazonian species is still incomplete, especially in remote areas, and major range extensions are relatively common (Lees et al. 2020). This knowledge gap also encompasses our understanding of habitat associations and the nature of seasonal movements (Jahn et al. 2020, Lees et al. 2020). The lack of more complete knowledge about species range limits and seasonal movements results in poor distribution maps (Lees et al. 2014). In extreme cases, range maps can mirror survey efforts in a region but not actual species distributions (Hortal et al. 2015). Many macroecological and biogeographic analyses rely on range maps (Oliveira et al. 2017, Fluck et al. 2020) and will be affected by poorly designed, outdated, or incomplete mapping of species distributions (e.g., Vale et al. 2017). Moreover, these biases can make it difficult to identify secondary contact zones and range limits, which will affect study design and hypothesis generation, as knowledge is incomplete and fragmented across Amazonia. Despite the fact that collection efforts have vastly improved over the past few decades (Vale and Jenkins 2012), with a huge increase in vouchered genetic resources, there are still numerous sampling gaps throughout Amazonia that contribute to a diminished knowledge regarding intra- and inter-specific lineage diversity.

Soares et al. (2023) raise an important issue regarding barriers to ornithological research in the Neotropics that directly affect Amazonian biogeography. The technological advancements in research methods, as seen, for example, in high-throughput molecular sequencing, have changed the way biodiversity research is done. However, unequal access to funding and equipment can often deter scientific development and training in Amazonian countries. As the scientific agenda is usually defined from a global North perspective, it affects what should be considered leading-edge and relevant (Soares et al. 2023). The demand for scientific impact and innovation does not necessarily fully fit the scientific agenda of the regions with the highest biological diversity (Nuñez et al. 2021). These regions, including Amazonia, lack basic components of biodiversity research that have yet to be studied, such as species natural histories, diversity and distribution patterns, and taxonomy. However, researchers working on these vital research topics struggle to attract funding that is often directed to the leading edge of the scientific agenda, dictated by highly capitalized research groups both in the region and in North America, and Western Europe (Soares et al. 2023). Basic biological research is a necessary step towards the integration of more complex modeling tools and analytical methods into the study of Amazonian biodiversity. For instance, information on the natural history of species (e.g., species' behaviors, traits, and basic biology) still remains a major bottleneck in Amazonian biogeography, which hinders the application of analyses that account for functional diversity and ecology (Lees et al. 2020). Also needed are incentives for better curation, management, and improvements in terms of faster updates and the development of integrated online databases, as well as increased data collection. As an example, many studies make use of birdtree.org data (Jetz et al. 2012) although it contains a large amount of missing and interpolated information for Amazonian species (Crouch et al. 2019), which also applies to trait databases (Wilman et al. 2014, Tobias et al. 2022), and could lead to spurious inferences, especially when associated with sampling biases (Hortal et al. 2015, Hughes et al. 2021). It is urgent that funding and support for studies focused on gathering basic natural history data on Amazonian birds be incentivized to help advance other areas of research in the region.

Collecting additional distribution, ecological, and trait data and improving their compilation and archiving will also be fundamental steps towards a more complete understanding of Amazonian biogeography (Fig. 2). This data is fundamental to describing ecological guilds, habitat specialization, and obtaining robust trait estimation, all of which will be important to test new hypotheses and improve model testing and analyses. Interdisciplinarity in research groups has shown its importance and will continue to be pivotal in advancing our understanding of landscape and climatic evolution in Amazonia and how it has shaped species histories (Thom et al. 2020, Sawakuchi et al. 2022). Dissecting Amazonian bird diversity into habitat-specific, trait-based, and ecological groupings will help to disentangle the complexities of how functional groups and ecosystems influence biogeographic patterns and their main drivers

(Schleuning et al. 2023). Increasing the availability of high-quality vouchered samples will be fundamental to exploring the complexities of bird diversification in Amazonia. Many collections still lack the necessary equipment (e.g., proper methods for storing genetic resources such as nitrogen tanks and ultra-cold freezers), and there is the difficulty of bringing consumables to remote areas. A large investment over the next decades will be necessary to improve natural history collections in Amazonian institutions to increase the quality of storage of genetic samples necessary for genomic analyses, fill sampling gaps, and access remote areas through field expeditions. Nevertheless, those will be important steps to studying diversification processes, species distributions, and their drivers in Amazonia.

Another factor impacting biodiversity research in Amazonia and elsewhere are convoluted and blurry legal regulations regarding access to genetic resources in different countries (Silvestri and Mason 2023). The Convention on Biological Diversity (United Nations 1992) and the Nagoya Protocol (United Nations 2010) establish the sovereign rights of States over their natural resources and advocate for a fair and equitable sharing of benefits arising from the utilization of genetic resources , including its application and commercialization (e.g., see https://learnnagoya.com/). These negotiations play an important role in the establishment of collaborative networks between countries, in particular between the Global North (often resource-rich) and the Global South (often biodiversity-rich) institutions, by ensuring equitable access and benefit-sharing. Benefit-sharing can positively impact biodiversity conservation (Godt 2009) and help protect traditional and indigenous knowledge associated with genetic resources (Robinson 2010; Wright 2020). Through these international agreements, countries are developing regulations for accessing their genetic resources and procedures for the fair and equitable sharing of benefits from their utilization. Despite acknowledging the importance of these regulations, researchers studying biodiversity are caught in a web of new regulations that are often not clear. Amazonia encompasses nine South American countries with distinct environmental laws. The distinct regulations established by these countries might directly impact the development of international collaborations and continental scale studies (Silvestri and Mason 2023). In some instances, overcomplicated regulations have worked against proper benefit sharing (Pauchard 2017) and impeded access to genetic resources for non-commercial research (Neumann et al. 2018). For example, samples from countries with more restrictive regulations (Carla Silvestri 2016) might be systematically excluded from studies, creating gaps in biogeographic and taxonomic knowledge. In Brazil, the "Lei da Biodiversidade" (Biodiversity Law; Law No. 13.123, May 20th, 2015) has directly impacted biodiversity research, creating demands for researchers even when access to genetic resources does not imply their exportation (Mc Kay et al. 2023). Moving forward, the biodiversity research community needs to effectively communicate with policy-makers (possibly through scientific societies) regarding the essential role that biodiversity research plays. Collaboratively developed best practices for access and benefit sharing should facilitate biodiversity research and help monitor and preserve biodiversity.

OUTSTANDING QUESTIONS AND FUTURE APPROACHES

The complexity of mechanisms driving species diversification in Amazonian birds shows that there is still much more to be understood about the underlying processes (Fig. 2). From improving ecological datasets to the development of reference genomes, scholars have a huge task ahead to fill the knowledge gaps in Amazonian biogeography. The knowledge that has to be generated in these multiple fields is complementary and cannot be ranked by importance. It should be mainly led by, or in collaboration with, scholars, communities, and entities based in the Amazonian region, who will define their priorities based on local expertise, respect for local cultures, collaboration with their communities, and the development of local graduate programs, while international networking will be key to achieving such a massive task (Carberry 2008, Nuñez et al. 2021, Trisos et al. 2021, Ribas 2023). Below, we present what we believe are future approaches or data gaps that need to be worked upon (Fig. 2), including, but not limited to: (1) an improved hypothesis-based approach based on combined geological and biological evidence, (2) advancing speciation genomics studies to better understand the complexity of some reticulated processes, and (3) informing conservation practices and generating quality reports that will help protect, develop, and create a stronger environment for the Amazonian peoples and its biodiversity to thrive.

Although the debate surrounding the effect of large rivers on diversification is still contentious, the fast development of detailed regional geological models (see Cracraft et al. 2020) is opening new opportunities to explicitly test their effect on population isolation and connectivity. Building basin-wide scenarios for the evolution of Amazonian organisms based on molecular data within a geological context is challenging given the lack of detailed geological information for the entire basin and the coarse resolution of continental-scale phylogeographic inferences. However, local studies focusing on specific, well-described geological events could directly tap into the mode of differentiation between co-distributed lineages. By focusing on local models from regions with well-described and recent geological changes, it might be possible to design studies that explicitly test the effects of environmental and landscape evolution on population isolation and gene flow (Fig. 2). By placing regional studies on a comparative framework that includes multiple co-occurring species, it will be possible to disentangle the effects of specific traits on differing patterns of population differentiation, gene flow, and demography (Fig. 2). Moreover, by incorporating the knowledge held by traditional and indigenous Amazonian populations, it will be possible to achieve collaborative and detailed information about habitat preferences and the natural history of birds.

While dependent on robust collections and ecological data, work on the genomics of speciation in Amazonian birds continues to advance to assess the occurrence of reticulate phylogenetic patterns, introgression, and hybridization. Based on a comprehensive understanding of the prevalence of gene flow between co-distributed species within Amazonia, future studies might be able to test if gene flow is associated with the ecology and geographic distribution of species. For instance, species with higher dispersal capability or species occurring in more dynamic (e.g., riverine habitats) or ephemeral (e.g., *Guadua* bamboo stands) environments might have a higher incidence of gene flow causing phylogenetic conflict (Mitchell et al. 2019, Johnson et al. 2023). Allopatric and peripatric differentiation are the main factors driving speciation, and closely related species are often isolated by physical barriers that can be overcome by continuous (e.g., individuals dispersing over the barrier) or pulsed (e.g., barrier displacement) migration. Higher environmental dynamism might lead to more opportunities for geographic isolation, followed by secondary contact, before reproductive barriers evolve between populations (Cutter and Gray 2016). As studies advance, more examples of the mixing of genetic pools resulting from gene flow that are the result of past landscape dynamics, like river captures, are being observed (Musher et al. 2022). The rate at which species develop reproductive barriers might also play an important role in the signal for gene flow, which is expected to be less frequent in lineages that evolve reproductive isolation more quickly (Weir and Wheatcroft 2011). Understanding the genomic mechanisms and traits that influence both dispersal propensity (i.e., gene flow) and the achievement of pre- or postzygotic isolation are essential areas of study to be pursued in Amazonian biogeography. Studying the processes leading to pre- and postzygotic isolation has the potential to contribute beyond the Amazonian biogeography discipline by entering the fields of evolutionary biology and comparative genomics.

Amazonia has been facing increased deforestation rates, fire disturbance (Feng et al. 2021, Gatti et al. 2021), damming of rivers affecting flood pulses and sediment discharge (Lees et al. 2016, Latrubesse et al. 2017), and legal and illegal mining (Vallejos et al. 2020), among other threats, at rates way higher than environmental change at evolutionary time scales (Barlow et al. 2018, Walker et al. 2019, Albert et al. 2023). These activities threaten Amazonian peoples as well as biodiversity. Although biogeographers have focused much of their attention on the past, it is important that research be carried out with a focus on the future and how biodiversity research might improve conservation practices by collaborating with and addressing the concerns of those living in the region. It is more urgent than ever for the whole scientific community to listen to Amazonian communities and work in concert with them to achieve social justice and conservation in the region (Oliveira et al. 2021, Medina et al. 2022, Ribas 2023). It stands as a challenge to biogeographers and biodiversity researchers alike to design studies that will advance not only the research agenda, but also the social and conservation agendas such that Amazonia maintains its role in regional and local climate control (Sampaio et al. 2007, Salazar et al. 2015), and provides for the future of its communities.

It has become clear that bird lineages respond differently to landscape and environmental change in Amazonia. However, the current challenge is to identify shared traits and species assemblies that reveal commonalities in diversification histories that can be linked to landscape evolution. The development of Amazonian bird biogeographic research has shown what seems to be obvious now: that the origins of the biota of the most biodiverse region of the planet cannot be explained by simple mechanisms or single hypotheses. The challenge now is to accumulate data and knowledge to be able to develop a synthesis of Amazonian diversification, which will be a complex and intricate interdisciplinary work. There are great opportunities for future generations of researchers based within Amazonia and beyond to do this with data and tools that will also continue to evolve.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTION

JMGC and GT conceived and wrote the initial version of the manuscript. LJM, AL, MAR, GDR, AA, VELA, MF, and CCR substantially contributed with their expertise, editing, expanding, and reviewing the final version of manuscript.

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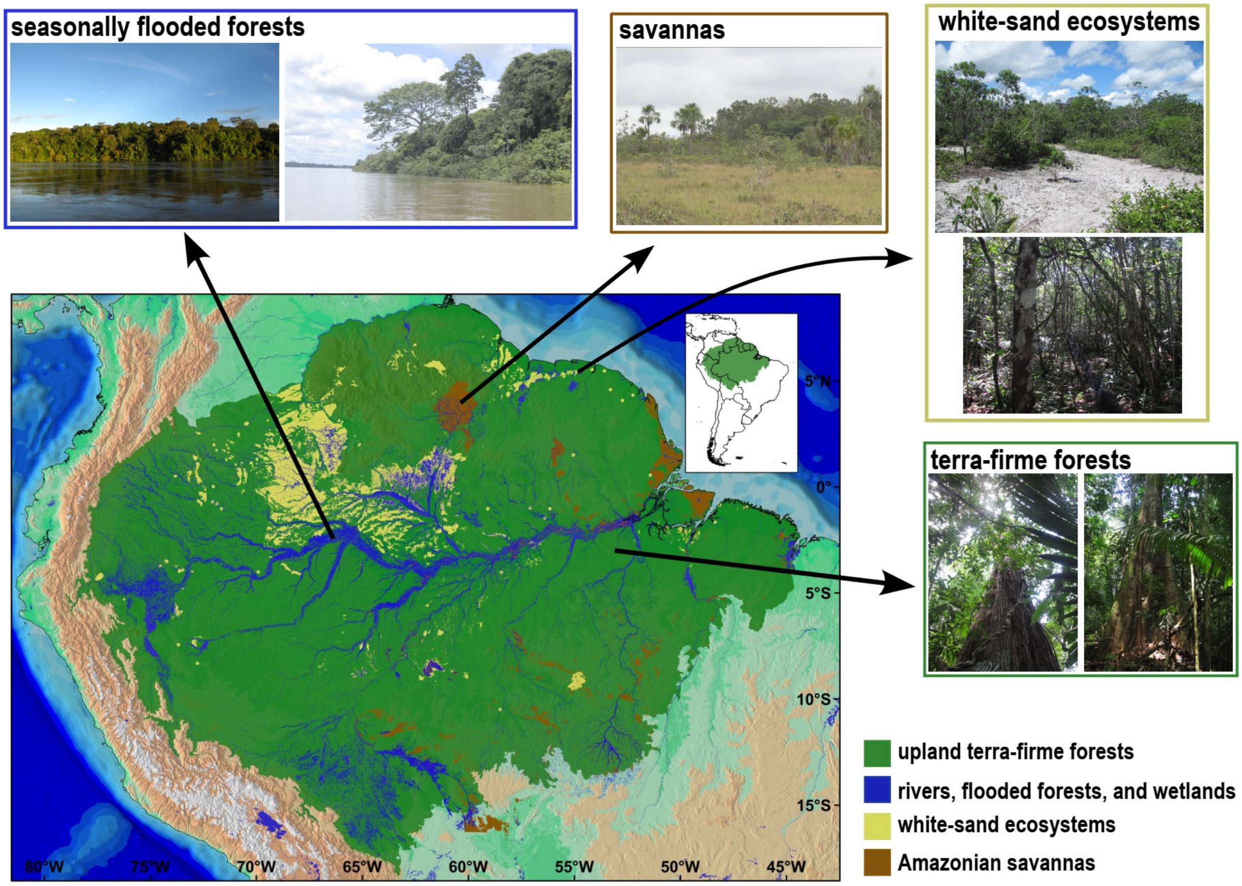
Figure 1. Map showing the extent and distribution of major Amazonian ecosystems. The small panels provide examples of the vegetation physiognomy in these ecosystems. Photos by JMG Capurucho and MFA Maximiano (flooded forest - picture on the right side - and savannas).

Figure 2. Diagram showing the main topics discussed in this review, their interconnections, and a roadmap to advancing biogeographic knowledge in Amazonia. The light green boxes are areas that still need further development but have ongoing research programs focusing on gathering this information. These will form the basis to, together with data in the blue boxes, provide an new integrative description of diversification patterns and biogeographic history of Amazonian birds. Red boxes indicate areas that require support or caveats to the advance of Amazonian biogeography research.


seasonally flooded forests
savannas
white-sand ecosystems
terra-firme forests
5°N
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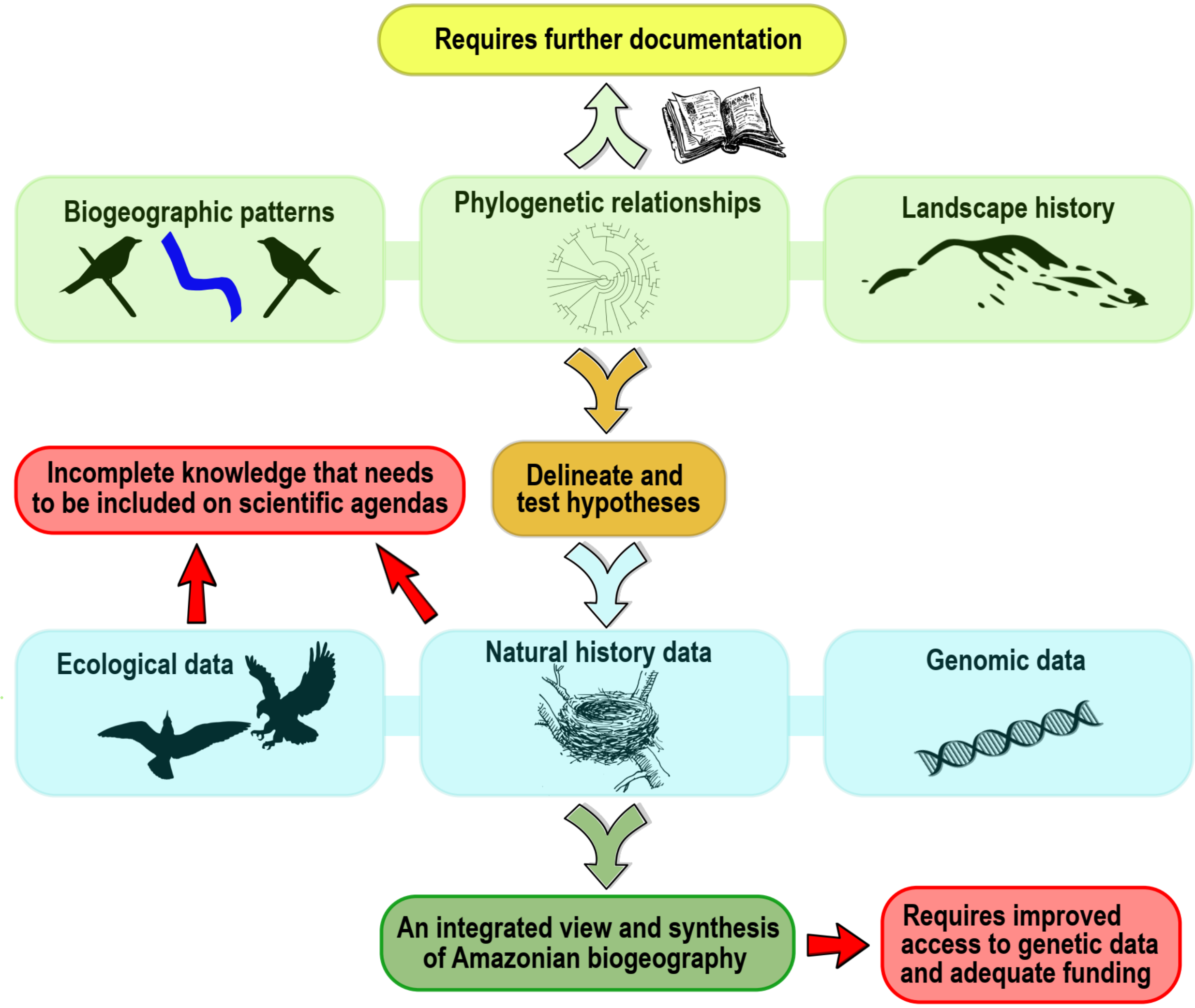
rivers, flooded forests, and wetlands
white-sand ecosystems
Amazonian savannas


Requires further documentation
Biogeographic patterns
Phylogenetic relationships
Landscape history
Delineate and test hypotheses
Incomplete knowledge that needs to be included on scientific agendas
Ecological data
Natural history data
Genomic data
An integrated view and synthesis of Amazonian biogeography
Requires improved access to genetic data and adequate funding