



## Diversity and evolution of Amazonian birds: implications for conservation and biogeography

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**Abstract:** Amazonia has been a focus of interest since the early days of biogeography as an intrinsically complex and extremely diverse region. This region comprises an intricate mosaic that includes diverse types of forest formations, flooded environments and open vegetation. Increased knowledge about the distribution of species in Amazonia has led to the recognition of complex biogeographic patterns. The confrontation of these biogeographic patterns with information on the geological and climatic history of the region has generated several hypotheses dedicated to explain the origin of the biological diversity. Genomic information, coupled with knowledge of Earth's history, especially the evolution of the Amazonian landscape, presents fascinating possibilities for understanding the mechanisms that govern the origin and maintenance of diversity patterns in one of the most diverse regions of the world. For this we will increasingly need more intense and coordinated interactions between researchers studying biotic diversification and the evolution of landscapes. From the interaction between these two fields of knowledge that are in full development, an increasingly detailed understanding of the historical mechanisms related to the origin of the species will surely arise.

**Key words:** Amazonia, biogeography, birds, conservation, diversification, rivers.

### INTRODUCTION

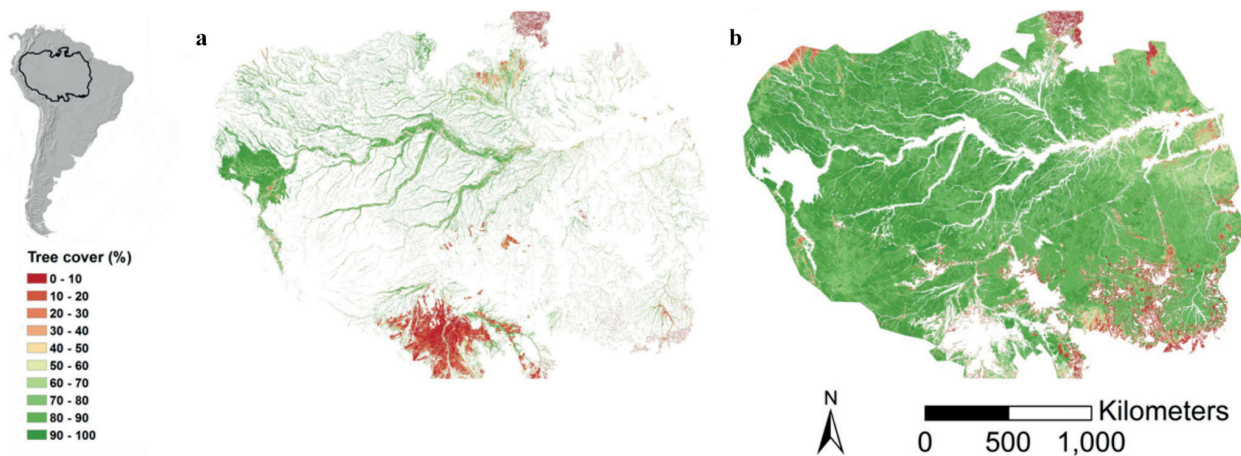
Amazonia has been a focus of interest since the early days of biogeography as an intrinsically complex and extremely diverse region (Wallace 1852, Haffer 1969). This region comprises an intricate mosaic that includes diverse types of forest formations, flooded environments and open vegetation (Cohn-Haft et al. 2007) (Figure 1). Increased knowledge

about the distribution of species in Amazonia has led to the recognition of complex biogeographic patterns (Antonelli et al. 2010, Ribas et al. 2012, Smith et al. 2014, Naka and Brumfield 2018). The confrontation of these biogeographic patterns with information on the geological and climatic history of the region has generated several hypotheses dedicated to explain the origin of the biological diversity (reviews in Haffer 2008 and Leite and Rogers 2013).

Since the proposition of these hypotheses, much knowledge has been accumulated, both with respect to biogeographic patterns (inter and

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**Figure 1** - Distribution of tree cover across the Amazon basin. (a) Floodplains and (b) uplands separated by the wetlands' mask (Hess et al. 2015). Figure from Flores et al. (2017).

intra-specific), and the evolution of Amazonian landscapes. In general, one can identify two main themes in Amazonian biogeography in which the accumulation of paleo-environmental knowledge has allowed the formulation and testing of hypotheses in an increasingly detailed way: the uplift of the Andes and its influence on the evolution and reconfiguration of the drainage system; and climatic oscillations due to glacial cycles during the Quaternary (Baker et al. 2014). Today it is clear that these histories are neither spatially or temporally independent, and despite many uncertainties, the association between biological and geological data has decisively helped to elucidate the relationship between environmental history and the origin of diversity in Amazonia (Baker et al. 2014). It is also clear that forest environments associated with different degrees of flooding (Figure 1) have had very different histories, as they respond differently to drainage evolution and paleoclimatic change (Harvey et al. 2017, Thom et al. 2018, Ribas et al. 2018).

The Quaternary climatic oscillations (2.6 Ma to the present) are traditionally associated with forest refuges, as proposed by Haffer (1969). Drainage evolution, on the other hand, is generally associated with Miocene events (23 to 5 Ma),

when the main phase of Andean uplift would have occurred (Hoorn et al. 2010, but see discussion in Baker et al. 2014). Due to this apparent temporal segregation of geological events, for a long time tests of diversification hypotheses have been based on dating the divergences to determine their causes: diversification in the Pleistocene would be associated with refuges while diversification in the Miocene would be associated to drainage evolution (Rull 2014). Meanwhile, the lack of simple and straightforward congruence among the different groups led to an alternative interpretation of a weak association between environmental history and biotic diversification in Amazonia (Smith et al. 2014).

However, the analytical approach needs to become more sophisticated (Papadopoulou and Knowles 2016). The accumulation of knowledge about the evolution of the Amazonian landscapes shows that different forces, initially associated with different hypotheses (eg. refuges, rivers), often considered as alternative, acted together spatially and temporally (Baker et al. 2014, Weir et al. 2015). In addition, environmental history has increasingly been shown to be complex. The climate of Amazonia did not vary uniformly during glacial cycles (Cheng et al. 2013, Wang et al. 2017),

and the response of forest and open formations to these oscillations is still much debated and poorly understood (Mayle et al. 2004, Cowling et al. 2001, Anhuf et al. 2006).

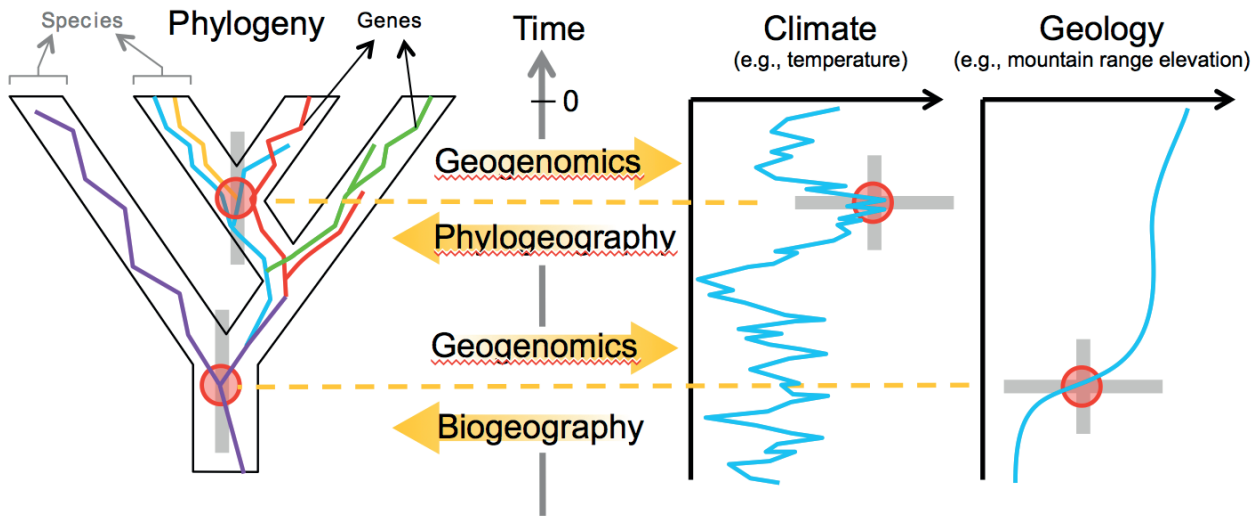
Most debates concerning the recent evolution of the Amazonian drainage have focused on the establishment of the transcontinental system, which has been suggested as the main driver of the onset of the *Terra Firme* formation in western Amazonian lowlands. A mid-Miocene age (9.4 to 9.0 Ma) for the onset of the trans-Amazon drainage has been linked to the period of decreasing deposition of the Solimões Formation (Solimões Fm) in western Amazonia and increased sedimentation rates at the Amazon Fan (Hoorn et al. 2010). However, the age of the upper Solimões Fm is still debated, and paleontological data suggest a late Miocene to early Pliocene age for the formation of the modern Amazon River (Latrubesse et al. 2010). In contrast, evidences from different proxies for defining the ages of the sedimentary deposits that overlap different areas of western and central Amazonia suggest younger ages for the establishment of the modern fluvial system, as Plio-Pleistocene (Nogueira et al. 2013) and mid to late Pleistocene (Rossetti et al. 2015). Recently, an alternative paleogeographic scenario suggests that the development of the modern drainage took place in steps since the late Oligocene-early Miocene until the Quaternary and not as a single event (van Soelen et al. 2017, Pupim et al. 2019). The recent development of research in sedimentology and paleoclimatology has provided increasingly detailed data, making possible a more specific association between landscape evolution and the spatial distribution of genetic diversity in the organisms that currently occupy the different environments (Figure 2) (Baker et al. 2014). Parallel to the advances in these areas of knowledge, significant advances in analytical methods in molecular phylogeny and phylogeography were also observed, making it possible to test these more detailed and complex scenarios (Toews et al. 2016).

Molecular phylogenetic and phylogeographic studies of groups for which taxonomy and sampling in Amazonia are better developed, as in birds and primates but also some groups of insects, frogs and small mammals, have repeatedly indicated that most current Amazonian species originated during the Pliocene and Pleistocene (Ribas et al. 2012, Boubli et al. 2015, Rull 2011, Garzón-Orduña et al. 2014, Smith et al. 2014, Pavan et al. 2016, Ribas et al. 2018) a timing that is partially consistent with a role for climate oscillations due to glacial cycles. However, most species are older than the LGM, meaning that the last glacial cycle has not disrupted pre-existing patterns of diversity and distribution (Ribas et al. 2012). Also, Quaternary drier climates seem to have been less pronounced in western Amazonia (Cheng et al. 2013, Wang et al. 2017), where the highest species diversity is concentrated today. This evidence suggests that a more thorough understanding of landscape evolution, not strictly focused on the effect of precipitation changes on vegetation as postulated by the Refugia hypothesis, is needed to decipher its relationship to biotic diversification. However, the uncertainty about the timing of the evolution of the drainage system and its associated environments has precluded such integration.

#### INTEGRATING HISTORY AND ECOLOGY

Since the proposal of phylogeography by Avise et al. (1987) the idea was to seek an integration of intra- and inter-specific genetic variability to understand the continuum of variation from polymorphism (population genetics) to divergence (phylogeny). This search involves an integration between historical data and data on the environments in which individuals occur today (Figure 2).

The importance of historical and ecological factors for community structuring is a consensus in the literature. However, few studies have determined the relative contribution of each of these factors.



**Figure 2** - In the phylogenetic tree (left), black ‘tubes’ represent species (i.e. the species tree), whose individuals are characterized by genes with different mutational histories (color lines within tubes; i.e. the gene tree). On the right, a climatic time series and temporal variation of a geologic feature are represented. Red circles and orange dashed lines highlight the correspondence between evolutionary and climatic/geologic events; gray bars represent confidence intervals for the timing of divergence (left) or the geologic/climatic events (right). Figure from Baker et al. (2014).

This is largely due to the lack of information on ecology and on the detailed patterns of occurrence of species (Hortal et al. 2015). Although many groups of organisms appear to be widely distributed in tropical regions, only recently studies have begun to document the detailed pattern of variation in species occurrence (Costa and Magnusson 2010) and the genetic structure within species, that often correspond to several independent evolutionary units (Aleixo 2004, Antonelli et al. 2010, Ribas and Miyaki 2004, Ribas et al. 2005, 2006, 2007, 2009, 2012, Schultz et al. 2016).

A good understanding of the patterns of occurrence and abundance of species in association with detailed information on the patterns of niches and habitats occupation within each community are critical for the testing of ecological and biogeographic hypotheses. Only through an integrated and multidisciplinary approach can we understand the great diversity of factors associated with the origin and maintenance of the most diverse biome on the planet, the Amazon Forest. This understanding is very important not only

from a theoretical point of view, but also to guide actions to conserve this megadiversity that is under increasing risk of destruction. Understanding the biogeographic patterns allows us to better estimate the impact of deforestation in certain regions of the Amazon, because it is possible to know which regions harbor greater diversity, or unique and endemic lineages, while understanding intra-population processes that shaped current diversity patterns helps us predict the consequences of fragmentation, future climate change and habitat loss.

#### IMPACT OF LARGE DAMS ON THE AVIFAUNA ASSOCIATED TO FLOODED ENVIRONMENTS

Despite being the world’s most species-diverse biome (Pimm et al. 2014, Jenkins et al. 2013), Amazonia includes a below-average proportion of threatened species (Vale et al. 2008). While this may seem an indication of resilience and robustness, caution is required for two main reasons: Amazonia currently experiences the highest absolute rate of forest loss (Soares-Filho et al. 2006) and the

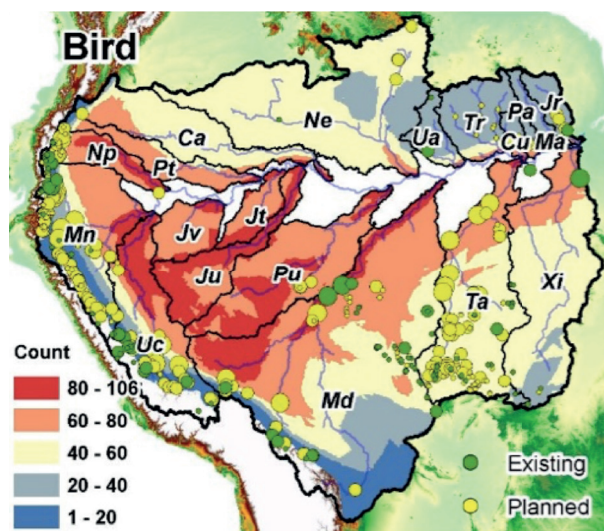
number of species classified as threatened is likely to be an artifact of poor taxonomic knowledge (Bates and Demos 2001, Whitney and Cohn-Haft 2014). This is especially important for the biota associated with flooded environments, as it is particularly understudied (Cohn-Haft et al. 2007) and the current model of hydropower development will focus the impact of the dam's lakes on these environments by adopting the run-of the river model (Latrubesse et al. 2017).

Surveys and meta-analyses of diversity patterns are dependent upon basic information of species delimitation. Phylogeographic studies of Amazonian vertebrates have often revealed more distinct evolutionary lineages than previously recognized by traditional taxonomy (e.g. Smith et al. 2014), and often the relationships among these lineages do not correspond to former generic or species limits (Ribas et al. 2005, 2006, 2007, 2012). This 'taxonomic shortfall' prevents meta-analyses based on current taxonomy from achieving an accurate representation of diversity patterns (Figure 1), and consequently from inferring processes and defining conservation strategies (Bates and Demos 2001, Hortal et al. 2015).

Comparatively, birds are among the taxonomically better known groups of Amazonian organisms, even though many new species continue to be discovered (Whitney and Cohn-Haft 2014). In addition, although the large-scale biogeography of Amazonian birds is comparatively well documented, there are multiple examples in which fine-grained patterns of diversity are being discovered that reflect landscape history (e.g. Ribas et al. 2012, d'Horta et al. 2013, Thom and Aleixo 2015). This is particularly true for upland forest birds, for which multiple taxonomic reviews have been published (Bates and Demos 2001, Ribas et al. 2012, Fernandes et al. 2013). In stark contrast, the avifauna associated with flooded environments is still poorly known, with few systematic revisions and a prevailing impression of uniformity of the

intraspecific diversity (Aleixo 2006, Cadena et al. 2011). Contrary to these first impressions, recent detailed descriptions of phenotypic variation and genetic diversity within flood-plain forest birds have documented that there is considerable unrecognized intraspecific diversity, and that when this is accounted for, common spatial patterns of distribution are revealed (Cohn Haft et al. 2007, Canton 2014, Choueri et al. 2017, Harvey et al. 2017, Thom et al. 2018). This evidence suggests that planning for hydropower generation in Amazonia is moving forward with poor knowledge about the species diversity that will be impacted (Figure 3).

Flooded habitat species are dependent upon environments created by rivers and the flooding cycle and their evolution are historically linked to the Amazonian drainage system (Moraes et al. 2016). Current reconstructions propose that western Amazonia was covered by a system of wetlands during a large period in the last 10 Ma, and that the current transcontinental drainage system is relatively recent (Latrubesse et al. 2010, Nogueira et al. 2013, Rossetti et al. 2015). This dynamic history may have had strong influence over the recent evolution of species adapted to flooded environments, which brought about changes in their distributions as well as possible disconnections between eastern and western populations. Such a scenario is suggested by phenotypic variation in several species of birds (Cohn-Haft et al. 2007) and has been confirmed through genomic analysis of parrots and passeriforms (Canton 2014, Thom et al. 2018). This dynamic history may also have resulted in distinct degrees of intraspecific genetic diversity, depending on how species have responded to the physical changes to their habitats. Quantifying this diversity is important for conservation planning (Figure 3), as populations with very low genetic diversity may be less capable of responding to environmental impacts and thus are more susceptible to population fragmentation



**Figure 3** - Flooded habitat birds (non-aquatic) species richness patterns of Amazonian river basins. Color scale from blue (low) to red (high) represent the number of species. Number of species based on overlapping distributions of each single species. Green and yellow circles are location of dams. Figure from Latrubesse et al. (2017). Amazon's 19 sub-basins are labeled with abbreviations: Andean-foreland Rivers: Marañon (*Mn*), Ucayali (*Uc*), Napo (*Np*), Putumayo (*Pt*), Caqueta (*Ca*); Cratonic rivers: Jari (*Jr*), Paru (*Pa*), Curuapenema (*Cu*), Maricuru (*Ma*), Tapajós (*Ta*), Xingu (*Xi*), Trombetas (*Tr*), Negro (*Ne*), Uatumã (*Ua*), Mixed terrain: Madeira (*Md*); Lowland rivers: Juruá (*Ju*), Purus (*Pu*), Jutai (*Jt*), Javari (*Jv*).

and extinction (Spielman, 2004). A better understanding of systematics and biogeography of Amazonian biota will be critical for any planning process involving developmental activities.

#### MOLECULAR DATA IN BIOGEOGRAPHY

The use of molecular data has brought two important novelties to biogeographic studies: the possibility of making temporal inferences and the possibility of studying the recent history of populations (Carstens and Richards 2007). Although the molecular data initially led to biogeographic studies focused on individual groups, diminishing the importance of the fundamentally comparative nature of classical biogeography, the evolution of data collection and analysis methodologies is allowing for a return to a comparative framework (Papadopoulou and Knowles 2016).

In the last decade, large-scale molecular data collection has become much easier and faster (McCormack et al. 2012). Next-generation sequencing techniques (NGS) have recently introduced the possibility of sequencing many regions of the genome in parallel, allowing a much faster and cheaper sequencing of thousands of loci. The selection of markers in this new era of genomic studies is based on how to reduce the genome for sequencing, i.e. select the set of thousands of markers to be studied. This can be done through traditional amplification of known regions and subsequent sequencing in parallel; digestion of the genome with restriction enzymes and size selection of fragments to be sequenced; or by using probes that bind to specific regions of the genome leading to sequencing of the adjacent regions (Harvey et al. 2016). The aim is to sequence a large number of homologous regions of appropriate size for phylogeographic analyzes. Despite some standing methodological difficulties, including how to combine fragments to perform each analysis and issues related to missing data (McCormack et al. 2012), several studies have successfully used NGS data to test biogeographic hypotheses using probes that bind to ultra-conserved genome regions (Smith et al. 2014) or SNPs obtained by DNA fragmentation and subsequent sequencing (GBS, ddRAD) (Harvey and Brumfield 2015, Weir et al. 2015, see review in Toews et al. 2016) (Figure 2).

This abundance of genetic information, coupled with the growing knowledge of Earth's history, especially the evolution of the Amazonian landscape, presents fascinating possibilities for understanding the mechanisms that govern the origin and maintenance of diversity patterns in one of the most diverse regions of the world (Figure 2). For this, we will increasingly need more intense and coordinated interactions between researchers studying biotic diversification and the evolution of landscapes (Baker et al. 2014, Cheng et al. 2013, Hoorn et al. 2010, Pupim et al. 2019). From the

interaction between these two fields of knowledge that are in full development, an increasingly detailed understanding of the historical mechanisms related to the origin of the species will surely arise.

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#### AUTHOR CONTRIBUTIONS

Both authors have discussed and gathered data on these topics for many years. CCR wrote the text, AA revised and complemented it.

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