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Isadora Fluck Essig

A INFLUÊNCIA DOS RIOS SOBRE A BIOGEOGRAFIA DE AVES NA AMAZÔNIA

Santa Maria, RS
2020

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Dissertação apresentada ao Curso de Pós-Graduação em Biodiversidade Animal, da Universidade Federal de Santa Maria (UFSM, RS), como requisito parcial para obtenção do título de **Mestre em Ciências Biológicas – Área Biodiversidade Animal**.

Orientador: Prof. Dr. Cristian de Sales Dambros

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2020

DEDICATÓRIA

Dedico este trabalho a Thaís Ariane Fluck, minha mãe e amiga.

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Por fim, faço destas palavras as minhas:

"If we but try to live uprightly, then we shall be all right, even though we shall inevitably experience true sorrow and genuine disappointments, and also probably make real mistakes and do wrong things, but it's certainly true that it is better to be fervent in spirit, even if one accordingly makes more mistakes, than narrow-minded and overly cautious. It is good to love as much as one can, for therein lies true strength, and he who loves much does much and is capable of much, and that which is done with love is well done."

-Vincent van Gogh, Amsterdam 3 de Abril de 1878.

Obrigada

RESUMO

CAUSAS DA DISTRIBUIÇÃO DE AVES DA AMAZÔNIA: UMA QUESTÃO DA ESCALA TAXONÔMICA

AUTORA: Isadora Fluck Essig
ORIENTADOR: Cristian de Sales Dambros

Uma das principais questões da biogeografia é o papel da cladogênese através de barreiras *versus* especialização ecológica na distribuição de espécies. Na Amazônia, se hipotetiza que os rios limitam a dispersão de espécies e promovem a cladogênese, afetando a distribuição das espécies. No entanto, estudos ecológicos recentes sugerem que a distribuição das espécies é mais afetada pelas condições ambientais (clima por exemplo) do que pelos rios, o que pode indicar que a especialização ecológica é mais importante para a composição da comunidade. Como os estudos evolutivos e ecológicos geralmente usam dados (por exemplo pequenos *versus* grandes grupos de espécies) e abordagens estatísticas distintos, o papel relativo das condições ambientais e dos rios na cladogênese e distribuição das espécies não está bem estabelecido. Criamos um banco de dados abrangente de ocorrências de aves (39.732 registros) para determinar a importância das condições ambientais (fatores ecológicos) e da cladogênese que ocorre através dos rios (fator evolutivo) para a distribuição de espécies endêmicas na Amazônia. Em seguida, comparamos a distribuição de clados endêmicos com resultados utilizando todas as aves, para determinar se os resultados obtidos de clados endêmicos podem ser extrapolados para escalas taxonômicas mais amplas (ou seja, comunidades inteiras, incluindo todos os clados). Os rios foram o fator mais importante para a cladogênese e distribuição dos clados endêmicos. No entanto, a distribuição de toda a comunidade de aves na Amazônia foi mais fortemente associada à temperatura do que aos rios. Esses resultados indicam que gradientes ambientais e barreiras geográficas têm sua importância para a distribuição de espécies dependente da escala taxonômica. Portanto, os resultados obtidos utilizando classes, ordem ou outro grupo taxonômico amplo não devem ser comparados a resultados obtidos através do uso de gêneros ou outros clados menos inclusivos.

Palavras-chave: Amazônia; rios; escala taxonômica; gradientes ambientais; distribuição de espécies.

ABSTRACT

CAUSES OF AMAZONIA BIRDS' DISTRIBUTION: A MATTER OF TAXONOMIC SCALE

AUTHOR: Isadora Fluck Essig
ADVISOR: Cristian de Sales Dambros

One of the main questions in biogeography is the role of cladogenesis across barriers vs. ecological specialization on species distribution. In Amazonia, rivers have long been hypothesized to limit species dispersal and promote cladogenesis, affecting species distribution. However, recent ecological studies suggest that species distribution is more affected by environmental conditions (e.g. climate) than by rivers, which could indicate that ecological specialization is more important to community assembly. Because evolutionary and ecological studies often use distinct data (e.g. small vs. large groups of species) and statistical approaches, the relative role of environmental conditions and rivers on species cladogenesis and distribution is not well established. We created a comprehensive database of bird occurrences (39,732 records) to determine the importance of environmental conditions (ecological factors) and cladogenesis across rivers (evolutionary factor) for the distribution of endemic species in Amazonia. We then compare the distribution of endemic clades vs. all birds to determine if results obtained from endemic clades can be extrapolated to broader taxonomic scales (i.e. whole communities including all clades). Rivers were the most important factor affecting the cladogenesis and distribution of endemic clades. However, the distribution of the whole bird community in Amazonia was more strongly associated with temperature than to rivers. These results indicate that environmental gradients and barriers importance to species distribution depends on the taxonomic scale. Therefore, results obtained from an entire class, order or other broad clade should not be compared to results obtained from genera or other less inclusive clades.

Keywords: Amazonia; rivers; taxonomic scale; environmental gradients; species distribution.

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INTRODUÇÃO

O que determina a distribuição da natureza ao longo do planeta? Essa é uma pergunta que tem movido muitas discussões entre os cientistas. Diferentes estudos e autores têm chegado a resultados controversos, levando ao questionamento se são características geográficas ou características ambientais que dirigem a estruturação da distribuição de espécies. Resultados controversos podem ser consequência das diferentes maneiras de se responder uma pergunta, assim como da escolha de qual grupo ou escala taxonômica utilizar. Enquanto estudos que utilizam diversas espécies e ampla escala geográfica sugerem que fatores ambientais são importantes para a distribuição de espécies ao longo do espaço (FLUCK et al., 2020; OLIVEIRA et al., 2017; SANTORELLI et al., 2018), estudos que levam em conta a história evolutiva das espécies revelam que barreiras geográficas, as quais restringem o movimento das espécies (i.e. dispersão) (HAYES e SEWLAL, 2004; POMARA, et al., 2014), são cruciais para a distribuição de certos grupos (RIBAS et al., 2012).

Entre os vários fatores que podem causar a diversificação de espécies na Amazônia está a formação de rios. Os grandes rios Amazônicos (que podem atingir mais de um quilômetro entre uma margem e outra; FLUCK et al., 2020) agem como barreiras geográficas, impedindo que os seres vivos se movimentem livremente de uma margem a outra, consequentemente afetando a dispersão e distribuição de espécies (HAYES e SEWLAL, 2004; POMARA, et al., 2014). Além disso, o surgimento de barreiras geográficas pode separar populações de uma mesma espécie e limitar o fluxo de genes entre os indivíduos, ocasionando a especiação alopátrica (RIBAS et al., 2012, BOUBLI et al., 2015). Os rios também são conhecidos por evitar o contato secundário entre espécies, assim mantendo os níveis de diversidade na Amazônia (NAKA e BRUMFIELD, 2018). Todos esses efeitos que os rios têm sobre os seres vivos podem estruturar a distribuição de espécies.

A partir de suas expedições à floresta amazônica em 1854, o naturalista Alfred Russel Wallace propôs que a distribuição das espécies pode ser estruturada de acordo com a configuração dos grandes rios, de forma que diferentes espécies ocorram em margens opostas do rio. Em 1985, Joel Cracraft apresentou a *"riverine hypothesis"*, sugerindo que a Amazônia é dividida em áreas de endemismo que carregam combinações únicas de espécies. Desde então, são muitos os estudos que têm explorado essa hipótese da configuração da diversidade em áreas de endemismo, de forma a investigar o efeito dos rios sobre os padrões de distribuição das espécies na Amazônia. Os estudos abrangem uma ampla gama de seres vivos, como cupins (DAMBROS et al., 2017), roedores (PATTON

et al., 1994), lagartos (SOUZA et al., 2013), anuros (GODINHO e DA SILVA, 2018) e aves (RIBAS et al., 2012). Mesmo com tantos estudos, o papel dos rios sobre a distribuição das espécies na Amazônia ainda é questionado. Enquanto estudos que utilizam pequenos grupos de espécies e suas relações evolutivas para investigar o efeito dos rios sobre a diversidade mostram que eles são de extrema importância, o efeito dos rios é mostrado ser muito baixo em estudos que utilizam informações sobre a composição de espécies em diferentes locais (abrangendo centenas ou até mesmo milhares de espécies), e sugerem que outros fatores como o clima sejam importantes para a estruturação da diversidade amazônica (FLUCK et al., 2020; OLIVEIRA et al., 2017; SANTORELLI et al., 2018).

Mas como um fator abiótico como a temperatura poderia afetar a distribuição de espécies? A floresta amazônica é conhecida por ter a temperatura sazonalmente estável em relação a florestas não tropicais. Sendo assim, as espécies se adaptam a uma faixa estreita de variabilidade na temperatura (JANZEN, 1967). Como consequência, as espécies não são capazes de se estabelecerem em locais com temperaturas que excedam sua tolerância fisiológica (ZUQUIM et al., 2012). Uma vez que diferentes locais na Amazônia diferem em seus aspectos climáticos, espécies que são adaptadas a sobreviver em faixas estreitas de temperatura não são capazes de ocorrer por toda a região amazônica (JANZEN, 1967). O efeito do clima sobre a distribuição de espécies já foi registrado para plantas (TUOMISTO et al., 2003; ZUQUIM et al., 2012) e vertebrados (MELO et al., 2009; VEECH e CRIST, 2007), de forma a criar uma substituição de espécies ao longo de gradientes ambientais (BUCKLEY e JETZ, 2008). Essa substituição pode ser resultado de processos evolutivos ao longo desses gradientes ambientais, como o processo de especiação ecológica (SCHLUTER, 2009; SALISBURY et al., 2012) ou simplesmente do estabelecimento de espécies com adaptações distintas (BUCKLEY e JETZ, 2008).

Ainda não existem comparações diretas entre as abordagens evolutiva e ecológica utilizando uma mesma base de dados e análises aplicadas a diversos grupos de espécies. Sendo assim, nós contribuímos para esta lacuna do conhecimento investigando como o surgimento dos rios, distância geográfica e fatores ambientais (temperatura, pluviosidade e elevação) afetaram processos evolutivos (*cladogenesis*: surgimento de novas espécies) e ecológicos (dissimilaridade na composição de espécies entre locais) de aves na Amazônia. Para isso, nós determinamos como a distância geográfica, rios e fatores ambientais se relacionam com 1) a cladogênese de grupos endêmicos (abordagem evolutiva) e 2) a distribuição de grupos endêmicos e comunidades inteiras (abordagem ecológica) na Amazônia. Como demonstrado por estudos evolutivos (RIBAS et al., 2012; FERNANDES et al., 2012; FERREIRA et al. 2017; ARAÚJO-SILVA, 2017; NAKA e BRUMFIELD, 2018), esperamos que a cladogênese de clados de aves endêmicas esteja associada a rios (*Psophia*; RIBAS et al., 2012), resultando em espécies distintas ocorrendo em margens

opostas. Por outro lado, esperamos que a mudança na identidade das espécies em comunidades inteiras seja mais associada a diferenças no ambiente. Portanto, a importância dos rios na distribuição de espécies deve ser mais acentuada para os clados endêmicos que se diversificaram na Amazônia, enquanto as diferenças no meio ambiente são mais importantes para a estruturação de comunidades inteiras. Sendo assim, nós esperamos que os resultados desse trabalho contribuam para o esclarecimento sobre o que está afetando os padrões de distribuição de espécies na Amazônia e se esse resultado depende da escala taxonômica e abordagem utilizada.

Estrutura da Dissertação

Esta dissertação está estruturada em formato *Original Research*, conforme as normas da revista *Ecography*.

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Causes of Amazonia birds' distribution: a matter of taxonomic scale

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Abstract

One of the main questions in biogeography is the role of cladogenesis across barriers vs. ecological specialization on species distribution. In Amazonia, rivers have long been hypothesized to limit species dispersal and promote cladogenesis, affecting species distribution. However, recent ecological studies suggest that species distribution is more affected by environmental conditions (e.g. climate) than by rivers, which could indicate that ecological specialization is more important to community assembly. Because evolutionary and ecological studies often use distinct data (e.g. small vs. large groups of species) and statistical approaches, the relative role of environmental conditions and rivers on species cladogenesis and distribution is not well established. We created a comprehensive database of bird occurrences (39,732 records) to determine the importance of environmental conditions (ecological factors) and cladogenesis across rivers (evolutionary factor) for the distribution of endemic species in Amazonia. We then compare the distribution of endemic clades vs. all birds to determine if results obtained from endemic clades can be extrapolated to broader taxonomic scales (i.e. whole communities including all clades). Rivers were the most important factor affecting the cladogenesis and distribution of endemic clades. However, the distribution of the whole bird community in Amazonia was more strongly associated with temperature than to rivers. These results indicate that environmental gradients and barriers importance to species distribution depends on the taxonomic scale. Therefore, results obtained from an entire class, order or other broad clade should not be compared to results obtained from genera or other less inclusive clades.

Keywords: Amazonia; rivers; taxonomic scale; environmental gradients; species distribution.

1 | INTRODUCTION

What are the causes of species diversity and distribution? Although this question has been extensively investigated by biogeographers and macroecologists (Haffer 1969; Wallace 1852; Cracraft 1985; Silva et al. 2019; Rangel et al. 2019), the role of evolutionary (e.g. cladogenesis across barriers) and ecological specialization (e.g. adaptations to the environment) on species distribution is still debated. In Amazonia, several studies support the role of rivers in promoting cladogenesis and shaping de distribution of endemic groups (Ribas et al. 2012, Fernandes et al. 2012; Ferreira et al. 2017; Araújo-Silva 2017, Naka and Brumfield 2018). However, ecological studies using a large number of species challenge the idea of rivers as the main cause for species distribution in the region (Oliveira et al. 2017, Santorelli et al. 2018), and suggest that species are distributed primarily according to their adaptations to environmental conditions (Fluck et al. 2020). These controversial findings could result from methodological differences between evolutionary and ecological studies (e.g. in taxonomic scale), and only a comparative study using both approaches can indicate the role of rivers and the environment in shaping species distribution.

Evolutionary studies suggest that cladogenesis, and consequently the distribution of sister clades, is primarily affected by rivers in Amazonia (Ribas et al. 2012; Weeks et al. 2016; Maximiano et al. 2020). Amazonian rivers can act as geographic barriers and limit gene flow between populations in opposite river banks, promoting allopatric speciation (Ribas et al. 2012). By promoting speciation, rivers cause distinct species to occur on opposite river margins (Wallace 1852, Ribas et al. 2012), leading to differences in species composition (Weeks et al. 2016) and contributing to the formation of endemism zones (Cracraft 1985).

Although rivers could affect the diversification and consequently the distribution of species in Amazonia, cladogenesis analyses are focused on only small and endemic clades (e.g. a single genus encompassing eight species; Ribas et al. 2012).

In contrast to evolutionary studies, ecological studies investigating the distribution of whole communities have found only a weak effect of rivers on the distribution of plants (Tuomisto 2016), termites (Dambros et al. 2017) and birds (Oliveira et al. 2017, Santorelli et al. 2018). These studies suggest that species are mostly affected by differences in the environment between sites, such as in soil conditions (Tuomisto 2003; Zuquim et al. 2012 for plants) and climate (Fluck et al. 2020 for birds). Results from these studies might also indicate that diversification along rivers has only a minor effect on the distribution of most species. Species with narrow adaptations replace each other along environmental gradients (Buckley and Jetz 2008; Zuquim et al. 2012). This replacement can result from the establishment of species with distinct adaptations to specific environmental conditions (Buckley and Jetz 2008), or from the adaptation of species or populations to distinct environments and subsequent ecological speciation (Schluter 2009, Salisbury et al. 2012).

Although diversification across rivers and species adaptations along environmental gradients are likely important for Amazonian diversity, it is not clear why the factors associated with the diversification of endemic clades are different from the factors associated with the structure of entire communities in Amazonia. Evolutionary and ecological studies have important methodological differences in the taxonomic scale considered, choice of clades under investigation, and the type of data used (e.g. museum records vs. presence/absence data). While evolutionary

studies are usually restricted to a few species or genera (Ribas et al. 2012, Batalha-Filho et al. 2014, Schultz et al. 2017, Ferreira et al. 2017, Araújo-Silva et al. 2017, Carneiro et al. 2018), ecological studies include hundreds or thousands of species (Dambros et al. 2017, Oliveira et al. 2017, Godinho and Da Silva 2018, Santorelli et al. 2018, Fluck et al. 2020). There are no direct comparisons between evolutionary and ecological approaches using the same database and applied to a diverse taxonomic group in which both previous phylogenetic and ecological approaches can be replicated.

We determine how geographic distance, rivers, and environmental factors are associated with 1) the cladogenesis of endemic groups (evolutionary approach) and 2) the distribution of both endemic groups and whole communities (ecological approach) in Amazonia. As has been shown in evolutionary studies (Ribas et al. 2012, Fernandes et al. 2012; Ferreira et al. 2017; Araújo-Silva 2017, Naka and Brumfield 2018), we expect cladogenesis of endemic bird clades to be associated to rivers (*Psophia*; Ribas et al., 2012), resulting in distinct species occurring across river margins (i.e. changes in endemic species composition). However, because several taxa in the whole bird clade have not diversified along Amazonian rivers, but as a part of much broader biogeographical processes (Jetz et al. 2012), we expect the change in species composition in the entire bird community to be more weakly associated to rivers. Therefore, the importance of rivers on the distribution of species should be stronger for endemic clades that diversified within Amazonia, whereas other factors, such as differences in the environment, should be more important for structuring whole communities.

2 | MATERIAL AND METHODS

2.1 | Study area

The Amazonian forest covers 6 million square kilometers in northern South America, comprising nine countries (Brazil, Bolivia, Colombia, Ecuador, Guyana, French Guyana, Peru, Suriname, and Venezuela; Da Silva et al. 2005), and harbor a wide range of vegetation types, such as rainforest, savannahs, flooded forests and more (Pires and Prance 1985). The forest has a predominantly warm climate, with mean seasonal temperature varying between 24 to 26°C and mean annual precipitation of 2300 mm (Fisch et al. 1998). Despite the seasonal stability (Janzen 1967), Amazonia has a great gradient of temperature due to differences in elevation (Körner 2007). For example, a difference in altitude of 2000m can culminate in a difference of 10°C (Supplementary material Hoorn 2010). In addition to providing a remarkable temperature gradient, the emergence of the Andes cordillera promoted gradual sediment deposits that were significant for the formation of different soils and dynamics of the hydrographic basin. This dynamism has led to the formation of several large rivers, such as the Amazon, Negro, Madeira, Xingu, Tapajós, and Branco (Hoorn et al. 2010).

2.2 | Data

Bird species occurrences were obtained from the literature. We created a species x site occurrence matrix based on previous studies published from 2000 to 2019. Data from studies published before 2000 were generally difficult to obtain because raw occurrence data was not available or the methods were not as precise as necessary for the analyses used in our ecological models. Published papers were found using the Google Scholar search tool. Only studies with the

combination of the words [“birds” OR “bird” OR “bird’s” OR “aves” OR “avifauna”] AND [“Amazon” OR “Amazonia” OR “Amazonian” OR “Guiana” OR “Guyana” OR “Suriname” “Venezuela” OR “Colombia” OR “Ecuador” OR “Peru” OR “Perú” OR “Bolivia”] in the title were included. Brazil was not used because most studies in Brazil were not conducted in Amazonia. However, the key-words “Amazon”, “Amazonia” and “Amazonian” retrieved studies conducted in the Brazilian Amazonian rainforest. Data were compiled from studies that 1) presented field methods so that sampling method (e.g. mist-net, point count) could be recognized, 2) described the locality of field activity; 3) identified individuals at the species level, 4) presented raw species occurrences (in a table, list of species, or supplementary material), 5) previously sampled data was not presented (i.e. original research). Data from islands and morphospecies (e.g. *Elaenia* sp.) which could not be compared among different studies were excluded from the data.

From the 1213 papers found, 107 met all the above criteria and were used for data compilation. The occurrence data encompassed 209 sites (Fig. 1A; see Supplementary material Appendix 1, Table A1) which are distributed in all biogeographic regions of Amazonia and cover virtually the entire range of climatic conditions and elevations in the region (see Supplementary material Appendix 1, Table A2). Because papers use different nomenclatures for species identification, species names were standardized using the South American Classification Committee nomenclature (SAAC), version from March 5th, 2018 (see Supplementary material Appendix 1, Table A1).

In addition to the occurrence data, we compiled 10,000 dated phylogenetic trees containing phylogenetic information for all birds of the world (9993) from the https://birdtree.org/ database (Jetz et al. 2012). Due to the high computational

demand that analyzing each tree separately would require, we randomly selected 10 out of the 10,000 phylogenies to run the analyses. Species or subspecies that had distribution range in IUCN but were not in the https://birdtree.org/ database were manually added to the trees. While the subspecies were attached to their sister species, the species were added to the root of their genus. We extracted environmental variables of mean temperature (bio1) and precipitation (bio12) from WorldClim (http://www.worldclim.org) with a resolution of 2.5 minutes. Data on elevation were extracted from NASA (https://asterweb.jpl.nasa.gov/gdem.asp) with a resolution of 10km.

2.3 | Data analysis

While evolutionary analyses determine the role of geographical and environmental factors on cladogenesis, ecological analyses quantify how these factors are associated with species distribution. To compare results from evolutionary and ecological models we used two independent analyses. Both the evolutionary and ecological analyses use the same data of bird species occurrences, phylogeny, and geographical and environmental data. Therefore, if current species distribution is caused by cladogenesis across barriers and along environmental gradients, both analyses should indicate rivers and climate as important.

To identify Amazonian bird endemics, we overlapped the Amazonian map and the IUCN range maps of all bird species. Because species range maps are not precise descriptors of species occurrences and often include areas outside the actual distribution of a species (Brooks et al. 2019), we relaxed the map overlap to consider a species as primarily endemic. Species with at least 70% of their range maps overlapping with the Amazonian map were considered endemics. Because

studies investigating biogeography and evolution of species in Amazonia often consider subspecies (Ribas et al. 2012), we included subspecies in our search for endemic clades. Clades with six or more endemic species or subspecies were extracted from 10 (out of 10,000) random phylogenetic trees to run the DEC (Dispersal-Extinction Cladogenesis; Ree and Smith 2008) analyses. We added branch lengths to subspecies belonging to these endemic clades according to previous phylogenetic studies on these clades (Ribas et al. 2012 for *Psophi*a; Ferreira 2018 for *Galbula*; Sousa-Neves et al. 2013 for *Xiphorhynchus*). *Reghmatorhina* and *Epinecrophylla* clades did not have previous studies on their evolution, so a standard value of 0.1 Mys was added to their branch lengths.

For the evolutionary analyzes, we have created exclusive occurrence tables for each endemic clade along the seven regions between rivers. Since the subspecies of the endemic groups are not easily discerned from species in fieldwork, we used distribution maps from the IUCN Red List Platform (https://www.iucnredlist.org/search) to recognize in which regions these subspecies occurred. Because this was a large-scale procedure, IUCN maps were fair to point out the presence and absence in the regions, even though they may produce false presences (Brooks et al. 2019). Furthermore, IUCN maps are extensively used in macroecological analysis and are shown to generate reliable results when used on an appropriate scale (Rodrigues and Diniz-Filho 2017, Rangel et al. 2018, Hurlbert and Jetz 2007). For standardization purposes, we use the same distribution maps of the subspecies extracted in endemic clades to include their presence in the occurrence data (points along the Amazon river) for ecological analyzes.

2.4 | Evolutionary analysis

We used a DEC (Dispersal-Extinction Cladogenesis; Ree and Smith 2008) model using different environmental and geographic factors to test their influence on the cladogenesis of Amazonian endemic clades (i.e. these analyses are performed using endemic clades only; Van Dam and Matzke 2016). To test the influence of different geographic and environmental factors on cladogenesis, we have constructed constraint matrices between seven areas separated by major rivers (Amazonia biogeographic areas; Fig. 1B). These areas are bounded by the Amazon, Negro, Madeira, Xingu, Tapajós, and Branco rivers and are known as the Amazonian interfluves – Guyana, Pantepui, Napo, Inambari, Rondônia, Tapajós and Xingu (Fig. 1b).

To infer how the cladogenesis of Amazonian endemic birds was affected by environmental and geographic factors, we used the BioGeoBEARS R package (Matzke 2013) using the dated phylogeny from Jetz (2012). BioGeoBEARS allows statistical comparison of biogeographical models, including DEC (Dispersal-Extinction Cladogenesis). The DEC model applied by BioGeoBears is a version of the Dispersal-Extinction Cladogenesis probabilistic model of the LAGRANGE program (Ree et al. 2005, Ree and Smith 2008, Matzke 2013, 2014). This model estimates values for the processes of dispersion (“d”; i.e. rate of dispersion or expansion of the distribution) and extinction (“e”; i.e. rate of extinction or contraction of the distribution) along phylogenetic branches through the provided data. Based on a model of geographic evolution, this method allows inferring how dispersal and extinction produced the geographic distributions of the species currently observed (Matzke 2013).

By applying constraint matrices indicating connectivity between the seven biogeographic areas defined by rivers, it is possible to modify the unconstrained DEC model (free dispersal between endemism areas) into a constrained DEC model (Dupin et al. 2017). Similarly, the model DEC model can be modified into a DEC + X model, which is a DEC model implemented using an adjacency matrix modified by a distance matrix representing geographical distance or differences in environmental variables between pairs of areas. The model has an additional parameter ("X") which modifies the dispersal probability as a function of distance specified in the matrix (Van Dam and Matzke 2016). The constrained matrix ("X") allows testing the effect of different environmental and geographical factors on species biogeographic history.

We implemented seven different models for each endemic clade to incorporate the effect of environmental variables, geographic distance, and rivers (presence and width) on cladogenesis (Table 1): 1) DEC unconstrained; 2) DEC constrained by the presence of rivers; 3) DEC + X constrained by geographical distance; 4) DEC + X constrained by the presence of rivers taking into account river width; 5) DEC + X constrained by differences in temperature; 6) DEC + X constrained by differences in precipitation; 7) DEC + X constrained by differences in elevation.

Because several phylogenetic hypotheses were available (10 phylogenies were used, see above), species in endemic clades had different phylogenetic relationships in each phylogeny. Therefore, models were fitted in each of these individual phylogenies, and we calculated the mean AIC (Akaike Information Criterion) value for models for the clade. The mean AIC values were used to determine which factor most affected the dispersion-extinction cladogenesis

process in each endemic clade. Similarly, we calculated the mean wAIC for each model to access the relative contribution of climatic, geographical distance, and rivers to the dispersion-extinction cladogenesis process. ΔAIC between the best and all other models was calculated to evaluate how models differed from each other.

2.5 | Ecological analysis

In addition to the effects of geographical barriers and the environment on cladogenesis, evolutionary processes across dispersal barriers and environmental filters should also affect the distribution of species (Silva et al. 2019). Ecological studies frequently compare changes in species composition between opposite sides of rivers and along environmental gradients (Pomara et al. 2014; Hayes and Sewall 2004) and can also incorporate phylogenetic information (Graham and Fine 2008, Leprieur et al. 2012). We used both taxonomic (Baselga 2012) and phylogenetic (Leprieur et al. 2012) community structure to study species distribution in Amazonia.

We used the pairwise Jaccard dissimilarity index (Baselga 2012) to measure differences in taxonomic composition among the 209 sites with available occurrence data (beta diversity) and the pairwise Jaccard dissimilarity index weighted by species phylogenetic distance to measure the phylogenetic dissimilarity (i.e. differences in evolutionary history) between sites (Leprieur et al. 2012). Because multiple phylogenetic hypotheses were used, we calculated a mean value for phylogenetic dissimilarity (Jaccard) for each pair of sites.

To compare the results from ecological analyses (whole bird community) to results from the evolutionary analyses described above (bird endemic clades), we

279 also measured taxonomic and phylogenetic dissimilarities for each endemic clade
280 separately.

281 To determine how geographical distance (i.e. spatial isolation), rivers, and
282 climate are associated with the taxonomic and phylogenetic dissimilarities between
283 sites, we constructed pairwise geographical, riverine, and environmental distance
284 matrices. To account for spatial isolation between sites, geographical distance was
285 calculated as the euclidean distance between all pairs of sites based on
286 geographical coordinates (latitude and longitude). The riverine distance matrix was
287 calculated as a binary matrix, in which “1s” represent pairs of sites separated by at
288 least one major Amazonian river and “0s” represent pairs of sites not separated by
289 major rivers. Environmental distances were calculated as the difference in
290 temperature, precipitation, and elevation for each pair of sites. We used a multiple
291 regression of distance matrices (Legendre et al. 1994) to associate the
292 geographical, riverine, and environmental distance matrices (predictor variables) to
293 the taxonomic and phylogenetic distance matrices (response variables). These
294 analyses were conducted for each endemic clade separately and the whole bird
295 community.

296 All analyses were conducted in the R program (R Development Core Team
297 2019) using the raster (Hijmans 2012), betapart (Baselga et al. 2017), ecodist
298 (Goslee and Urban 2007), rgdal (Bivand et al. 2011) vegan (Oksanen et al. 2010),
299 APE (Paradis et al. 2004), rgeos (Bivand and Colin, 2017), phytools (Revell 2012),
300 speciesgeocodeR (Zizka and Antonelli 2015), FD (Laliberté et al. 2014),
301 BioGeoBEARS (Matzke 2013) and picante (Kembel et al. 2010) packages.

302

3 | RESULTS

We found records for 1783 species distributed in all Amazonian regions (Fig. 1a; see Supplementary material Appendix 1, Table A1). Most previous studies were conducted in the Guyana region (n = 31), whereas the Pantepui was the region with the lowest number of previous studies (n = 5). From all species recorded, nine endemic clades appeared at least twice in the ten random trees: *Psophia, Galbula, Rhegmatorhina*, Myrmotherula, Myrmelastes*, Thamnomanes*, Epinecrophylla, Lepidothrix* and *Xiphorhynchus* ("*" indicates when a clade included at least one sister species from other genus forming a monophyletic clade; see Supplementary material Appendix 1, Table A4), encompassing 73 from the 1783 species. These clades were used in the analyses of individual endemic clades.

3.1 | Cladogenesis models

Based on AIC values (see Supplementary material Appendix 1, Table A4) and mean AIC values for each model per clade, the models including rivers as barriers to dispersal (DEC rivers and DEC rivers width) best explained the cladogenesis of six endemic groups. In contrast, the model including dispersal constrained by temperature was the best fitting model for three groups (see Supplementary material Appendix 1, Table A5). However, except for *Psophia*, models including rivers, geography, or environment had similar fit to the data (ΔAIC; see Supplementary material Appendix 1, Table A4).

Based on weighted AIC values (wAIC), rivers was the factor with the highest importance for the cladogenesis of six endemic groups. Temperature was the most important factor for the other three groups (Fig. 2 – grey bars; see Supplementary

material Appendix 1, Table A6). The clades with the highest contribution of rivers were also those with the lowest contribution of temperature. Geographic distance, precipitation, and elevation had low importance for the cladogenesis of all clades (Fig. 2-grey bars).

3.2 | Ecological models

When testing for the association between taxonomic dissimilarity and predictor variables for each individual endemic group, presence of rivers was the factor with the highest explanatory power for four clades, geographic distance was the factor with the highest explanatory power for two clades and differences in temperature was the factor with the highest explanatory power for three clades (see Supplementary material Appendix 1, Table A7). When using phylogenetic dissimilarities instead of taxonomic dissimilarities, the presence of rivers was the factor with the highest explanatory power for five clades and geographic distance was the factor with the highest explanatory power for three clades (see Supplementary material Appendix 1, Table A8). Only the *Myrmotherula* clade had its phylogenetic dissimilarities mostly explained by differences in temperature (Fig. 2 – black bar; see Supplementary material Appendix 1, Table A7).

In the analyses using all bird species (i.e. whole community, encompassing 1783 species), taxonomic and phylogenetic dissimilarity was explained mostly by differences in temperature ($R^2_{taxo} = 0.12$; $R^2_{phylo} = 0.05$; $P < 0.001$) and the presence of rivers separating regions ($R^2_{taxo} = 0.09$; $R^2_{phylo} = 0.04$; $P < 0.001$; Table 2). However, rivers were not hard limits for species composition – sites separated by rivers often had similar taxonomic and phylogenetic composition of species (i.e. low beta diversity; shared species; Fig. 1a).

4 | DISCUSSION

By comparing the results from evolutionary (DEC) and ecological models (multiple regression on distance matrices), we found that rivers are the main factor affecting the cladogenesis and distribution of endemic clades, in contrast to the relatively weak effect of environmental differences and geographical distance. These results corroborate previous studies suggesting that cladogenesis across rivers has a strong effect on the current distribution of endemic species in Amazonia (Ribas et al. 2012, Cracraft 1985). However, a small fraction of the Amazonian bird genera evolved entirely within Amazonia and have only species endemic to this region (endemic clades encompassed 73 out of 1873 species). Contrary to results found for endemic species, ecological models using whole community data revealed differences in temperature as the most important factor shaping the phylogenetic and taxonomic composition of species in Amazonia.

Differences in temperature was the most important factor associated with bird phylogenetic and taxonomic dissimilarity between sites (Table 2) – i.e. species identity differs in sites with different mean annual temperature. This association could also be explained by indirect effects mediated by other variables correlated to temperature (i.e. altitude; Janzen 1967; Fluck et al. 2020), but differences in other climatic and topographic variables were not as important in our models (Table 2). Because the Amazonian rainforest has a relatively stable seasonal temperature compared to non-tropical regions, species in the tropics may have narrow adaptations to climatic conditions (Read et al. 2018, Janzen 1967). The temperature gradient extending from Andes and Tepuis towards central Amazonia may be associated with the evolution of adaptations and specialization of species in the region (Luruziaga-Aveiga and Weir 2019, Rahbek et al. 2019). Narrow

adaptations and specialization to specific temperature ranges may lead to changes in species composition along this gradient and prevent individual species from occurring across the entire Amazonian region. We were not able to obtain reliable soil and vegetation data from all sampling locations, but these factors have also been associated with species composition in local studies (e.g. Dambros et al. 2016, Pomara et al. 2014; Costa et al. 2005). Therefore, these gradients may be correlated to temperature and affect the distribution of species in the region.

Although the temperature gradient was the most important factor associated with changes in species composition, rivers also contributed to changes in phylogenetic and taxonomic composition to a lesser extent (Table 2). These changes are especially strong for endemic clades (Fig. 2) and across the wide Amazon river, where a break in species composition between communities in the north and south of the river is evident (warmer colors mostly restricted to the north of the Amazon river in Fig. 1). The importance of rivers for all birds in our study is also stronger than reported previously for Passerine birds (Fluck et al. 2020). These differences can be due to the use of species records instead of the range maps used in previous studies and the addition of more than 619 bird species, especially from non-volant clades (e.g. *Psophia*) which are likely to have limited dispersal across rivers. When only endemic clades are used for analyses, evolutionary and ecological models are congruent for most clades and indicate rivers as important for cladogenesis and species distribution (Fig. 2). Collectively, our results and results from previous studies suggest that evolutionary processes associated with the presence of rivers (i.e. allopatric speciation) can determine the distribution of at least some endemic bird species. Even though these effects can

400 be detected at the community level, the distribution of species at broad taxonomic
401 scales is primarily associated with differences in the environment (Table 2).

402 Comparing data obtained from multiple studies represents a challenge due
403 to differences in sampling effort and methodology. Our study is the first to use the
404 same data to contrast evolutionary and ecological approaches, shedding light on
405 one of the most debated topics in Amazonian biogeography (Ribas et al. 2012,
406 Santorelli et al. 2019). We demonstrated that both evolutionary and ecological
407 approaches point to rivers affecting the cladogenesis and distribution of endemic
408 clades (Fig. 2). In contrast, our results suggest that rivers are not the most
409 important factor explaining the distribution of all birds in Amazonia. These results
410 suggest that findings obtained from small clades cannot be extrapolated to whole
411 communities and that differences obtained from evolutionary and ecological
412 approaches might be mainly due to differences in taxonomic scale (see also
413 Maximiano et al. 2020).

414 In conclusion, our results suggest that environmental gradients are the main
415 cause for the distribution of large communities of species in Amazonia. However,
416 rivers have influenced the cladogenesis and the distribution of endemic clades.
417 The Andean uplift has shaped the distribution of species in Amazonia, marking the
418 origin of many rivers (Hoorn 2010). At the same time, the Andean uplift shaped not
419 only geographical barriers in Amazonia, but also created gradients in elevation
420 (Rangel et al. 2019), climate (Hoorn 2010), and soils (Higgins et al. 2011).
421 Although species differ in their response to these gradients in Amazonia, it is still
422 not clear how these species evolved distinct adaptations. Only by incorporating
423 species evolution along environmental gradients and in response to the presence
424 of geographical features, researches will be able to fully understand the causes for

the current species distribution in Amazonia from fine to broad taxonomic scales. Future studies investigating the causes for species distribution must be aware that the importance of environmental gradients and barriers depends on the taxonomic scale. Results obtained from an entire class, order or other broad clade should not be compared to results obtained from genera or other less inclusive clades.

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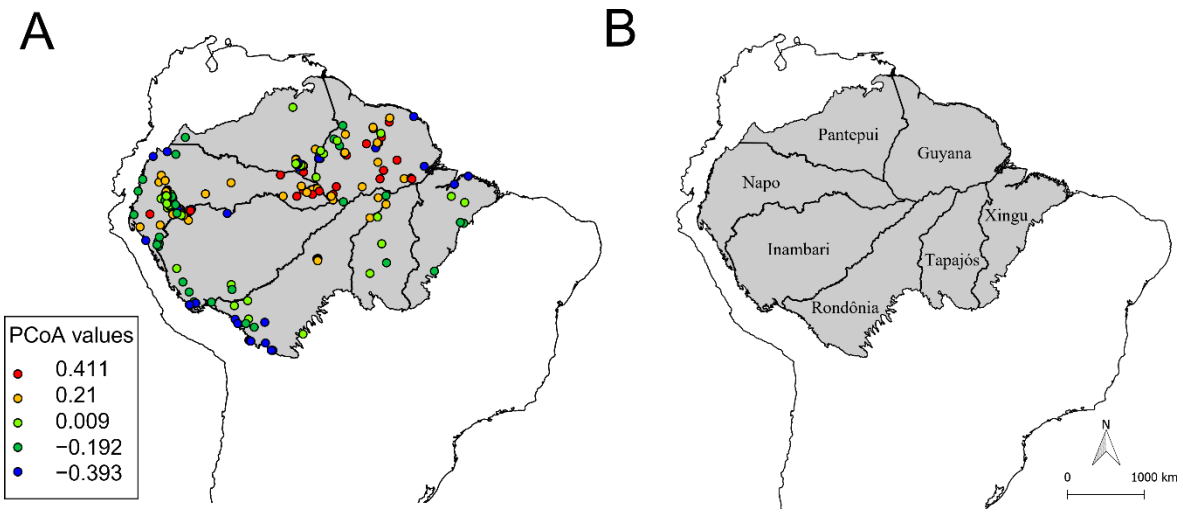
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606 **FIGURES**



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609 Figure 1 – Maps of the bird communities with available data (A) and endemism
610 areas (B) following Cracraft (1985), Ribas (2012), Borges e Silva (2012) and Naka
611 (2011). In (A), phylogenetic dissimilarity between sites summarized in one PCoA
612 axis is represented by the color gradient, which indicates the ordering scores from -
613 0.393 to 0.411. Ordering scores were obtained from a Principal Coordinates
614 Analysis (PCoA) using the Jaccard phylogenetic dissimilarity index (Leprieur et al.
615 2012).

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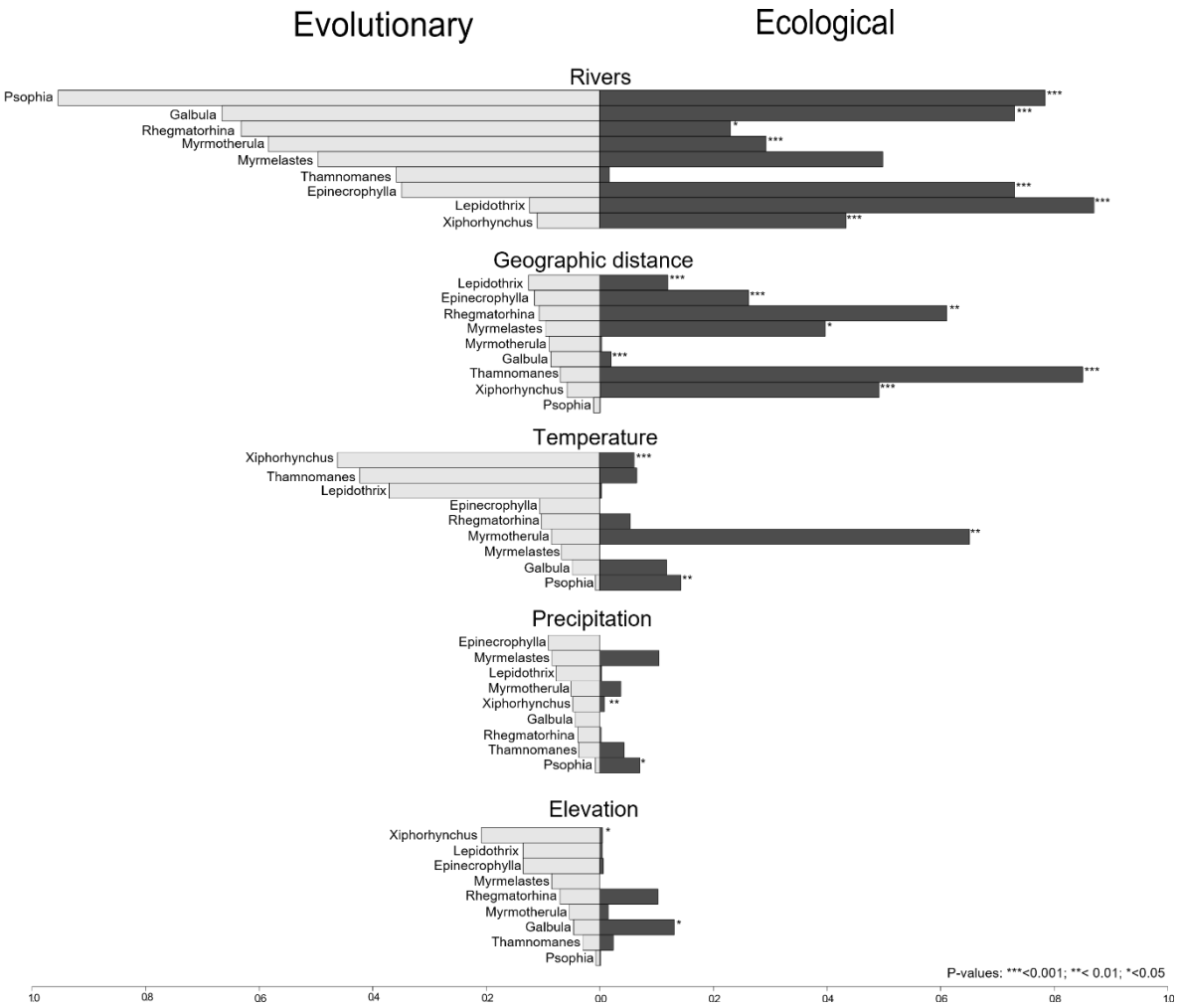


Figure 2 - Comparison between results of cladogenetic (evolutionary) and ecological models. Explanatory factors (rivers, geographic distance, temperature, precipitation, and elevation) on cladogenesis (gray bars) and distribution (phylogenetic dissimilarity between sites; black bars) for each endemic group are represented in a scale from 1 to 0. To evaluate the contribution of each factor on the cladogenesis of each group, we used mean wAIC values (see Supplementary material Appendix 1, Table A6), and to measure the effect of each factor on species distribution of each group we used relative values of R^2 (see Supplementary material Appendix 1, Table A8). The relative values of R^2 were calculated by dividing the coefficients associated with each factor by the sum of all coefficients in the Multiple Regression of Distance Matrices .

638 **TABLES**

639 Table 1 – Cladogenesis (DEC) models fitted to groups of endemic birds. Each DEC
640 model was modified to test for the effect of different factors on the birds'
641 cladogenesis process.

Model	Variable	Question
DEC unconstrained	Non (free dispersal between areas)	Has the group cladogenesis occurred without any restriction between areas?
DEC constrained by the presence of rivers	Presence of rivers	Has the presence of rivers affected group cladogenesis?
DEC+X constrained by distance	Distance (km)	Has distance between areas affected group cladogenesis?
DEC+X constrained by rivers' width	Rivers' width	Has rivers' width affected group cladogenesis?
DEC + X constrained by temperature	Mean temperature (^{o}C) of areas between rivers	Has the difference in mean temperature between areas affected group cladogenesis? (i.e. environmental distance)
DEC + X constrained to precipitation	Mean precipitation (mm) of areas between rivers	Has the difference in mean precipitation between areas affected group cladogenesis? (i.e. environmental distance)
DEC + X constrained to elevation	Differences in mean elevation (m) of areas between rivers	Has the difference in mean elevation between areas affected group cladogenesis?

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643 Table 2 –Effect of geographical distance, environmental differences (temperature,
644 elevation, and annual precipitation), and presence of rivers on bird taxonomic and
645 phylogenetic dissimilarities in multiple regression analyses. Taxonomic and
646 phylogenetic dissimilarities were measured using the Jaccard dissimilarity index
647 (Baselga 2012, Leprieur et al. 2012).

	Taxonomic dissimilarity	**Phylogenetic dissimilarity**
Variable	**R^2**	**R^2**
Geographic distance	0.053***	0.009**
Average annual temperature	0.117***	0.055***
Elevation	0.012**	0.011*
Annual Precipitation	0.025***	0.007*
Rivers	0.086***	0.036***

648 P-values: ***<0.001, **<0.01, *<0.05
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662 **APPENDIX**

663 Table A1 – Data collection. File (.csv) containing compiled bird checklists in
664 Amazonia and published in scientific papers available in Google Scholar (see main
665 text for search queries).

666 Table A2 – Mean environmental range encompassed in the data (i.e. sites for bird
667 checklists).

	Amazonia			Study sites		
Variable	**max**	**min**	**mean**	**Max**	**min**	**mean**
Temperature	28.1	7.1	25.55	27.4	9	25.29
Precipitation	5238	550	2298	4109	818	2275
Elevation	255	0	133	255	0	130.6

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669 Table A3 – River width information used to constrain the matrix used in the model
670 DEC+X. Euclidean distances were measured manually using Google maps tool
671 “measure distance”. The mean width for each river was obtained by measuring the
672 distance between river margins at intervals of 50km. Adapted from Fluck et al.
673 (2020).

River	Amazon	Negro	Madeira	Xingu	Tapajós	Branco
Width (km)	2,83	2,21	1,37	1,55	4,66	1,07

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675 Table A4 – Model fitting. File (.csv) containing information about the d, e, and x
676 parameters, AIC, ΔAIC values for each model fitted for each endemic group for
677 each phylogenetic hypotheses.

Table A5 – Mean AIC per group and model. As the groups were represented by more than one phylogenetic hypothesis and the models were fitted in each one of these hypotheses, we made an average of AIC of each model for each group.

	DEC unconstrained	**DEC constrained by the presence of rivers**	**DEC+X constrained by distance**	**DEC+X constrained by river width**	**DEC + X constrained by temperature**	**DEC + X constrained to precipitation**	**DEC + X constrained to elevation**
Lepidothrix	66.7412	70.1222	67.3518	68.3744	**65.2196**	68.3382	67.3444
Myrmotherula	48.8184	**46.43**	49.6976	48.9812	49.7952	50.8156	50.7156
*Rhegmatorhina**	113.4234	109.887	111.8294	**109.8642**	112.3684	113.9046	113.0224
*Myrmelastes**	65.62175	**64.5865**	66.73025	65.5675	67.50325	67.05125	67.04375
Xiphorhynchus	60.218	61.80925	61.58125	61.4435	**57.38025**	61.75775	58.81375
Psophia	42.5128	35.886	42.8254	**34.8128**	43.6732	43.5062	43.6414
Galbula	72.944	**70.532**	73.53333	71.24593	74.63333	74.78533	74.68867
Epinecrophylla	64.28067	**64.05867**	65.34333	65.158	65.50867	65.80533	65.01
*Thamnomanes**	53.56	51.02	53.863	53.938	**50.269**	55.123	55.546

683 Table A6 – Mean wAIC values of each model representing different factors
684 to compose Fig. 2 (grey bars). As the sum of wAIC values per group is equal
685 to one, the wAIC values represent the relative contribution of each factor per
686 group. Similarly to the approach used for AIC values, because groups were
687 represented by more than one phylogenetic hypothesis and the models
688 were fitted in each one of these hypotheses, we made an average of wAIC
689 of each model for each group

Factor	***Psophia***	***Lepidothrix***	***Epinecrophylla***	***Galbula***	***Myrmelastes****	***Myrmotherula***	***Rhegmatorhina****	***Thamnomanes****	***Xiphorhynchus***
No restrictions	0.0128	0.1679	0.2048	0.1103	0.1720	0.1381	0.0498	0.0815	0.1141
Rivers	**0.9538**	0.1234	**0.3484**	**0.6650**	**0.4957**	**0.5835**	**0.6314**	0.3582	0.1098
Geographic distance	0.0111	0.1256	0.1152	0.0864	0.0961	0.0891	0.1069	0.0700	0.0577
Temperature	0.0072	**0.3706**	0.1059	0.0480	0.0669	0.0848	0.1024	**0.4224**	**0.4617**
Precipitation	0.0078	0.0770	0.0906	0.0439	0.0843	0.0509	0.0391	0.0376	0.0476
Elevation	0.0073	0.1355	0.1351	0.0462	0.0850	0.0536	0.0702	0.0302	0.2090

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Table A7 – Relative R^2 values for each factor affecting taxonomic dissimilarity between sites. The relative values of R^2 were obtained by dividing the coefficients of each factor (results from multiple regression model on distance matrices) by the sum of coefficients of all factors.

Factor	***Psophia***	***Lepidothrix***	***Epinecrophylla***	***Galbula***	***Myrmelastes****	***Myrmotherula***	***Rhegmatorhina****	***Thamnomanes****	***Xiphorhynchus***
Rivers	**0.7557**	**0.8644**	**0.9111**	0.1788	0.2859	0.3725	**0.8886**	0.0530	0.4046
Geographic distance	0.0422	0.1310	0.0833	0.1438	**0.6054**	0.1104	0.1015	0.2954	**0.5893**
Temperature	0.1170	0.0007	0.0049	**0.5534**	0.0012	**0.4775**	0.0069	**0.6143**	0.0037
Precipitation	0.0838	0.0023	0.0000	0.1011	0.1074	0.0116	0.0003	0.0109	0.0020
Elevation	0.0013	0.0018	0.0006	0.0229	0.0001	0.0280	0.0026	0.0263	0.0004

711 Table A8 – Relative R^2 values for each factor affecting phylogenetic dissimilarity
712 between sites. The relative values of R^2 were obtained by dividing the
713 coefficients of each factor (result of the regression of matrices) by the sum of
714 coefficients of all factors. Values used to compose figure 2 (black bars).

Factor	***Psophia***	***Lepidothrix***	***Epinecrophylla***	***Galbula***	***Myrmelastes****	***Myrmotherula***	***Rhegmatorhina****	***Thamnomanes****	***Xiphorhynchus***
Rivers	**0.7846**	**0.8709**	**0.7313**	**0.7310**	**0.5000**	0.2933	0.2304	0.0176	0.4340
Geographic distance	0.0006	0.1199	0.2624	0.0199	0.3967	0.0035	**0.6110**	**0.8506**	**0.4914**
Temperature	0.1431	0.0030	0.0001	0.1177	0.0004	**0.6515**	0.0543	0.0655	0.0616
Precipitation	0.0701	0.0023	0.0000	0.0000	0.1038	0.0372	0.0021	0.0425	0.0081
Elevation	0.0016	0.0039	0.0061	0.1314	0.0001	0.0145	0.1022	0.0238	0.0048

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