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**Filogeografia comparada de Passeriformes com uma distribuição circum-Amazônica**

**SÃO PAULO**

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# **Comparative phylogeography of Passerine birds with a circum-Amazonian distribution**

**Filogeografia comparada de Passeriformes com uma distribuição circum-Amazônica**

**Original Version**

Thesis submitted to the Graduate Program of the Museu de Zoologia da Universidade de São Paulo in partial fulfillment of the requirements for the degree of Doctor of Science (Systematics, Animal Taxonomy and Biodiversity).

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## **Abstract**

There are a number of common distributional patterns that have provided the foundations of our current knowledge of Neotropical biogeography. A distinctive pattern is the so-called “circum-Amazonian distribution”, which expands across the forested lowlands south and east of Amazonia, the Andean foothills, the Venezuelan Coastal Range, and the Tepuis. To date, there is no clear understanding of the processes giving rise to this distribution. To understand the evolutionary history of taxa exhibiting this pattern it is necessary to test biogeographic hypotheses offering mechanistic explanations. Comparative phylogeography allows more accurate phylogeographic hypotheses for these taxa, as well as better population genetic parameters. Comprehensive comparative studies aiming at unraveling the evolutionary and biogeographic mechanisms underlying the circum-Amazonian distribution have not been conducted yet, and only scarce descriptive information has been published. Therefore, the objective of this work was to elucidate the historical and biogeographic mechanisms underpinning circum-Amazonian distribution by performing comparative genomic analyses of a group of Suboscine passerines. Ultraconserved Elements (UCEs) were obtained for eight taxonomic groups to estimate population parameters and genealogical trees. For the *Thamnophilidae* species were inferred demographic histories with *mom2*. The best models of each taxon were analyzed in a comparative framework to relate them with previously proposed biogeographic hypotheses for the Neotropics and to propose plausible biogeographical scenarios for the circum-Amazonian pattern. The circum-Amazonian distributional pattern has two main phylogeographic units: an Andean (plus Central America region) and an eastern-forested region (Atlantic Forest ecoregion, forested areas around southeast of Amazonia), interconnected by a northern and southern corridor, allowing biotic interchanges

between them (mainly from the southern) and hybridization. Species-tree analyses recovered (a) an Andean clade with two Andean subgroups in the northern Peru and central Andes, and (b) an eastern-forested clade including northern and central/southern Atlantic Forest subgroups. The demographic histories of the Thamnophilidae taxa suggest that diversification of the circum-Amazonian taxa have a strong influence of climatic fluctuations during the Pleistocene, with interconnected refugia allowing phenotypic/genetic differentiation but maintaining a considerable level of gene flow during varying dry/cool and warm/humid periods. In addition, the results of this work opened interesting taxonomic questions about some taxa that could be covered in the future (*T. ruficapillus/torquatus* complex, *Xiphocolaptes* complex).

## Resumo

Existe um número de padrões de distribuição comuns que forneceram os fundamentos do nosso atual conhecimento da Biogeografia Neotropical. Um padrão distintivo é o chamado padrão de distribuição circum-Amazônico, apresentado por grupos filogeneticamente relacionados habitando as florestas de baixada ao sul-leste da Amazônia, as encostas úmidas dos Andes, a área costeira da Venezuela e os Tepuis. Atualmente não existe um entendimento claro dos processos que deram surgimento a este padrão de distribuição. Para compreender a história evolutiva dos táxons exibindo este tipo de padrão é necessário testar hipóteses biogeográficas que ofereçam explicações mecanicistas. A Genômica comparativa permite hipóteses filogeográficas mais exatas para estes táxons, assim como melhores parâmetros demográficos. Estudos comparativos abrangentes visando em esclarecer os mecanismos evolutivos e biogeográficos relacionados a distribuição circum-Amazônica não tem sido elaborados ainda, e só informação descritiva escassa tem sido publicada. Portanto, os objetivo fundamental do projeto foi elucidar os mecanismos históricos e biogeográficos subjacentes à distribuição circum-Amazônica desenvolvendo análises genômicas comparativos de um grupo de Passeriformes Suboscines. Dados do gene ND2 e de Elementos Ultraconservados (UCEs) foram obtidos de oito grupos taxonômicos para estimar parâmetros populacionais e árvores genealógicas. Histórias demográficas foram inferidas só para as espécies da família *Thamnophilidae* usando *mom2*. Os melhores modelos de cada táxon foram analisados num marco comparativo para relaciona-os ás hipóteses biogeográficas propostas para o Neotrópico e propor cenários possíveis para a distribuição circum-Amazônica. O padrão de distribuição circum-Amazônico possui duas unidades filogeográficas principais: uma unidade Andina (incluindo a região de Centro América) e uma segunda unidade incluindo as regiões florestais do

leste (Mata Atlântica, áreas florestais ao sudeste da Amazônia). Estas unidades estão interconectadas por corredores ao norte e sul da distribuição, permitindo intercâmbios de biota entre elas (principalmente pelo corredor sul). SNAPP identificou o clado Andino subdividido em norte do Peru e central Andes, e um segundo clado das Florestas do Leste incluindo dois subgrupos, um do norte e outro do centro-sul da Mata Atlântica. As histórias demográficas dos Thamnophilidae sugerem que a diversificação na distribuição circum-Amazônica foi altamente influenciada pelas flutuações climáticas durante o Pleistoceno, com refúgios interconectados gerando diferenciação fenotípica/genética mas mantendo certo grau de fluxo gênico nos períodos secos/frios e quentes/húmidos. Adicionalmente, algumas questões taxonômicas sobre alguns táxons estudados que poderiam ser estudadas no em futuros estudos (o complexo *T. ruficapillus/torquatus* e o gênero *Xiphocolaptes*).

## General Introduction

Neotropical biomes and ecosystems exhibit high biodiversity and a wide range of ecological/geological characteristics (Connell, 1978; Stotz *et al.*, 1996; Myers *et al.*, 2000; Rull, 2011; Richardson & Pennington, 2016).

The Neotropics contains about 100,000 species of seed plants (37% of the world's species, Antonelli & Sanmartín, 2011), more of 3,000 species of amphibians (50% of all amphibian richness, Young *et al.*, 2004) and have high levels of richness in reptiles (Böhm *et al.*, 2013). In the same way, the Neotropical areas harbor approximately 3,800 species of birds (Stotz *et al.*, 1996) a 36% of all known landbird species and the highest level of endemism in the world (Newton & Dale, 2001), and probably these values are being underestimated.

Several theoretical and empirical approaches have been performed to identify and understand the processes involved in the evolution of such high diversity in the Neotropics (e.g. Sick, 1967; Haffer, 1969; Vuilleumier, 1971; Brown, 1979; Cracraft, 1985; Cracraft & Prum, 1988; Hooghiemstra & van der Hammen, 1998; Garzón-Orduña *et al.*, 2014; Antonelli *et al.*, 2018; Rull, 2018).

Mainly, these efforts have focused in the analysis of the Amazonian region. Thus, several hypotheses about the origin and maintenance of diversity of the Amazonia have been proposed (reviewed by Haffer, 1997 and Rull, 2018). Two of these hypotheses are based in the presence of rivers acting as barriers among populations/species. In the first one, the River Hypothesis (Sick, 1967; Capparella, 1988), the rise/presence of rivers in the Amazonian basin are the main cause in the separation of animal ancestral populations in this region (originally, the idea about rivers acting like barriers was outlined by Wallace, 1854). In the second one, the River-refuge Hypothesis

(Haffer, 1993), the isolation of ancestral populations in the Amazonia was a consequence of (a) several emerging rivers and (b) “ecologically unsuitable terrain” in the northern and southern Amazonia during the dry glacial periods in the Quaternary. Also, the Paleogeography Hypothesis (Croizat, 1976), states that geological processes (tectonic movements and level sea fluctuations) influence (indirectly) the diversity/distribution of species/subspecies allowing the isolation and re-connection of Amazonian populations. Lastly, the Refugia Hypothesis proposes that the biodiversity in Amazonia was molded by a series of climatic fluctuations during the Cenozoic, producing a reduction of the Neotropical Forests (Haffer, 1969; Vanzolini & Williams, 1970). (Cracraft, 1985) proposed other alternative to the “refugia” hypothesis; using the South American Avifauna, stated that endemism areas in these regions could be older (and, subsequently, the origin of its biodiversity) than the Pleistocene.

All these hypotheses have been subject to wide discussion, and several tests have been implemented to corroborate or refute their assumptions (Mayr & O’Hara, 1986; Salo, 1987; Nores, 1999; Loughheed *et al.*, 1999; Colinvaux *et al.*, 2000; Haffer & Prance, 2001; Haffer, 2008; FernAndes *et al.*, 2012; Maldonado-Coelho *et al.*, 2013; Garzón-Orduña *et al.*, 2015; Rocha & Kaefer, 2019, among others). For instance, Bennett *et al.*, (2012) broadly discuss about the origin of biodiversity in Neotropics and the influence of the ‘refugia’ proposed by Haffer (1969), while Ramírez-Barahona & Eguiarte (2013), Leite *et al.*, (2016) and Arruda *et al.*, (2017) tested the influence of climatic fluctuations during the Pleistocene in Neotropical regions. In the same way, Albert *et al.* (2018) review the impact of the change of course of the Amazon River in the diversification of Neotropics, and Nazareno *et al.* (2018) tested the importance of the riverine barriers (Wallace hypothesis) in some species of plants. Côrtes *et al.* and Moggi *et al.* (2015) tested the Pleistocene arcs as driver of diversification in the South American Seasonally Forests for some



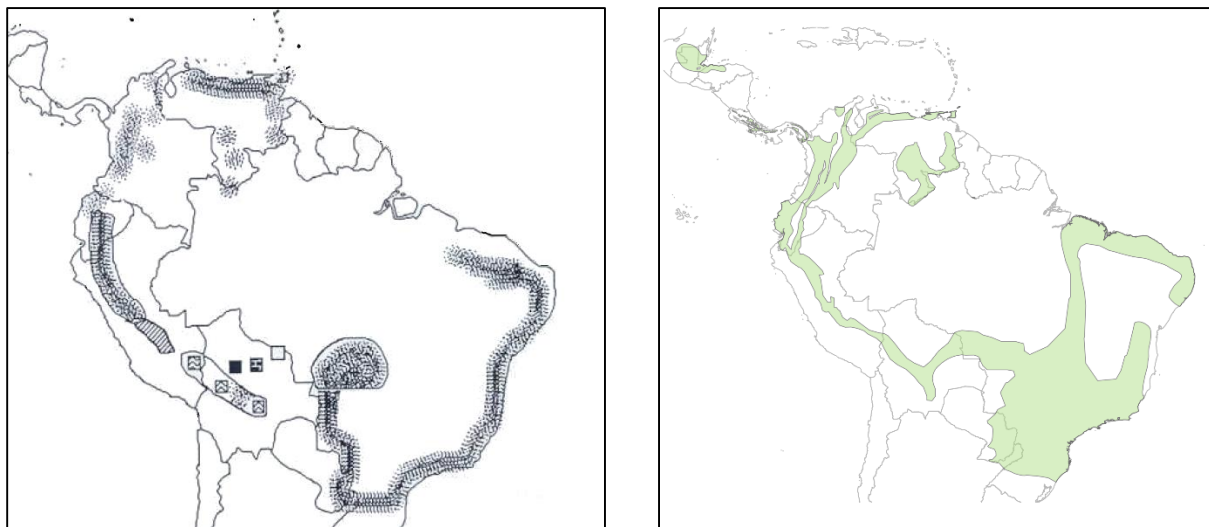
species of plants. Finally, in a study based on 27 avian lineages, Smith *et al.* (2014) propose that the high diversification of Neotropical birds was not mainly affected by the changes in the South American landscape, but also due to dispersal events creating isolation and speciation.

Because of this bias in the quantity and quality of studies about Amazonia in relation to others Neotropical regions, the information about the evolutionary and biogeographic processes acting on the non-Amazonian regions is relatively scarce. However, some theoretical and empirical approaches have been performed to identify and understand the processes involved in the biodiversity of non-Amazonian areas/taxa. Initially, multiple works covered general descriptions and classifications of the different Neotropical regions (e.g. Haffer, 1969; Cabrera & Willink, 1980; Rivas-Martínez & Tovar, 1983; Cracraft, 1985; Dinerstein *et al.*, 1995; and Morrone, 2014). Others were focused in open lowlands from South America, like the Cerrado, the Caatinga and the Chaco (Prado & Gibbs, 1993; da Silva, 1995; Bridgewater *et al.*, 2004; Mayle, 2006; Roig-Juñent *et al.*, 2006; and Caetano & Naciri, 2011). In the same way, the Andean region (Fjeldså, 1992; Knapp, 2002; Doan, 2003; Brumfield & Edwards, 2007; Ribas *et al.*, 2007; Graham, 2009; Cadena *et al.*, 2016; Chazot *et al.*, 2016; Cuesta *et al.*, 2016) and the Atlantic Forest have been studied (Damasceno *et al.*, 2014; Amaral *et al.*, 2016; Dalapicolla *et al.*, 2018). Among these works, there is no consensus in the explanations about the basic evolutionary processes/patterns acting on these regions.

### **The circum-Amazonian distribution pattern**

Despite a wide variety of proposed evolutionary and biogeographic mechanisms intended to explain Neotropical diversity, our understanding remains scarce for some of these patterns. For

instance, a considerable number of birds are distributed in those areas surrounding Amazonia but are absent from Amazonia itself (Remsens *et al.*, 1991; Bates, 1997; Lovette, 2004), and we have no clear understanding of the mechanisms responsible for those distributions. Such distributional pattern is known as the “circum-Amazonian distribution” (Figure 1) and is characterized by the presence of phylogenetically related groups mainly in “(a) *montane forested areas on the humid slopes of the Andes and the Coastal Range of Venezuela or the Tepui region; and in (b) lowland forested areas south and east of the lowland forests of Amazonia*” (Remsens *et al.*, 1991).



**Figure 1.** Circum-Amazonian distribution pattern sensu Remsens *et al.* (1991). Left map: Distribution of *Platyrinchus mystaceus* (modified from Remsens *et al.* (1991). Right map: Distribution of *Dysithamnus mentalis* (BirdLife International, 2016).

In the first study describing the circum-Amazonian pattern, Remsens *et al.* (1991) describe that species like *Platyrinchus mystaceus*, some *Hemitriccus*, *Dysithamnus mentalis*, *Phyllomyias burmeisteri*, and the *Elaenia* species *albiceps*, *parvirostris*, and *obscura*, among others, share this distributional pattern. Subsequent works have identified other taxa as circum-Amazonian. Bates (1997) stated that two species of *Tiaris*, *T. obscura* and *T. fuliginosa*, have a geographical

distribution congruent with the proposed by Remsen *et al.* (1991). Also, populations of *Phaeothlypis* (Lovette, 2004); and the species *Synallaxis ruficapilla* and *S. moesta* (Batalha-Filho *et al.*, 2013) share this pattern. Some species of genus *Cercomacra* (*C. melanaria*, *C. ferdinandi*, *C. carbonaria*, and *C. nigricans* complex) fit partially into this distributional pattern (see Tello *et al.*, 2014). In a recent study, Savit & Bates (2015) described the intraspecific genetic structure of the burnished-buff tanager (*Tangara cayana*), another ‘circum-Amazonian’ bird.

There are also examples in non-passerines such as the genus *Pionus*, in which the *sordidus-maximiliani* complex seem to exhibit complementary geographical ranges resulting in a circum-Amazonian distribution (see Ribas *et al.*, 2007). Moreover, the circum-Amazonian distribution pattern can also be found in other non-avian groups such as some insects and plants (e.g. Prado & Gibbs, 1993; Erwin, 2000; Canals & Johnson, 2000; Knapp, 2002; Irmeler, 2009).

Nevertheless, whereas the diversity and distribution patterns in adjacent Neotropical regions have been the focus of more studies, this complex pattern of distribution has not received enough attention, and the events and evolutionary processes behind it have not been thoroughly revealed.

## **Comparative Phylogeography**

Phylogeography is a relatively recent and successful field that, in a broad definition, aims at studying the geographical history of a particular clade using populations as terminals instead of species (see Avise *et al.*, 1987; Zink, 2002). Phylogeography starts with the rise of mitochondrial DNA sequencing, allowing analyses to identify genealogical patterns among individuals, and link these patterns with the geographic distributions of populations (Avise, 2009). The advent of new

mathematical and molecular tools now allows comparison of genealogical patterns (based in the estimates of gene flow/divergence among species) across different lineages/taxa ('Multi-species phylogeographic' studies) co-occurring in time and space (Hickerson *et al.*, 2010). Such multi-taxon approach is known as comparative phylogeography (Arbogast & Kenagy, 2001) and its main objective is to search for concordant splits within contemporaneous, co-distributed species (Bermingham & Avise, 1986). In this way, the level of "phylogeographic congruence is a measure of the historical stability of the current species assemblage" (Zink, 2002), namely, a particular evolutionary reconstruction (a hypothesis) on co-distributed species affected by similar climatic/geological events would be more 'supported' while more individuals phylogeographic patterns being congruent. This approach would be analog to some analyses in historical biogeography that use phylogenies and "area cladograms" of several groups to identify common biogeographic patterns across space (see Nelson & Platnick, 1981; Humphries & Parenti, 1999). Among the methodologies developed to access the level of phylogeographic congruence of co-distributed taxa, the hierarchical approximate Bayesian Computational (hABC) framework proposed by Hickerson *et al.* (2006). This methodology allows to quantify the probability of simultaneous divergence among populations/taxa, estimating demographic parameters (e.g. across-species demographic variation, divergence times, inter-gene variability in coalescent times, DNA mutation rate heterogeneity, among others, see Hickerson *et al.*, 2007) from multiple phylogeographic datasets (from these populations/taxa) in a single analysis. Posteriorly, this pipeline was upgraded to test evolutionary and biogeographical scenarios (e.g. dispersal/vicariance/extinctions); to include climatic, ecological and geological (palinological) data into the prior parameters of tested model(s); and, to allow the use of multi-locus DNA sequences data (see Huang *et al.*, 2011). This method has been widely used. For instance,

Hickerson & Meyer (2008) implemented a hierarchical approximate Bayesian computation (hABC) to test vicariance/dispersal explanations of allopatric diversification across co-distributed cowrie gastropods (Cypraeidae, Mollusca), and Bell *et al.* (2011) used five species co-distributed rainforest frogs multi-locus datasets to test evidence of single/multiple vicariance events in the Australian Wet Tropics rainforests. Recently, Robinson *et al.* (2014) applied a hABC method to infer population history from genomic data, using as example populations of *Biorhiza pallida*.

### **Ultraconserved Elements**

Initially, the empirical works in comparative phylogeography were based on the DNA information from the mitochondrial, nuclear or a few individual genes (Hickerson *et al.*, 2006). With the advent of Massively Parallel Sequencing (MPS, Shendure & Ji, 2008), the possibility to obtain multiple sets of sequences from genomes has increased (Edwards *et al.*, 2015; Edwards *et al.*, 2016).

Additionally, the use of highly conserved genomic sequences or 'ultraconserved elements' (UCEs, see Bejerano *et al.*, 2004) allows the use of a large set of universal markers to infer relationships among lineages (Faircloth *et al.*, 2012; Faircloth *et al.*, 2015). UCEs are “highly conserved regions of organismal genomes shared among evolutionary distant taxa” whose function in the genome is associated with gene regulation (Pennacchio *et al.*, 2006) and development (Sandelin *et al.*, 2004; Woolfe *et al.*, 2004). For any given UCE, levels of sequence variation increase as one moves away toward the flanking regions. Therefore, sequence data from this gradient of variation, allows sampling several levels of sequence diversity that reflect different evolutionary timescales (Faircloth *et al.*, 2012). Hence, UCEs can be used with MPS protocols to generate huge numbers of orthologous sequence data among taxonomically diverse groups. In recent reviews, Heyduk *et*

*al.* (2016) and Harvey *et al.* (2016) show the advantages/precautions in the use of the target enrichment methodologies, like as UCEs.

Since their application as molecular markers in phylogeny and evolution, the UCEs has been increasing recently. For instance, UCEs have proven to be useful in the reconstruction of phylogenetic relationships in Hymenoptera (Faircloth *et al.*, 2015), in New World Sparrows (Passerellidae, Bryson Jr. *et al.*, 2016), phylogeny and genetic relationships in the salamander *Plethodon serratus* (Newman & Austin, 2016). Also, the estimation of demographic and population parameters based on UCE data has been shown to improve relative to those based on mtDNA or other genomic markers (Smith *et al.*, 2013; Harvey *et al.*, 2013; Zarza *et al.*, 2016; Myers *et al.*, 2019).

## **Justification**

Here, I implemented a comparative phylogeographic approach to study the evolutionary history of a number of passerine birds with circum-Amazonian distribution using genomic data (UCEs). First, I tested whether these circum-Amazonian distributions are the result of a congruent history across taxa or whether it is the result of lineage-specific histories. Also was possible test whether congruent topologies are associated to dispersal and vicariance events, which allow me to do inferences on the various proposed hypotheses for Neotropical diversity (e.g. paleogeography, refugia and riverine hypotheses). Additionally, it was possible to estimate the level of influence of the environmental variables on the species of these regions, and the constraints imposed by these factors. Furthermore, the genealogical/evolutionary information of each lineage was useful to determine levels of demographic structure and the dynamics among isolated populations from the

same lineages (e.g. migration rates, speciation), which generated information on the role of lineage-specific histories and idiosyncrasies in shaping circum-Amazonian populations.

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## Chapter I

Out of northeastern Brazil: demographic and evolutionary history of the Variable Antshrike,  
*Thamnophilus caerulescens* (Aves, Thamnophilidae)

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## Abstract

The Neotropics exhibit a wealth of distributional patterns that are often shared by a number of co-distributed species. A distinctive pattern is the so-called “circum-Amazonian distribution”, which is observed in species that do not occur in Amazonia but rather in forested habitats around it forming a continuous belt that extends south and east of Amazonia, the Andean foothills, and often into the Venezuelan Coastal Range and the Tepuis. Although this pattern is widespread across a wealth of animals and plants, the historical and biogeographic mechanisms giving rise to it remain poorly understood. The Variable Antshrike (*Thamnophilus caerulescens*) is a sexually dimorphic subsocial passerine bird that is distributed along the southern portion of the circum-Amazonian belt. It comprises eight currently recognized subspecies that exhibits extreme levels of plumage variation. Our objective was to describe the phylogeographic and demographic history of *Thamnophilus caerulescens* using Ultraconserved Elements (UCEs). We inferred population structure and divergence times, as well as modeled the demographic history of the species based on comprehensive sampling across the entire distribution of the species. Structure analyses allowed to identify three genomic clusters within the species: a) northeastern Atlantic Forests; b) southeastern Cerrado, central, and southern Atlantic Forests, and c) Chacoan and Andean populations. Demographic analyses revealed a history of gene flow, mainly between birds from the central and southern Atlantic Forest, the Chacoan, and Andean populations. Differentiation took place during the Pleistocene, with a possible origin in the northern Atlantic Forest during the Pliocene. The recent diversification of the Variable Antshrike was probably affected by series of humid and dry periods throughout the Quaternary, allowing the intermittent connection between



the central-southern Atlantic Forests and the Chacoan – Andean populations, and, to a lesser extent, with the northern Atlantic Forest populations.

## Introduction

The Neotropics harbor the highest levels of species diversity and endemism across multiple taxonomic groups (Halffter, 1992; Mittermeier *et al.*, 1998; Myers *et al.*, 2000; Olson *et al.*, 2001; Dinerstein *et al.*, 2017). In general, the spatial distribution of Neotropical organisms results from large-scale geological processes, such as the uplift of the Andes, that generate opportunities for allopatric differentiation and promote diversification into novel environments (Hooghiemstra *et al.*, 2002, Graham, 2009, Hoorn *et al.*, 2010, Herzog *et al.*, 2011, Prieto-Torres *et al.*, 2018). These processes are also shaped by species' ecological affinities and dispersal abilities to disperse across barriers and persist over time (Burney & Brumfield, 2009; Smith *et al.*, 2014), resulting in a complex mosaic of distributional ranges, often shared by large numbers of co-distributed species, from which some general patterns have emerged. For instance, coarse distributional limits of South American taxa have allowed us to recognize the main domains of forested areas, such as the Atlantic Forest and Amazonia, or open areas such as the Llanos and the Cerrado (Darlington, 1957; Sánchez-González *et al.*, 2008; Morrone, 2014; Prieto-Torres *et al.*, 2018). However, there is prevalent taxon-specific and scale-dependent variation in demographic and geologic histories that obfuscate our understanding of the mechanisms driving the evolutionary history of co-existing populations (Smith *et al.*, 2014).

Distributional patterns of Neotropical birds are largely bounded by the main biogeographic domains. Yet, there are numerous instances in which several widely distributed co-occurring taxa exhibit rather odd distributions that expand beyond the boundaries of these domains. One of these common patterns is known as the circum-Amazonian distribution (*sensu* Remsen *et al.*, 1991), which largely mirrors the extend of Seasonally Dry Tropical Forests – SDTF (*sensu* Mooney *et al.*, 1995) surrounding Amazonia (Chaco, Caatinga, Interandean valleys) but that expands into

neighboring forested formations in seasonal savannah environments (Cerrado, Llanos, Pampas) and humid forests (Atlantic Forest, Andean Foothills, Guiana Shield). The circum-Amazonian distribution is shared by a considerable number of species of birds, insects, and plants (Bates, 1997; Lovette, 2004; Knapp, 2002; Irmeler, 2009) but we still lack a thorough understanding of the historical events and evolutionary processes generating this pattern.

Although a wealth of hypotheses about the origin and maintenance of diversity in the Neotropics has been proposed for the Amazonia (reviewed by Haffer, 1997), they can be relevant shed light on the circum-Amazonian patterns of distribution. For example, hypotheses based in the presence of rivers acting as barriers between populations – the Riverine Hypothesis (Sick, 1967; Capparella, 1988; Wallace, 1854) – could explain the distribution of some species with an incomplete/intermittent circum-Amazonian distribution (an idea proposed for Amazonian taxa, initially by Wallace, 1854). In the same way, the Refugia Hypothesis (Haffer, 1969; Vanzolini & Williams, 1970), that proposes that the biodiversity in Amazonia was molded by a series of climatic fluctuations during the Cenozoic producing a reduction of the Neotropical Forests, could be extrapolated to explain the diversification of species of this distribution. In addition, the combined effect of these rivers and the refugia created during the dry glacial periods in the Quaternary would be another suitable explanation for circum-Amazonia taxa (River-refuge Hypothesis Haffer, 1993). Lastly, it is possible that geological processes (tectonic movements and level sea fluctuations) influence (indirectly) the diversity/distribution of species/subspecies allowing the isolation and re-connection among the different areas of the circum-Amazonian region(s) (Paleogeography Hypothesis, Croizat, 1976).

The Variable Antshrike (*Thamnophilus caerulescens*) is a suboscine passerine that exhibits circum-Amazonian distribution. It inhabits the forest understory, second-growth woodland, and

patches of thickets and trees in more open regions, and can be found in patches of degraded remnants of forest (Zimmer & Isler, 2019). The Variable Antshrike is sexually dimorphic and exhibits extreme levels of plumage variation across its range. Hence, taxonomists have recognized a number of subspecies, some of which have been recently synonymized (see Zimmer & Isler, 2019), that exhibit clinal variation in vocalizations and plumage (Brumfield, 2005; Isler *et al.*, 2005). Although this high levels of phenotypic variation lacking clear-cut geographic structure are extraordinary in the avian world, a thorough understanding of the mechanisms giving rise to the remain poorly understood.

Ultraconserved Elements (UCEs Bejerano *et al.*, 2004) are highly conserved genomic sequences that allow the use of a large set of universal markers to infer relationships among lineages (Faircloth *et al.*, 2012; Faircloth *et al.*, 2015). The estimation of demographic and population parameters based on UCE data has been shown to improve relative to those based on mtDNA or other genomic markers (Smith *et al.*, 2013). For example, Zarza *et al.* (2018) used UCEs to identify the demographic patterns in some groups of vertebrates. In the same way, Myers *et al.* (2019) infer historical demography in a species of snakes. Also, UCEs were used to delimitation of species (Ješovnik *et al.*, 2017; Pie *et al.*, 2017).

Here, we describe the large-scale phylogeographic and demographic history of *Thamnophilus caeruleus* using genome-scale. Specifically, we used ultraconserved Elements (Faircloth *et al.*, 2012; UCEs) to a) describe the populational structure and estimate divergence times, and b) identify plausible historical and evolutionary processes responsible for generating the circum-Amazonian distributional pattern of *T. caeruleus*. Specifically, we aim at testing scenarios such as a possible isolation among their populations after an initial period of expansion due to climatic fluctuations in the Cenozoic, and assess migration events between populations during the

Quaternary. To this end, we use demographic modeling to test for different scenarios contemplating different rates and directions of migration and growth rates across populations of *T. caerulea*. In addition, we describe a plausible phylogeographic scenario of the species and propose one possible change to refine the taxonomy of this polytypic taxon. The evolutionary and demographic information of the populations of *T. caerulea* will be useful to shed light on the role of lineage-specific histories and idiosyncrasies in shaping circum-Amazonian populations.

## Final remarks

The lineages identified here for *Thamnophilus caeruleescens* are congruent with the geographical distribution of the species; having an isolate clade from northeastern Atlantic Forests, and other two with high level of admixture, plumage and vocal variation in the central-southern Atlantic Forests (plus eastern Cerrado) and Andes + Chaco. The level of admixture, times of divergence and demographic history support a scenario of recent diversification in the taxon, with climatic fluctuations during the Quaternary as its main influence. Specifically, the isolation of *cearensis* group could be increased by the presence of São Francisco River as a secondary barrier, illustrate an actual process of speciation. In this way, we think that the *cearensis* group (northern Atlantic Forest) has the potential to be considered a full taxonomic species. Finally, the species *T. caeruleescens* needs a complete taxonomic review to corroborate this affirmation.

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## Chapter II

### Comparative phylogeography of passerine birds with a circum-Amazonian distribution

#### Abstract

There are a number of common distributional patterns that have provided the foundations of our current knowledge of Neotropical biogeography. A distinctive pattern is the so-called “circum-Amazonian distribution”, which expands across the forested lowlands south and east of Amazonia, the Andean foothills, the Venezuelan Coastal Range, and the Tepuis. To date, there is no clear understanding of the processes giving rise to this distribution. To understand the evolutionary history of taxa exhibiting this pattern it is necessary to test biogeographic hypotheses offering mechanistic explanations. Comparative phylogeography allows more accurate phylogeographic hypotheses for these taxa, as well as better population genetic parameters. Comprehensive comparative studies aiming at unraveling the evolutionary and biogeographic mechanisms underlying the circum-Amazonian distribution have not been conducted yet, and only scarce descriptive information has been published. Therefore, the objective of this work was to elucidate the historical and biogeographic mechanisms underpinning circum-Amazonian distribution by performing comparative genomic analyses of a group of Suboscine passerines. Ultraconserved Elements (UCEs) were obtained for eight taxonomic groups to estimate population parameters and genealogical trees. For the *Thamnophilidae* species were inferred demographic histories with *moments*. The best models of each taxon were analyzed in a comparative framework to relate them with previously proposed biogeographic hypotheses for the Neotropics and to propose plausible

biogeographical scenarios for the circum-Amazonian pattern. The circum-Amazonian distributional pattern has two main phylogeographic units: an Andean (plus Central America region) and an eastern-forested region (Atlantic Forest ecoregion, forested areas around southeast of Amazonia), interconnected by a northern and southern corridor, allowing biotic interchanges between them (mainly from the southern) and hybridization. Species-tree analyses recovered (a) an Andean clade with two Andean subgroups in the northern Peru and central Andes, and (b) an eastern-forested clade including northern and central/southern Atlantic Forest subgroups. The demographic histories of the *Thamnophilidae* taxa suggest that diversification of the circum-Amazonian taxa have a strong influence of climatic fluctuations during the Pleistocene, with interconnected refugia allowing phenotypic/genetic differentiation but maintaining a considerable level of gene flow during varying dry/cool and warm/humid periods. In addition, the results of this work opened interesting taxonomic questions about some taxa that could be covered in the future (*T. ruficapillus/torquatus* complex, *Xiphocolaptes* complex).

## Introduction

A major breakthrough in the understanding of earth's biodiversity is the different evolutionary, biogeographical, and environmental processes affecting the distribution of the species and the response to these processes (Darlington, 1959). In this sense, it is expected that species with similar geographical distributions would have also common history of processes/events molding their habitats (Humphries & Parenti, 1999). Relatively new groups of analysis were developed in order to identify and understand the relationship between co-distributed species and the biogeographical/evolutionary processes affecting them, called as Comparative Phylogeography (CP) (Arbogast & Kenagy, 2001; Hickerson *et al.*, 2010). The main objective of CP is to search for concordant splits within contemporaneous, co-distributed species (Bermingham & Avise, 1986). In this framework, the level of "phylogeographic congruence is a measure of the historical stability of the current species assemblage" (Zink, 2002), namely, a particular evolutionary reconstruction (a hypothesis) on co-distributed species affected by similar climatic/geological events would be more 'supported' while more individuals phylogeographic patterns being congruent. The CP has been applied in the study of multiple co-distributed taxa (Barker *et al.*, 2015; Potter *et al.*, 2017), mainly in areas of interest as the Neotropics (Françoso *et al.*, 2016; Rincon-Sandoval *et al.*, 2019; Sartorato Zanchetta *et al.*, 2019).

As proved by several studies, the Neotropical biomes and ecosystems exhibit high biodiversity and a wide range of ecological/geological characteristics (Myers *et al.*, 2000; Rull, 2011; Richardson & Pennington, 2016; Dinerstein *et al.*, 2017). In this way, extensive work has been developed to explain and understand this high diversity in the Neotropics, as the processes involved in that phenomenon, arising a varying number of hypotheses, based in both theoretical



and empirical approaches (e.g. Sick, 1967; Haffer, 1969; Vuilleumier, 1971; Brown, 1979; Cracraft, 1985; Hooghiemstra & van der Hammen, 1998; Garzón-Orduña *et al.*, 2014). These hypotheses cover proposals from ecological perspectives like the Gradient Hypothesis (Endler, 1982) to those based on geographical isolation as Refuges (Haffer, 1969; Vanzolini & Williams, 1970) and Rivers (see Wallace, 1854; Sick, 1967), and Paleogeographic ones as the Arch and the Lagoon Hypotheses (Patton & Silva, 1997; Marroig & Cerqueira, 1997). All these hypotheses have been subject to wide discussion, and several tests have been implemented to corroborate or refute their assumptions (Mayr & O’Hara, 1986; Salo, 1987; Nores, 1999; Loughheed *et al.*, 1999; Colinvaux *et al.*, 2000; Haffer, 2008; FernAndes *et al.*, 2012; Maldonado-Coelho *et al.*, 2013; Garzón-Orduña *et al.*, 2015; Rocha & Kaefer, 2019, among others).

Despite the large variety of proposed evolutionary and biogeographic mechanisms intended to explain Neotropical diversity, our understanding remains scarce for some of these patterns. For instance, a considerable number of birds are distributed in the surroundings of the Amazonia but they are absent in the Amazonia itself (Remsens *et al.*, 1991; Bates, 1997; Lovette, 2004), and there is no clear understanding of the mechanisms involved in that kind of distributions. Such distributional pattern is known as “circum-Amazonian distribution” (Figure 1) and is characterized by the presence of phylogenetically related groups mainly in “(a) montane forested areas on the humid slopes of the Andes and the Coastal Range of Venezuela or the Tepui region; and in (b) lowland forested areas south and east of the lowland forests of Amazonia” (Remsens *et al.*, 1991). Remsens *et al.* (1991), in the first study describing the circum-Amazonian pattern, described that species as *Platyrinchus mystaceus*, *Hemitriccus* spp., *Dysithamnus mentalis*, *Phyllomyias burmeisteri*, and *Elaenia albiceps*, *E. parvirostris*, and *E. obscura*, among others, share this distributional pattern. Subsequent works have identified other taxa as circum-

Amazonian. Bates (1997) stated that two species of *Tiaris*, *T. obscura* and *T. fuliginosa*, have a geographical distribution congruent with the proposed by Remsen *et al.* (1991). More examples of species exhibiting this circum-Amazonian pattern were presented by Lovette (2004) in the case of *Phaeothlypis* and by Batalha-Filho *et al.* (2013) in *Synallaxis ruficapilla* and *S. moesta*. Additionally, some species of *Cercomacra* (*C. melanaria*, *C. ferdinandi*, *C. carbonaria*, and the *C. nigricans* complex) and *Tangara cayana* fit partially into this distributional pattern (see Tello *et al.*, 2014; Savit & Bates, 2015). There are also examples in non-passerines such as the genus *Pionus*, in which the *sordidus-maximiliani* complex seem to exhibit complementary geographical ranges resulting in a circum-Amazonian distribution (see Ribas *et al.*, 2007). Moreover, the circum-Amazonian distribution pattern was identified in other non-avian groups such as some insects (references related to insects) and plants (references related to plants) (e.g. Prado & Gibbs, 1993; Erwin, 2000; Canals & Johnson, 2000; Knapp, 2002; Irmiler, 2009). Nevertheless, whereas the diversity and distribution patterns in adjacent Neotropical regions have been the focus of several studies, this complex pattern of distribution has not received enough attention, and the events and evolutionary processes behind it have not been thoroughly revealed.

Here, we implemented a comparative phylogeographic approach to infer common evolutionary histories from eight taxa of Passeriformes with circum-Amazonian distribution, using genomic information from Ultraconserved Elements (UCEs, Bejerano *et al.*, 2004). The UCEs are highly conserved genomic sequences that allow the use of a large set of universal markers to infer relationships among lineages (Faircloth *et al.*, 2012; Faircloth *et al.*, 2015), and they can be used to estimate demographic and population parameters (Smith *et al.*, 2013; Zarza *et al.*, 2018; Myers *et al.*, 2019; Oswald *et al.*, 2019). We estimated the populational parameters and demographic history for each species, followed by the comparative analysis of their evolutionary histories.

Lastly, we proposed plausible scenarios in order to explain the formation of this distributional pattern based mainly in the proposed hypotheses of diversification for the Neotropics.

## Conclusions

In this first phylogeographic comparative approach to the understanding of the circum-Amazonian distributional pattern using genomic data of Passerines, we found general congruence among the populational structure, phylogenetic relationships, and demographic histories of the taxa analyzed. We defined two main units: the Andean and the Brazilian forested phylogeographic region(s), disjointed complete or partially via a **northern** (northern Andes  $\leftrightarrow$  Tepuis  $\leftrightarrow$  Atlantic Forest) or **southern interconnection** (southern Atlantic Forest  $\leftrightarrow$  central Andes). Contact zones among clusters included individuals with considerable levels of admixture, supports the possibility of events of hybridization among populations, mainly in the northern – southern interconnections. Species trees analyses inferred well-supported clades from central/southern and northern Atlantic Forest populations. In the same way, we identified central Andean clades (northern Peru and central Peru - Bolivia), but a bigger sampling effort will be necessary in the north Andean region. Demographic histories of the *Thamnophilidae* taxa seems to be product of a recent diversification with climatic fluctuations throughout the Quaternary as its main influence, fitting into a Refugia context previously proposed by other authors. However, at least to *D. mentalis* and the *Thamnophilus palliatus/tenuepunctatus* complex, alternative hypotheses (like corridors of STDfS vegetation during the Pleistocene) could not be discarded. In addition, our results raise new question about the taxonomy and systematics of the circum-Amazonian species (the *T. ruficapillus/torquatus*, *T. palliatus/tenuepunctatus*, and the *Xiphocolaptes* complexes). Future studies about the circum-Amazonian distribution have to cover other taxonomic groups outside Aves, phenotypic and ecological data, and the implementation of comparative methodologies that

can include all those parameters for estimation of demographic/evolutionary scenarios that explain in deep the past and current dynamics of the circum-Amazonian distributional pattern.

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