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Life history and ecology might explain incongruent population structure in two co-distributed montane bird species of the Atlantic Forest

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ABSTRACT

Comparative phylogeography is a powerful approach to investigate the role of historical and environmental processes in the evolution of biodiversity within a region. In this regard, comparative studies of species with similar habitat preferences are valuable to reduce the confounding influence of habitat association when interpreting phylogeographic patterns. In the Atlantic Forest of South America, phylogeographic studies of highland and lowland species have shown distinct population structure patterns so far, suggesting that such species have responded differently to Pleistocene glacial cycles. Herein, we performed a comparative analysis using molecular data and paleodistribution models of two Montane Atlantic Forest (MAF) co-distributed passerine birds with similar habitat requirements but with distinct life-history traits and ecologies: the frugivore lek-breeding Blue Manakin (*Chiroxiphia caudata*) and the insectivore and socially monogamous Drab-Breasted Bamboo Tyrant (*Hemitriccus diops*). We aimed to shed light on the role of contrasting life histories and ecologies onto the demography and population structure of MAF species. We sampled both species throughout most of their distribution range, sequenced a mitochondrial and a nuclear molecular marker, and used standard phylogeographic methods to investigate population structure and ecological niche modeling (ENM) to infer the species' paleodistributions. Our analyses recovered a phylogeographic break in *H. diops* in the region of the Doce River, but no genetic structure in *C. caudata*. We also found higher differentiation among subpopulations within each lineage of *H. diops* than among subpopulations of *C. caudata*. We suggest that these discrepancies in population structure might be due to distinct life-history traits and their impact on gene flow and generation time. For example, while *H. diops* is an insectivore species, *C. caudata* is a frugivore and the latter ecological aspect likely selects for a higher dispersion distance. Additionally, because *C. caudata* is a lek-breeding species, it has a longer generation time than *H. diops*. These traits could hinder genetic differentiation when populations become geographically isolated. Nonetheless, both species showed some common biological features, such as signatures of synchronous population expansion and larger distribution ranges during the Last Glacial Maximum, possibly due to similar cold tolerance.

1. Introduction

Comparative phylogeography is a powerful approach to understand how co-distributed species responded to historical events within a region (Avise et al., 2016; Prates et al., 2016; Riddle, 2016), including the important links between population processes and regional patterns of diversity (Bermingham and Moritz, 1998). Congruent phylogeographic structures among co-distributed species are most likely explained by similar responses to the same biogeographical and environmental processes, while discordant patterns indicate independent responses (Bermingham and Avise, 1986; Bermingham and Moritz, 1998; Avise, 2000; Arbogast and Kenagy, 2001; Zink et al., 2001; Hickerson et al., 2010). In this context, discrepancies in phylogeographic patterns among co-distributed species could result from differences in (i) colonization time of a given region, (ii) response to geographic barriers, (iii) selective gradients, (iv) gene flow levels, (v) rates of molecular

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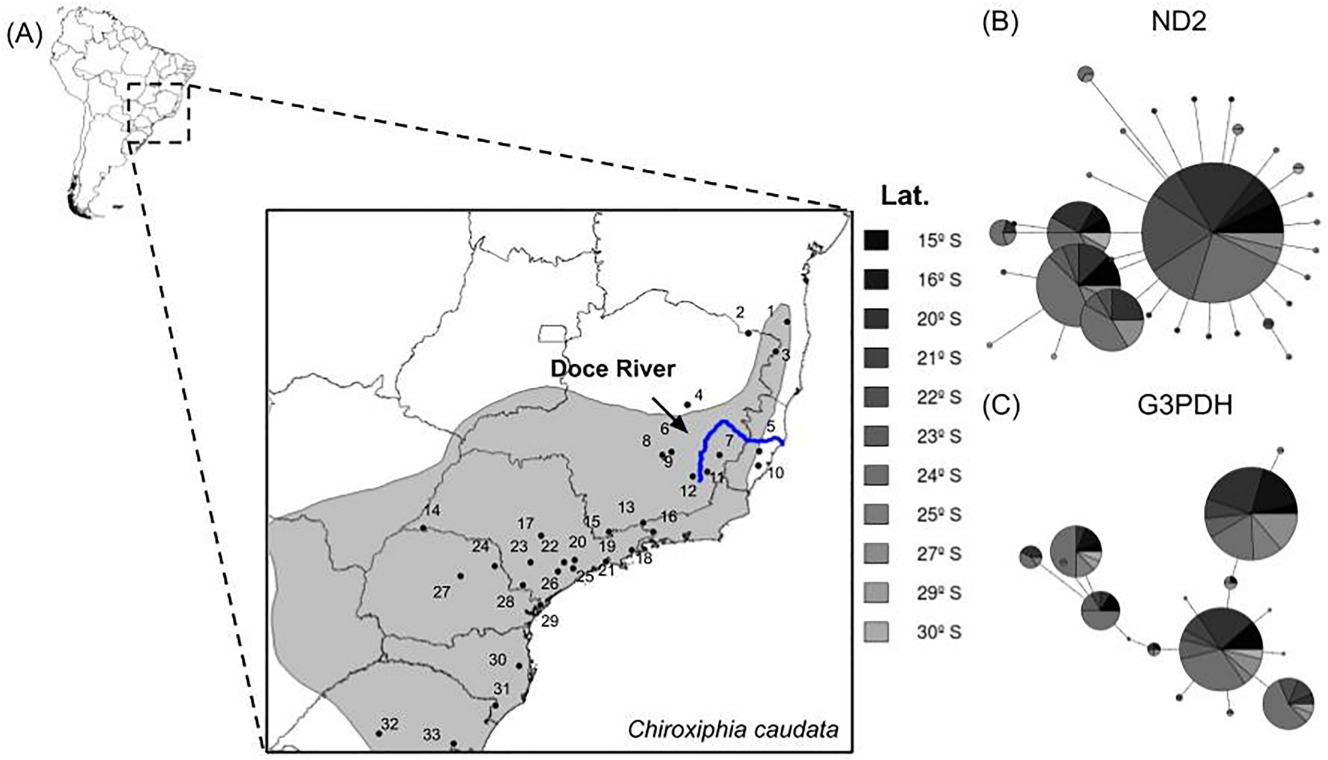

Fig. 1. Sampling localities and haplotype network for *Chiroxiphia caudata*. (A) Map with sampling localities. The gray area represents the distribution range for *C. caudata* and the dots represent the sampled localities. Numbered localities are listed on Supp. Mat 1. (B) Mitochondrial ND2 haplotype network and (C) nuclear G3PDH haplotype network, colored according to the latitude of each locality.

evolution, (vi) effective population sizes and (vii) generation time (Zink, 1996). However, phylogeographic incongruences among co-distributed species inhabiting similar habitats may also result from other aspects of organisms' biology and testing congruence among organisms that differ in their life-history traits can shed light onto the role of ecology in the diversification process (Ditchfield, 2000; Sullivan et al., 2000; Gutiérrez-García and Vázquez-Domínguez, 2011; Paz et al., 2015). In fact, recent conceptual frameworks in comparative phylogeography emphasize the contribution of biological attributes as an important factor to explain phylogeography patterns, as opposed to emphasis mostly on historical events (Papadopoulou and Knowles, 2016; Zamudio et al., 2016).

The role of life-history and ecology on the phylogeographic patterns of tropical organisms is still largely unexplored, including in montane systems. Tropical montane regions are considered a cradle of biodiversity and their elevated diversity is often explained by the interplay between historical climate changes and complex topography creating many opportunities for allopatric differentiation as well as by high population persistence in pockets of habitats that remain stable over time, thereby decreasing the likelihood of population extinction (Fjeldså et al., 2012). Specifically, as the climate became warm during interglacial periods, suitable habitat for mountain species likely shifted upwards and their inability to cross warm valleys promoted genetic isolation (Wiens, 2004; Kozak and Wiens, 2006; Knowles and Massatti, 2017). The interplay between glacial cycles and topography can be important in the diversification of montane species with narrow thermal breadth, as is likely the case of tropical species (Janzen, 1967; Polato et al., 2018).

Such biogeographic processes are often invoked to have had an important role in the building up of the astonishing diversity found in Neotropical mountain regions (Fjeldså et al., 2012; Antonelli, 2015). However, their importance in promoting and maintaining biodiversity is still largely unknown in the Montane Atlantic Forest (MAF). These montane forests along the eastern edge of South America can reach up to 2500 m a.s.l. and hold a high degree of biological endemism (Stotz et al., 1996). Even though a blossoming body of research on phylogeography in the last decade has investigated the processes originating and maintaining biodiversity in the Atlantic Forest (AF) (e.g. Cabanne et al., 2008; Carnaval et al., 2009; Maldonado-Coelho, 2012; Raposo do Amaral et al., 2013), few have studied the evolutionary history of MAF organisms (but see Amaro et al., 2012; Batalha-Filho et al., 2012; Raposo do Amaral et al., 2018b). Highland and altitudinal generalist species, due to their distinct climate ranges, and therefore likely distinct climate tolerances, could have distinct responses to historical processes such as Pleistocene glacial cycles. In fact, the distinct diversification patterns found so far in MAF organisms have been attributed either to orogenic activity or the interplay between historical climate changes and the complex topography of the region (Raposo do Amaral et al., 2018b). On the other hand, processes advocated to explain phylogeographic patterns of organisms with broad elevational ranges rely mostly on the role of range fragmentation and genetic differentiation due solely to historical climate changes (e.g. Cabanne et al., 2008; Maldonado-Coelho, 2012). This illustrates how highland and altitudinal generalist species could have distinct responses to the Pleistocene glacial cycles that result in discrepant diversification histories.

Phylogeographic comparisons across organisms with broadly similar habitat associations and congruent geographic distributions are valuable to reduce the confounding influence of environmental factors such as habitat dependence and climatic variation on patterns of population differentiation. In this regard, we aimed to perform a comparative analysis using molecular data and paleodistribution models of two forest dependent and co-distributed MAF passerine birds but with distinct life-history traits and ecologies: the Blue Manakin (*Chiroxiphia caudata*) and the Drab-Breasted Bamboo Tyrant (*Hemitriccus diops*). These species occur in the understory and mid-story of forests and range from the northernmost montane forests in the state of Bahia into lower elevation forests in the state of Rio Grande do Sul in Brazil, eastern Paraguay and northeastern Argentina (Fig. 1). *C. caudata* and *H. diops*

can be found up to 1800 and 1500 m.a.s.l., respectively (Mallet-Rodrigues et al., 2010). Despite their largely sympatric distribution, the two species differ in some life-history and ecological attributes: *C. caudata* is a species with a lek mating system while *H. diops* seems to be a socially monogamous and territorial species; *C. caudata* is a frugivore generalist whereas *H. diops* is insectivorous (Ridgely et al., 1989; Parrini, 2015). To our knowledge this is the first comparative analysis throughout the range of two sympatric AF endemic bird species, allowing us to explore whether species with similar current range distribution and habitat dependence responded in a similar fashion to the same historical events. Given their similar ranges and level of forest dependence, differences in their phylogeographical patterns could be related to distinct life-histories and ecologies. Thus, we address the following questions: (1) do they have similar population structure?, (2) was their genetic structure shaped by the same historical processes?, and (3) have they experienced synchronous historical population size changes? Overall, we aimed to shed light onto the role of cold tolerance and distinct species' ecology in recent diversification events of the MAF biota.

2. Materials and methods

2.1. Sampling

We gathered samples throughout most of the geographical distribution of both species: 115 individuals of *C. caudata* from 33 localities (Fig. 1, Suppl. Mat. 1) and 80 individuals of *H. diops* from 21 localities (Fig. 2, Suppl. Mat. 2). The genetic samples consisted of blood and tissues collected specifically for this project, loans from other institutions and one sequence for each species available in GenBank (see Acknowledgements for collecting permit numbers and Suppl. Mat. 1 and 2 for GenBank accession numbers, specimen and tissue collection holdings).

2.2. Molecular markers and molecular analyses

We used two molecular markers: the mitochondrial gene NADH dehydrogenase subunit 2 (ND2) and the intron 11 of the nuclear gene glyceraldehyde 3-phosphate dehydrogenase (G3PDH). Total DNA was extracted with a protocol using phenol, chloroform, and isoamyl alcohol (modified from Bruford et al., 1992). The quality and amount of the DNA extraction were checked by electrophoresis in 1% agarose gel. High-quality extractions were diluted to ~20 ng/μl for subsequent analyses.

DNA amplification through PCR consisted in a mix containing 2.5 μl 10x buffer (Tris-HCl 10 mM pH 8.3, KCl 50 mM, $MgCl_2$ 2.5 mM), 1 μl dNTP (2 mM of each nucleotide), 1 μl of each primer (10 μM), 18.4 μl of Milli-Q water, 0.1 μl of *Taq* polymerase (5 U/μl, GE Health Care), and 1 μl of DNA. The primers used for each reaction were: LMet (Ribas et al., 2005) and H6313 (Sorenson et al., 1999) for the ND2, and GAPDL890 and GAPDH950 (Friesen et al., 1997) for the G3PDH. PCR was performed using TC9600 and TC9700 thermocyclers (Applied Biosystems) under the following conditions: initial denaturation at 94 °C for 4 min; 40 cycles of 95 °C for 1 min, varying annealing temperature for 30 s, and 72 °C for 40 s; and final extension at 72 °C for 9 min. For the ND2, a touch-down PCR was performed with temperatures decreasing from 60 °C to 50 °C by 1 °C per cycle. For the G3PDH, the annealing temperature was kept constant at 56 °C throughout the cycles. Amplification success was checked with gel electrophoresis and amplified DNA was purified with polyethylene glycol 20% (Paithankar and Prasad, 1991) or with Exonuclease I (Fermentas, 20 U/μl) and FastAP Alkaline Phosphatase (Fermentas, 1 U/μl) mixed at 1:4 proportion.

DNA sequencing was performed with Sanger sequencing using Big

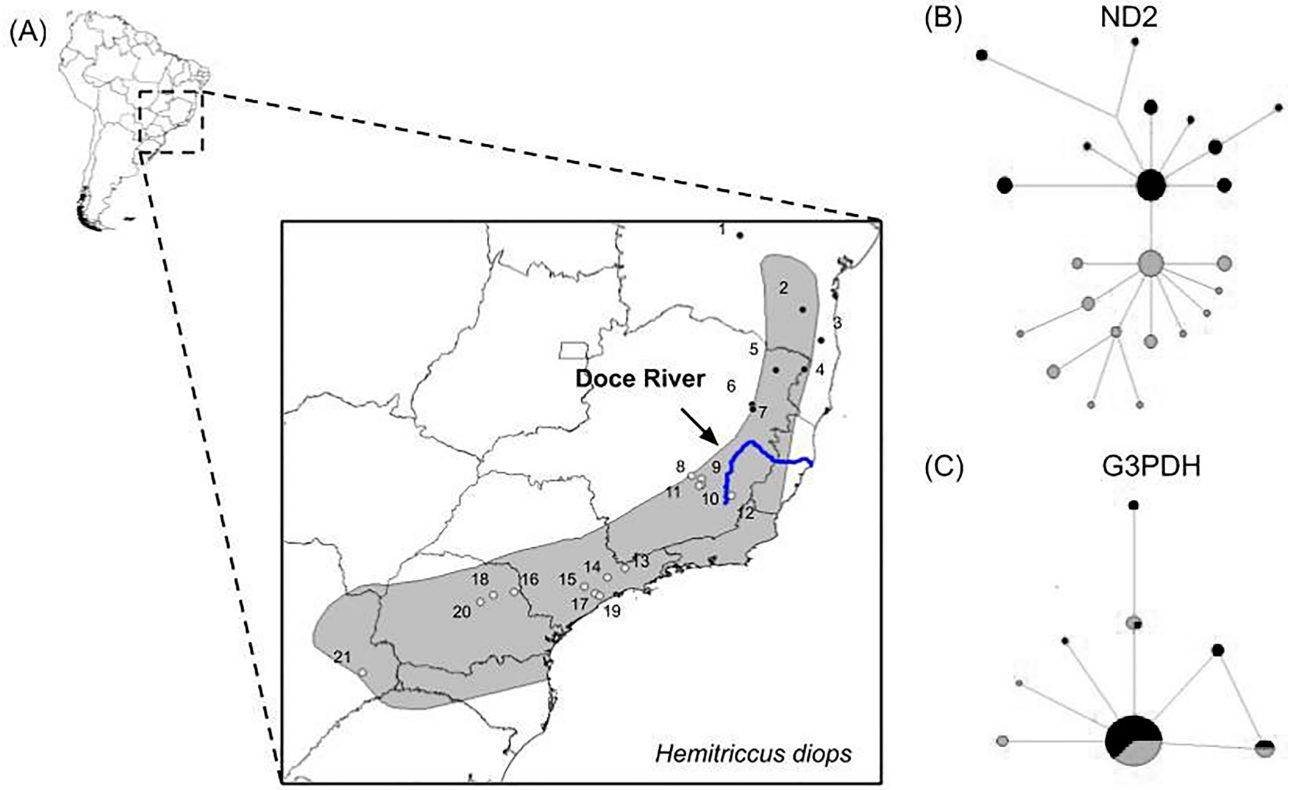

Fig. 2. Sampling localities and haplotype network for *Hemitriccus diops*. (A) Map with sampling localities The gray area represents the distribution range for *H. diops* and the dots represent the sampled localities and the location of haplogroups. Numbered localities are listed on Supp. Mat 2. (B) Mitochondrial ND2 haplotype network and (C) nuclear G3PDH haplotype network, colored according to each of the two distinct haplogroups identified in the ND2 haplotype network.

Dye Terminator Cycle Sequencing Kit (Applied Biosystems) with the same primers used in the PCR. After the reaction, the product was precipitated by washing it first with 80 μl of isopropanol 75% and then with ethanol 70%. The reaction was analyzed using automated genetic analyzers (ABI 3100 or ABI 3130, Applied Biosystems).

2.3. Data analysis

Sequence chromatograms were analyzed and contigs were produced using CodonCode Aligner 3.6.1 (CodonCode Corporation). We used CLUSTAL W (Thompson et al., 1994), as implemented in the software MEGA 5 (Tamura et al., 2011), to align the contigs. For the ND2 sequences, we used MEGA 5 to translate them and verify the existence of unexpected stop codons and to check their nucleotide composition, as expected for mtDNA. For G3PDH, we used PHASE (Stephens et al., 2001), as implemented in DnaSPv5 (Librado and Rozas, 2009), to determine their gametic phase. Individuals with gametic phases determined with probability lower than 80% were removed from the subsequent analyses. We used the PHI test, implemented in the software SplitsTree (Huson and Bryant, 2006), to check for the presence of recombination in our samples. The PHI test was chosen due to its robustness to the presence of potential population expansion (Bruen et al., 2006).

2.4. Population structure and demographic history

The phylogeographic structure was inferred by the haplotype network, constructed for each marker using the Median-Joining method (Bandelt et al., 1999) in the software NETWORK 4.5.1.0 (http://fluxus-engineering.com). The haplotypes were colored based on the samples' geographic location. We also used an Analysis of Molecular Variance (AMOVA) to investigate the presence of structure among our populations. AMOVA was performed using Arlequin 3.5 (Excoffier and Lischer, 2010). For *H. diops*, given that the ND2 haplotype network revealed two genetically distinct lineages, we used a hierarchical AMOVA, nesting the localities within the two lineages. AMOVA was performed using localities that had three or more sampled individuals, and the genetic distance was calculated based on Φ_{ST} (Excoffier et al., 1992).

We measured genetic diversity using the following summary statistics: number of segregating sites (S), haplotype diversity (Hd), number of haplotypes (h), and nucleotide diversity (π). We generated Bayesian Skyline Plots to infer demographic history in both species. However, they were unreliable due to large error estimates in all cases and are not presented here. Thus, to test for changes in population size we used the Fu's Fs (Fu, 1997) and the R_2 (Ramos-Onsins and Rozas, 2002). All the summary statistics were calculated with DnaSPv5. For *H. diops*, we measured all the summary statistics for each lineage independently.

2.5. Ecological niche modeling

We used MaxEnt 3.4 (Phillips et al., 2006) to create the Ecological Niche Models (ENM) of *C. caudata* and *H. diops*. These models were used to infer their distribution at current conditions, the Medium Holocene (MH,~0.006 mya), the Last Glacial Maximum (LGM, ~0.022 mya), and the Last Interglacial (LIG; ~0.12–0.14 mya). For the MH and LGM, we only used the Atmospheric Oceanic Global Circulation Models (AOGCM) available for both of these time points, namely: CCSM4, MIROC-ESM, and MPI-ESM-P, developed through Coupled Model Intercomparison Project Phase 5 (CMIP5) (https://esgf-node.llnl.gov/projects/cmip5/). We used occurrence points from the localities sampled herein, localities from individuals deposited at the Zoology Museum of the University of São Paulo (MZUSP), and the online biological collection databases speciesLink (http://www.splink.org.br) and GBIF data portal (http://www.gbif.org/). We obtained 214 points of occurrence for *C. caudata* and 61 points for *H. diops*. Some individuals had imprecise data of collecting localities and additional information was harvested in the Ornithological Gazetteer of Brazil (Paynter and Traylor, 1991). Only one record per geographical coordinate was used. We visually analyzed the coordinate points on DIVA-GIS (Hijmans et al., 2004), to reduce the likelihood of including points outside the known species´ range. To reduce the impact of sample collection bias (bias arising from some places being more densely sampled than others), we randomly subsampled the occurrence points to guarantee that only one coordinate per 0.5° × 0.5° grid was used. To obtain the accuracy of models, we used 75% of the records as training samples and the remaining 25% as test samples and calculated area under the curve (AUC) values for the training and test models. We generated five replicates of each model.

To generate our ENM we used seven Bioclim variables at 2.5 arcmin resolution (~4.5 km at the Equator). We decided not to use the 19 Bioclim variables to reduce collinearity problems during model construction (Terribile et al., 2012), and selected seven variables that showed low correlation. Then, we used the variables mean diurnal range, temperature seasonality, maximum temperature of the warmest month, precipitation of wettest month, precipitation of driest month, precipitation seasonality, and precipitation of warmest quarter. We cropped the Bioclim layers to only represent South America (between latitudes 14°N and 57°S, and longitudes 30°W and 85°W). For each variable, we also calculated the mean value for each cell across different AOGCMs for a period (in MH and LGM) using the raster package (Hijmans and van Etten, 2014) in R 3.4.4. We chose this approach in order to yield a single paleodistribution model for each period (instead of a different model for each AOGCM).

3. Results

3.1. Molecular data

For *C. caudata*, we obtained sequences of 932 bp from 102 individuals of the mitochondrial marker ND2 and 303 bp from 82 individuals of the nuclear marker G3PDH. For *H. diops*, we obtained sequences of 910 bp from 66 individuals of the mitochondrial marker ND2 and 323 bp from 60 individuals of the nuclear marker G3PDH. We only retained sequences of G3PDH with high phasing probabilities: 63 individuals of *C. caudata* and 44 individuals of *H. diops*. The PHI test indicated that no signal of recombination was detected on the G3PDH for *C. caudata* ($p = 0.16$). However, recombination was detected in *H. diops* ($p = 0.023$) and we selected a non-recombinant fragment of 66 bp that had the highest level of polymorphism (eight haplotypes).

3.2. Phylogeographic structure

The haplotype network of the ND2 did not reveal a clear phylogeographic structure for *C. caudata* (Fig. 1). On the other hand, the ND2 haplotype network for *H. diops* recovered a phylogeographic break near the Doce River, with one phylogroup north (herein Northern lineage) and another mostly south (Southern lineage) of this river (Fig. 2). The two groups are separated by one mutation between the central and most common haplotypes in each lineage. No haplotype sharing was detected in the same locality. However, Southern lineage haplotypes were also recovered at both sides of the tributaries of the Doce River in the headwater region (Fig. 2). Haplotype networks for the G3PDH did not recover phylogeographic structure for any species. Similar results were found with AMOVAs. For *C. caudata*, we did not find significant structure among the populations with ND2 ($\Phi_{ST} = 0.002$, $p > 0.05$) and although we found a significant signature of structure with G3PDH ($\Phi_{ST} = 0.094$, $p < 0.01$), the low Φ_{ST} showed that most of the genetic variation was contained within populations rather than among them. For *H. diops*, we detected significant structure between the two lineages in the ND2 AMOVA ($\Phi_{CT} = 0.391$, $p < 0.01$) but not for the G3PDH AMOVA ($\Phi_{CT} = -0.009$, $p > 0.05$). However, we did detect

Table 1
Summary statistics per lineage for each molecular marker. N = sample size. S = number of substitutions. h = number of haplotypes. Hd = haplotype diversity. π = nucleotide diversity. sd = standard deviation. Fs and R_2 = population expansion tests.

Species	Lineage	Marker	N	S	h	Hd (sd)	π (sd)	Fs	R_2
C. caudata		ND2	102	36	30	0.88 (0.02)	0.0028 (0.0002)	−29.12**	0.02**
		G3PDH	126	10	14	0.86 (0.02)	0.0077 (0.0004)	−2.93	0.12
H. diops	North	ND2	36	14	13	0.88 (0.04)	0.0024 (0.0003)	−6.28**	0.065*
		G3PDH	52	4	6	0.37 (0.08)	0.0071 (0.0019)	−3.43*	0.064
	South	ND2	35	13	14	0.88 (0.04)	0.0020 (0.0002)	−9.49**	0.055**
		G3PDH	36	4	5	0.54 (0.09)	0.0094 (0.0019)	−1.72	0.081

significant structure among populations within the lineage groups with both markers in this species (for the ND2, $\Phi_{SC} = 0.134$, $p < 0.01$; for the G3PDH, $\Phi_{SC} = 0.136$, $p < 0.01$). Overall Φ_{ST} (i.e. structure among all populations), also was significant for both markers (for the ND2, $\Phi_{ST} = 0.473$, $p < 0.01$; for the G3PDH, $\Phi_{ST} = 0.128$, $p < 0.01$).

3.3. Demographic history

Given that no phylogeographic structure was found for *C. caudata*, the following analyses were performed assuming that all samples belonged to a single panmictic population. On the other hand, since *H. diops* presented a phylogeographic structure, the following analyses considered samples as part of either the Northern lineage or the Southern lineage. Signatures of population expansion were detected with Fu's Fs and R_2 for the ND2 in all groups: all samples of *C. caudata* and both lineages of *H. diops* (Table 1). In G3PDH, only Fs for Northern lineage of *H. diops* exhibited significant evidence of population growth (Table 1).

3.4. Ecological niche modeling

Our ENMs exhibited good accuracy, as evidenced by the area under the curve values (AUC ≥ 0.9). For *C. caudata*, the current distribution is mostly south of the Doce River with lower probability of occurrence north of the river. There were overall larger suitable areas during the LGM, but mostly on the continental shelf which was above the sea level at the time (Fig. 3). During the LIG, the suitable area was smaller than today and mostly in the southern part of the current distribution. For *H. diops*, the current model predicts more suitable areas as being south of the Doce River. The LGM model indicates a larger past distribution, with two isolated areas of high suitability on both sides of the Doce River. The LIG model shows a smaller distribution, mostly south of the Doce River. In this species, the models also predict the existence of suitable habitats in continental shelf areas (Fig. 3).

4. Discussion

Our study is the first to compare the phylogeography of two co-distributed bird species across their range in AF. We identified that they exhibit discordant and concordant population history aspects. On one hand, they differ in their phylogeographic structure, with one species presenting a shallow but clear phylogeographic break (*H. diops*) while the other exhibiting no population structure (*C. caudata*). Additionally, the subpopulations of *C. caudata* are less differentiated from each other than the subpopulations within each *H. diops* lineage. This suggests that despite occupying high elevation forests and being cold-tolerant, these species have responded distinctively to the same historical events. On the other hand, Fs and R_2 statistics suggested that both species experienced population expansion. These results and the paleodistribution models imply a common demographic response to an underlying expansion of the forest during the LGM. Our results also suggest that differences in life-history and ecological traits may explain the contrasting phylogeographic structures and that cold-tolerance itself seems to be of less importance as a driver of population differentiation. In the following, we further discuss the processes likely underlying the commonalities and discrepancies in the population histories of these species.

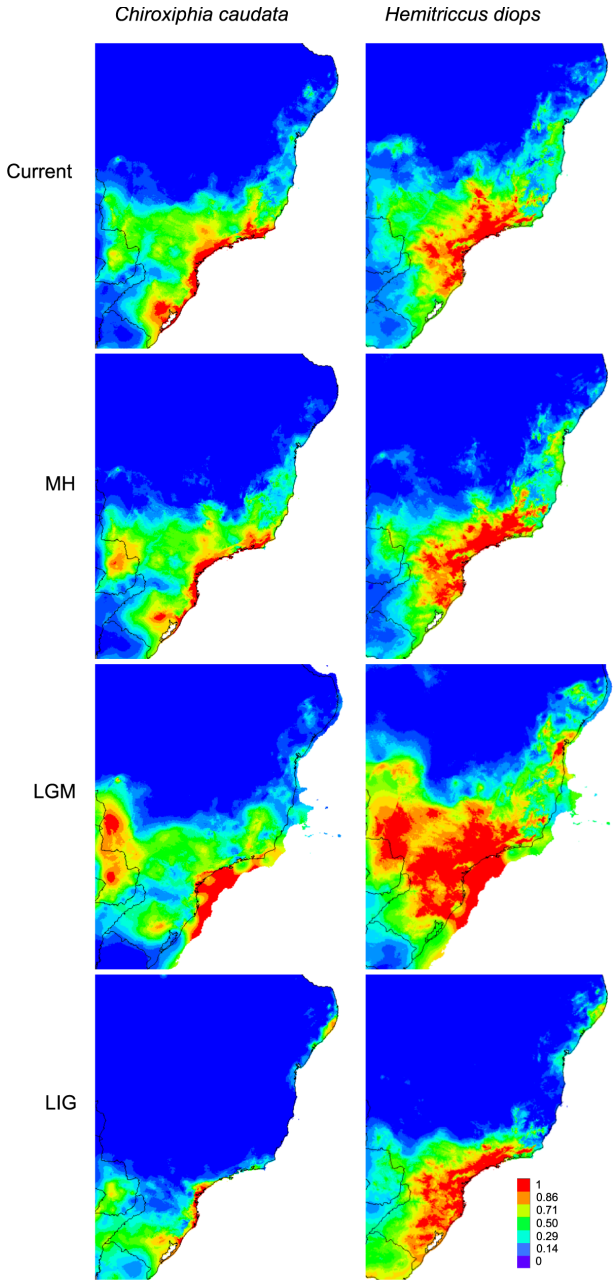

Fig. 3. Ecological niche models (ENMs) of the Montane Atlantic Forest birds *Chiroxiphia caudata* and *Hemitriccus diops* for current conditions, mid Holocene (MH), last glacial maximum (LGM), and last interglacial (LIG). Warmer colors indicate a higher species suitability, as depicted in the legend.

4.1. Phylogeographic discordance between species

The incongruent phylogeographic structure recovered might be related to species differences in life history and ecology. Specifically, population structure could have been influenced by distinct levels of philopatry as a consequence of diet and mating system. In our study, while *H. diops* mostly feeds on insects on bamboo leaves, *C. caudata* is a frugivorous species (Parrini, 2015). Also, *C. caudata* is a lek-breeding species whereas *H. diops* is seemingly territorial and does not form leks. Frugivorous species are expected to have higher dispersal distances since this is a more ephemeral food resource in time and space (Levey and Stiles, 1992). Likewise, frugivorous birds, including manakin species, are known to exhibit elevational seasonal movements in the neotropics (Loiselle and Blake, 1991; Boyle, 2008; Barçante et al., 2017). It is unknown if *C. caudata* performs altitudinal movements in the Atlantic Forest, but a congeneric species, *Chiroxiphia boliviana*, apparently migrates upslope during the breeding season in the Bolivian Andes (Villegas et al., 2016). In addition, females in lekking species have to visit several leks in an area before mating (Foster, 1981), and the need to visit many leks could select for higher dispersal distances in females of lek-breeding species relative to non-lekking, territorial species. These behaviors, in turn, could have increased gene flow among different subpopulations in *C. caudata*, leading to no phylogeographic structure in this species. This is further supported by our AMOVA results, which indicate that populations of *C. caudata* are less differentiated from each other than populations within each *H. diops* lineage. In fact, high philopatry level can directly affect genetic differentiation in a micro-evolutionary scale (Wright, 1943; Wakeley and Aliacar, 2001), and populations of species with higher dispersal have been shown to be less differentiated than populations from species with lower dispersal (e.g. canopy *vs*. understory species, Burney and Brumfield, 2009; Smith et al., 2014). Thus, a higher propensity to disperse in frugivorous and lek-breeding species could partially explain the discordance in the phylogeographic structure of *C. caudata* and *H. diops*.

Mating system can also have a direct effect on generation length, which as a result may influence levels of divergence. The structure of leks was studied in another closely related *Chiroxiphia* species whose males have an average tenure time to attain alpha status of approximately 10 years (McDonald, 1993). In contrast, females start breeding when 2–3 years old and have a generation time of 4.9 years (McDonald, 1993), which is about three times larger than the average generation time of non-lekking passerine birds (ca. 1.7 years; Saether et al., 2005). The presumed longer generation time of *C. caudata* relative to *H. diops* means that both sexes in the first would have experienced fewer generations if isolated by any given biogeographical event. Consequently, isolation time in allopatry would be shorter in *C. caudata* and could not have been long enough to leave a genetic signature (i.e. detectable with two molecular markers). In contrast, the shorter generation time of *H. diops* could have favored the accumulation of differences between geographically isolated populations. This is true even if we consider that the discrepancy in generation time is larger between males than between females of *C. caudata* and *H. diops*, which would impact mostly the divergence and geographical structure of nuclear genes. Indeed, differences in female generation length between these species are likely large enough to have influenced population differentiation in the mtDNA.

Lek-breeding systems also result in a very skewed sex ratio in reproductive success. Although most females are expected to reproduce successfully, mainly the alpha males of each lek will reproduce at a given time (Foster, 1981; DuVal and Kempenaers, 2008). In addition, a significant proportion of male birds die before they could even reach the alpha status, hence further increasing the distortion between the sexes in their genetic contribution to the next generation (McDonald, 1993). This skewed sex ratio reduces effective population size and therefore can increase the magnitude of genetic drift. In a scenario of strong drift, two isolated populations are expected to differentiate from each other at a faster rate. Therefore, when comparing systems with high (i.e. *C. caudata*) and supposedly no (i.e. *H. diops*) skews in mating number towards males, the former is predicted to exhibit stronger genetic structure in nuclear genes. However, a skewed reproductive success restricted to males is not expected to influence the geographic variation in mtDNA. Here, we did not recover meaningful nuclear genetic differentiation across geography in any of the two species and our results may suggest that other factors, such as the ones discussed above, were likely more important in explaining discrepancies in phylogeographic structure. Finally, one cannot rule out that this only reflects low resolution in individually sequenced nuclear genes (e.g. Raposo do Amaral et al., 2018a); hence, a proper test of this idea would await a genomic analysis.

Alternatively, observed differences in phylogeographic structure can be a result of geographically distinct patterns of isolation in glacial refugia. The ENM projection to the LGM (Fig. 3) shows a high probability of occurrence of *H. diops* in two refugia and lower probability of occurrence of *C. caudata* to the north of the Doce River. Therefore, it is also possible that the present-day populations of *C. caudata* were restricted to only one southern refugium during the LGM, with subsequent range expansion northwards following the onset of a warmer and more humid climate. Although the persistence in only one refugium could explain the absence of a phylogeographic break in *C. caudata*, differences in philopatry and generation time ought to be invoked to explain higher genetic structuring within the lineages of *H. diops*, as given by the AMOVA results. Other MAF passerine species with no phylogeographic structure have previously been reported (Batalha-Filho et al., 2012; Cabanne et al., 2013). These montane species are also cold-tolerant and could have been shielded from harsher periods of the Pleistocene. However, population divergence has also been found in other MAF birds (Raposo do Amaral et al., 2018b) and this study, as well as our comparative analyses, imply that the presence or absence of phylogeographic structure may be weakly related to the montane lifestyle. Instead, life-history and ecology might play a more prominent role in the response of each montane species to historical climatic changes.

4.2. Demographic concordance between species

We detected genetic signatures of population expansion on both species, as well as larger distributional range during the LGM. In fact, the distribution of both species during the LGM, as inferred by ENM, suggests that they could have been largely sympatric, although with lower probability of occurrence for *C. caudata* in most of the distribution area (Fig. 3). This suggests that both species might have had larger population sizes during periods of lower average temperature and precipitation, as expected for cold-tolerant species. However, it is evident in the ENM that despite both species showing larger range distributions, *H. diops* showed a continuous distribution throughout the LGM, while *C. caudata* distribution was more fragmented. This implies that even being currently sympatric and forest-dependent, they have distinct climate niches and were likely less sympatric throughout the Pleistocene.

Our paleoclimatic ENM showed that both species were more widespread during glacial periods, which is congruent with the hypothesis that the MAF and their associated organisms increased their distribution during the LGM (Raposo do Amaral et al., 2018b). These results are congruent with previous studies showing larger range distributions during the LGM (Amaro et al., 2012) or signatures of population expansion in cold-tolerant MAF species (Batalha-Filho et al., 2012) and with the hypothesis of stable forest regions south of the Doce River throughout the Pleistocene (Carnaval et al., 2014). Nonetheless, it is unclear whether the observed genetic signatures of population expansion, as given by the Fu's Fs and R_2 tests, are referring to expansion after or during the glacial periods. Given that those species currently have a smaller range distribution, genetic signatures of population size decline

would have been expected. It is possible that the use of a few molecular markers constrained our inference to older demographic events and we did not have power to detect changes in a more recent timescale (i.e. decline after the LGM). Furthermore, if populations experienced a last severe bottleneck, the signals of older bottlenecks can be erased. A larger number of loci will be relevant to better assess the timing of demographic changes throughout the Pleistocene.

4.3. Population structure in H. diops

The shallow phylogeographic structure in *H. diops* suggests that the two recovered lineages probably diverged during the Pleistocene. This implies that this split cannot be reconciled with the major orogenic activity in the Doce River valley (ca. 480 million years ago; Neto et al., 1995; Tedeschi et al., 2016). Additionally, extensive and continuous montane forests are present along its headwaters, where this and other AF species (including other montane species) are found (Maldonado-Coelho, 2012). The permeability of the small tributaries of the Doce River in the headwaters is supported by the evidence that individuals with haplotypes of the Southern lineage were found on both sides of the river. Hence, the signatures of demographic expansion and the larger range of the past distributions during the LGM indicated that population divergence in *H. diops* might be a consequence of historical range fragmentation during interglacial periods.

The Doce River coincides with the phylogeographic break of other species of birds endemic to the AF (Cabanne et al., 2008; Maldonado-Coelho, 2012). The northern bank of the Doce River coincides with the Bahia Refugium and the southern bank coincides with the São Paulo Refugium (Carnaval and Moritz, 2008). The presence of two mitochondrial lineages suggest that populations of *H. diops* were able to persist in the south and in the north, instead of persisting in just one of these regions and later dispersing to the other, as proposed by some of the previous (Carnaval et al., 2009) and more recent (Carnaval et al., 2014) hypotheses about the AF refugia.

5. Conclusions

Our study revealed both incongruent and congruent evolutionary history patterns in two sympatric MAF passerine birds with distinct ecologies and life-histories. The incongruent population structure pattern shown in our comparative study indicates that life history and ecological traits can be important in diversification processes. Further investigations of these traits are needed to clarify their micro-evolutionary role. Congruent aspects we observed were the genetic signatures of population expansion and broader range distributions during the LGM. Additionally, we documented a phylogeography break for *H. diops* that is congruent with the Doce River, supporting the hypothesis that this river could be a secondary barrier delimitating distinct biogeographical regions within the AF.

Author contribution

This study was part of the Master's thesis of TSR, who contributed to data collection, design, analysis, and writing. HBF was involved in conceptualization, formal analysis, visualization, and writing. LFS contributed to data collection. CYM contributed to lab resources, design, and writing. MMC contributed to data collection, design, analysis, and writing.

Declaration of Competing Interest

None.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2020.106925.

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