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Phylogeography and population dynamics of Antbirds (Thamnophilidae) from Amazonian fluvial islands

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Abstract

Aim: To investigate the evolution of the avifauna associated to Amazonian fluvial islands, focusing on the Negro River archipelagos.

Locations: Fluvial islands in the Amazon Basin.

Methods: One generalist floodplain species (*Hypocnemoides melanopogon*) and three river island specialists (*Myrmotherula assimilis*, *Myrmoborus lugubris* and *Thamnophilus nigrocinereus*) were studied (Thamnophilidae). We sequenced two mitochondrial genes and genotyped eight microsatellite loci. Phylogenetic relationships among intraspecific lineages and divergence times were estimated using Bayesian Inference. Haplotype networks, AMOVA (analysis of molecular variance) and Mantel tests were used to verify the spatial organization of genetic diversity. Gene flow and population structure were evaluated using a dissimilarity index, Bayesian inference and allele frequencies. Historical demography was inferred through neutrality tests and Extended Bayesian skyline plots (EBSP).

Results: River island specialists have evolved distinct lineages in different Amazonian tributaries, but exhibit very weak population structure within the Negro river basin. The generalist floodplain species had no population structure along the Amazon basin or within the Negro river basin. Signals of weak and recent (Pleistocene) population expansion were recovered for all species.

Main conclusions: River islands specialists show stronger population structure within Amazonia than floodplain generalists. They show a common spatial and temporal pattern of divergence between populations from the Negro islands and western Amazonia (upper and middle Solimões), which may be related to Amazonian drainage evolution. Island specialists had low genetic diversity within the Negro basin, while the higher and unstructured diversity pattern found in the floodplain generalist species may be a consequence of higher dispersal caused by the seasonal flooding pulse. River islands populations have a recent and dynamic history of contact and isolation, with small historical fluctuations of population sizes, which is in sharp contrast with the patterns found in upland forest birds.

KEYWORDS
Anavilhanas, central Amazonia, fluvial islands, insular habitats, Jaú, Negro river, population dynamics

1 | INTRODUCTION

Intrinsic ecological characteristics, such as dispersal ability and distinct strategies of habitat use, may lead to different population genetic patterns even in species inhabiting the same geographical region, and thus subjected to the same landscape history (Burney & Brumfield, 2009). In Amazonia, many taxa specialized in lowland forest habitats (*terra firme* forests) have their distributions delimited by large rivers (e.g. Ayres & Clutton-Brock, 1992; Haffer, 1969; Kaefer, Tsuji-Nishikido, Mota, Farias, & Lima, 2012; Ribas et al., 2012). These taxa often have limited dispersal capacity or tend to avoid open areas (e.g. Fernandes, Cohn-Haft, Hrbek, & Farias, 2014; Fernandes, Wink, & Aleixo, 2012), so that river channels and floodplains are strong barriers to dispersal, favouring genetic structuring of populations (Beja et al., 2010; Fernandes et al., 2014). Paradoxically, these same rivers can facilitate gene flow for floodplain specialists, implying in a lack of genetic structure for such species throughout the basin (Aleixo, 2006; Cadena, Gutiérrez-Pinto, Dávila, & Chesser, 2011). Nevertheless, to consider the continuous floodplain habitats of Amazonas River and its tributaries as corridors to gene flow can be a biased view, considering the high diversity of microhabitats found and the diverse ways in which species can use them (Parolin et al., 2004; Rosenberg, 1990).

Beyond barriers or corridors, Amazonian rivers are responsible for regulating habitats that occupy approximately 300,000 km^2 of the basin (Wittmann, Schöngart, & Junk, 2010). The physicochemical characteristics of their waters create the environments of *várzea* (white water rivers) and *igapó* (black or clear water rivers) which show distinct physiognomies, primary productivity, plant species diversity and composition (Prance, 1979; Parolin et al., 2004; Wittmann et al., 2010). Amazon rivers floodplains are subjected to strong seasonal cycles whose duration and amplitude are highly spatially and temporally variable through the basin (Junk et al., 2011). Additionally, fluvial dynamics and palaeoclimatic changes are responsible for shaping these landscapes through time (Franzinelli & Igreja, 2002; Irion, Müller, & Morais, 2009; Latrubesse & Franzinelli, 2005), shaping the evolution of fluvial terraces that currently extend for tens of kilometres (Gonçalves-Jr, Soares, Tatumi, Yee, & Mittani, 2016; Soares, Tatumi, & Riccomini, 2010).

A highly specialized and endemic fauna and flora occupies river-created habitats, with about 15% of non-aquatic Amazonian birds being restricted to floodplains (Remsen & Parker, 1983; Wittmann et al., 2010). Because the seasonal flooding of Amazonian rivers creates locally ephemeral environments, it has been thought that these species must possess dispersal capabilities to deal with the dynamic nature of their habitat (Remsen & Parker, 1983). Hence, the continuity and dynamism of floodplains could explain the lack of genetic structure found in the few specialist species that have been studied so far (Aleixo, 2006; Cadena et al., 2011).

At least 20 Amazonian floodplain resident birds show a high level of microhabitat specialization with a clear preference for using fluvial islands, being partially or totally dependent on a habitat with spatially limited distribution in the riverine landscape (Armacost-Jr & Capparella, 2012; Rosenberg, 1990). The evolution of the Amazonian drainage network may strongly influence the evolution of river islands and their specialist biota, especially historical changes in sedimentation dynamics related to variation in sea level or rainfall (Gonçalves-Jr et al., 2016; Irion et al., 2009; Latrubesse & Franzinelli, 2005; Soares et al., 2010).

In this study, we examined genetic diversity and population dynamics of four antbird species (Thamnophilidae) that occur in fluvial islands of the Negro River Basin, one of the largest tributaries of the Amazon River. The influence of ecological characteristics on the genetic patterns was assessed by including a floodplain generalist and three fluvial islands specialist species. In addition, to evaluate the relationship between these populations with conspecifics from other Amazonian fluvial islands, we included a more limited sampling obtained from other Amazonian river systems. Phylogeographical patterns were related to the recent climatic and tectonic evolution of the Amazon basin, focusing on the lower Negro River.

2 | MATERIALS AND METHODS

2.1 | Study region

The lower Negro river comprises two main archipelagos (Figure 1). While the Jaú archipelago is smaller and located in a narrow channel zone, Anavilhanas is a conspicuous landscape feature with approximately 300 islands with distinct geomorphological physiognomies (Latrubesse & Franzinelli, 2005). A third archipelago, Mariuá, occurs 60 km upstream of the Jaú islands (Figure 1). These environments are affected seasonally by the flood pulse driven by the South America summer monsoon (SASM, Zhou & Lau, 1998) that alters the connectivity among islands and habitat availability (Latrubesse & Franzinelli, 2005; Sioli, 1984).

2.2 | Study species and sampling

Some species of Antbirds (Thamnophilidae) occur on fluvial islands, with varying degrees of dependence on these environments (Remsen & Parker, 1983; Rosenberg, 1990). Four species with different degrees of island specialization were selected for this study. *Hypocnemoides melanopogon* (Sclater, 1857) is a floodplain generalist that uses forest edges close to lakes and rivers, and occurs in a large portion of northern Amazon basin (Zimmer & Isler, 2003) (Table S1 in Appendix S1). *Myrmoborus lugubris* (Cabanis, 1847), *Myrmotherula assimilis* (Pelzeln, 1868) and *Thamnophilus nigrocinereus* (Sclater, 1855) are island specialists, occasionally found on river margins (Armacost-Jr & Capparella, 2012; Remsen & Parker, 1983; Rosenberg, 1990). This habitat specialization of the three latter species is reflected in their geographical distribution, which is restricted to large river channels (Zimmer & Isler, 2003).

To understand population dynamics in the complex insular system of the lower Negro River, six and nine islands of Jaú and Anavilhanas respectively were sampled (Table S2 in Appendix S1). Samples of 51 *H. melanopogon*, 31 of *M. lugubris*, 32 *M. assimilis* and 27 *T. nigrocinereus* individuals were collected, while samples

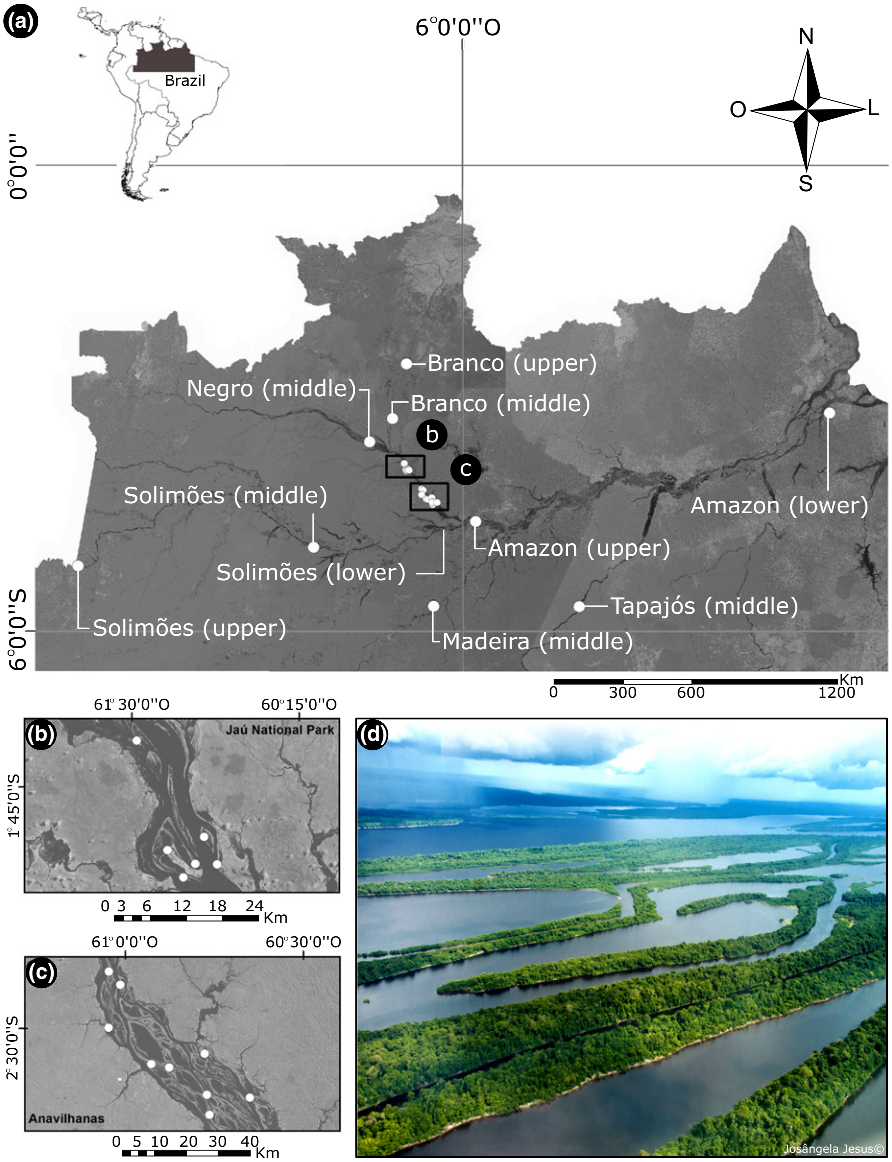

FIGURE 1 (a) Study area in Brazilian Amazon Basin; (b) Jaú islands; (c) Anavilhanas archipelago; sampling points are represented by white circles; (d) aerial view of Anavilhanas islands

from other localities were obtained as loans (Tables S2 and S3 in Appendix S1).

2.3 | Molecular data acquisition

Genomic DNA was extracted and mitochondrial DNA genes cytochrome *b* (*cytb*) and NADH Dehydrogenase 2 (*ND2*) were amplified (Table S4 in Appendix S2). Eight polymorphic microsatellite heterologous primers developed for Thamnophilidae were used to assess variability in nuclear DNA (Table S5 in Appendix S2).

2.4 | Microsatellite data analyses

The occurrence of null alleles was verified with MICROCHECKER 2.2.3 (Van Oosterhout, Hutchinson, Wills, & Shipley, 2004). Deviation from Hardy–Weinberg equilibrium (HWE), estimates of inbreeding coefficient (*Fis*) and linkage disequilibrium (LD) were made using GENEPOP 4.3 (Raymond & Rousset, 1995), applying Bonferroni correction. Observed and expected heterozygosities (H_o and H_e, respectively) were inferred using ARLEQUIN 3.5 (Excoffier & Lischer, 2010). Allele richness (A_r) was calculated using FSTAT 2.9.3.2 (Goudet, 2001). A hierarchical analysis of molecular variance (AMOVA) was used to examine how the genetic variability is distributed across the landscape. We looked for significant correlations between genetic and geographical distances using Mantel tests. Both analyses were performed in ARLEQUIN. To estimate gene flow, pairwise *FST* comparing archipelagos were computed per species, considering the occurrence of null alleles using FREENA (Chapuis & Estoup, 2007). Population structure was inferred using STRUCTURE 2.3.4 (Pritchard, Stephens, & Donnelly, 2000), considering locprior and no-admixture model. Allele frequencies were correlated among populations. We ran five iterations of 100,000 generations with 10% burn-in, testing K=10 populations. Plots of the absolute values of ln Pr(X|K) were generated by STRUCTURE HARVESTER 0.6.93 (Earl & VonHoldt, 2012).

2.5 | Mitochondrial DNA analyses

The model of sequence evolution was selected using the Bayesian information criterion in PartitionFinder 1.1.0 (Lanfear, Calcott, Ho, & Guindon, 2012). Phylogenetic analysis was performed in MRBAYES 3.2 (Ronquist et al., 2012) with four parallel Markov chain Monte Carlo (MCMC) chains and 5,000,000 generations, discarding initial 25% as burn-in, and using closely related species as outgroups (Isler, Bravo, & Brumfield, 2013).

The timing of origin of the Negro basin clades was estimated using BEAST 1.8 (Drummond & Rambaut, 2007). *Hypocnemoides maculicauda* was used as the outgroup for *H. melanopogon*, while for *M. lugubris*, *M. assimilis* and *T. nigrocinereus*, conspecific lineages from other Amazonian rivers were used as outgroups, based on our previous phylogenetic analyses (MRBAYES, Figure S1). The Yule speciation process, an uncorrelated lognormal relaxed clock (Drummond, Ho, Phillips, & Rambaut, 2006) and a rate of evolution of 2.1% divergence per million years for *cytb* (Weir & Schluter, 2008) were used. We ran MCMC with 10,000,000 generations, discarding 10% as burn-in. Convergence was confirmed in TRACER 1.6 (Rambaut et al., 2014) and AWTY (Wilgenbusch, Warren, & Swofford, 2004).

The genealogy of haplotypes was visualized in NETWORK 4.6 (Bandelt, Forster, & Röhl, 1999). BAPS 6.0 (Corander, Cheng, Marttinen, & Tang, 2013) was employed to verify the occurrence of population structure. Summary statistics (number of haplotypes, haplotype diversity and nucleotide diversity) were calculated in DNASP 5.0 (Librado & Rozas, 2009). A hierarchical AMOVA was performed using the same scenarios evaluated for the nuclear markers, based on global values of genetic distance-based Φst. A pairwise matrix of dissimilarity index Φst comparing the different archipelagos was built. Mantel tests were used to evaluate the relationship between geographic and genetic distances. These analyses were computed in ARLEQUIN. To assess historical population demography within the Negro river basin, Tajima's *D* (Tajima, 1989) and Fu's *Fs* (Fu, 1997) were estimated based on 10,000 coalescent simulations in DNASP, and Extended Bayesian Skyline Plots (EBSP) were generated in BEAST. The Bayesian MCMC was run for 100,000,000 generations, discarding the initial 10% of samples as burn-in. Convergence of runs was evaluated on TRACER.

3 | RESULTS

3.1 | Phylogeographical context of the Negro basin populations

As all studied species have distributions that are larger than the Negro basin, mtDNA phylogeographical analyses were performed to determine the evolutionary relationships of the samples from this region in the larger spatial context. For *H. melanopogon*, samples from western Amazon (upper Solimões) appeared within the Negro river basin clade (Figure S1 in Appendix S3). Within *M. assimilis* and *M. lugubris*, samples from western Amazon (upper and middle Solimões) appeared as the sister group to an eastern clade including samples from the Negro basin, as well as the Amazon River and tributaries (Figure S1). Divergence between western and eastern Amazonia was dated to about 800 ka for *M. lugubris* (CI: 1.30 ma–300 ka) and 400 ka for *M. assimilis* (CI: 700–200 ka, Figure 2). For *T. nigrocinereus*, the Negro river basin clade originated at about 600 ka (CI: 800–250 ka; Figure 2).

3.2 | Population structure within the Negro basin

3.2.1 | Microsatellite data

Eight microsatellite loci were polymorphic for *H. melanopogon* and *T. nigrocinereus*, while five exhibited polymorphism in *M. lugubris* and *M. assimilis* (Table 1). Linkage disequilibrium was not detected in any species. Several loci were not in HWE after Bonferroni correction, with some deviations being restricted to specific archipelagos (Table S6 in Appendix S3). The possible occurrence of null alleles was indicated for these loci. The mean observed heterozygosity ranged between 0.18 (*M. lugubris*) and 0.53 (*T. nigrocinereus*; Table 1).

Most nuclear genetic diversity has no correlation with geography (Table 2). The absence of geographic structure within the Negro river basin was also evident for *T. nigrocinereus* due to a significant correlation between genetic and geographic distances (p=.004, Figure S2 in Appendix S3). Accordingly, despite STRUCTURE results indicating k = 5 for *H. melanopogon* and *M. lugubris*, and k = 2 for *M. assimilis* (Figure S3 in Appendix S3), the small difference between likelihood values indicates the existence of just one population (Pritchard et al., 2000). Pairwise *FST* matrix between archipelagos considering all the species indicates genetic similarity (Table S7 in Appendix S3).

3.2.2 | Mitochondrial data

Sequences of *cytb* (911–1020 bp) and *ND2* (944–1027 bp) were obtained for 175 individuals. The generalist floodplain species *H. melanopogon* exhibited 29 haplotypes in 33 individuals with nucleotide diversity (π) of 0.005 (Table 3). In contrast, the number of haplotypes found for the specialist species in the same region are 17 to *M. lugubris* (34 individuals, π=0.002), 18 to *M. assimilis* (26 individuals, π=0.002) and 19 to *T. nigrocinereus* (30 individuals, π=0.001; Table 3).

Accordingly, *H. melanopogon* haplotypes were differentiated by several mutational steps, did not exhibit any relationship with geographic regions and only one population was identified in the BAPS (Bayesian Analysis of Population Structure) analysis (Figure 3). For the island specialist species, some geographic signal was present, but there were shared haplotypes between Anavilhanas and Jaú (*M. lugubris* and *M. assimilis*) and among Anavilhanas, Jaú and Branco river (*T. nigrocinereus*; Figure 3). Population structure analysis identified two lineages for *M. lugubris* (prevailing in Anavilhanas and Jaú, respectively) and *T. nigrocinereus* (one in Jaú and another widespread within the Negro basin), and three for *M. assimilis* (one exclusive to Anavilhanas, dashed lines, Figure 3).

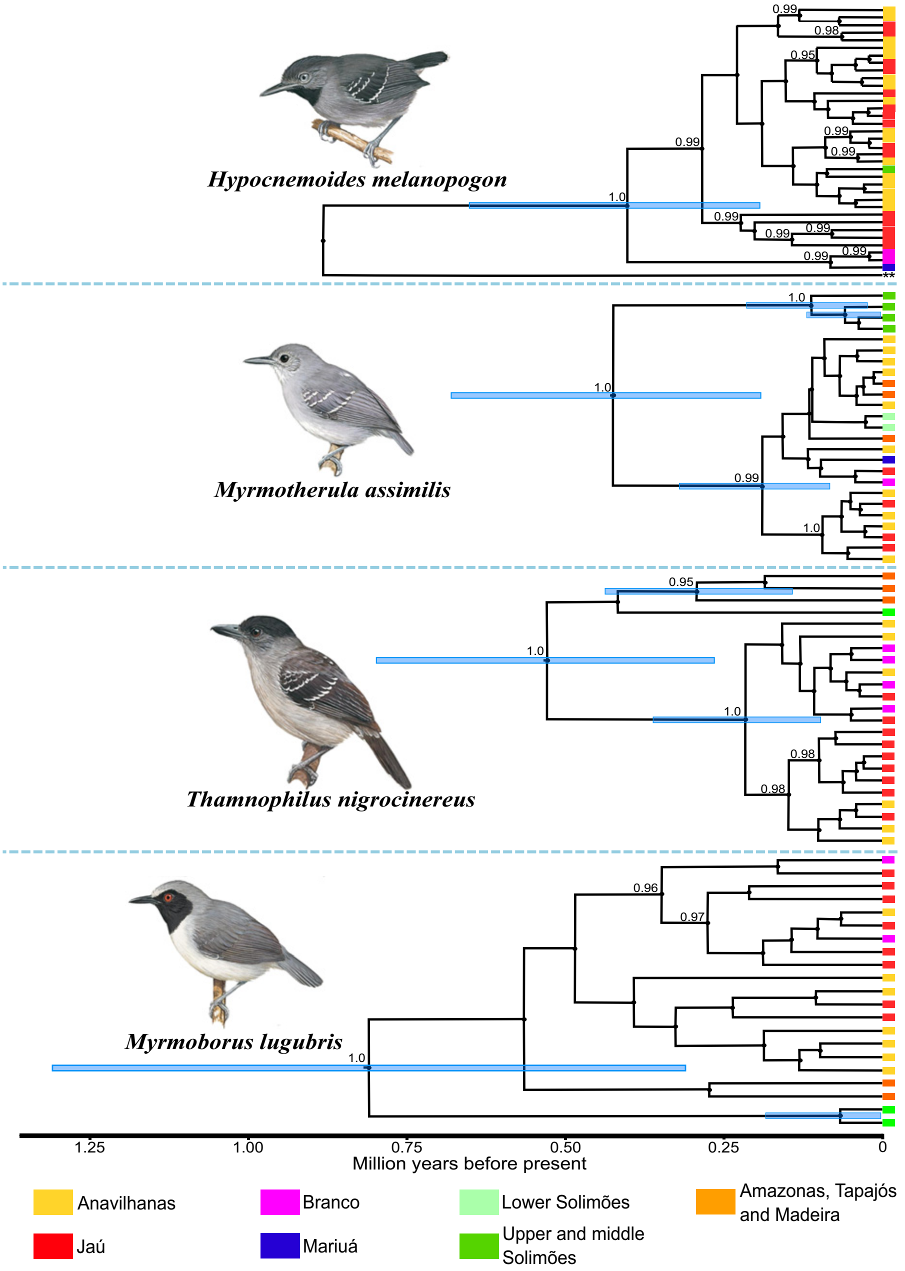

FIGURE 2 Divergence times among intraspecific lineages of the four studied species. Numbers close to nodes are posterior probabilities. Nodes without these values had support lower than 0.95. Blue bars are confidence intervals of divergence time estimates. Vertical bars indicate collection localities: Green: upper and middle Solimões; Light green: lower Solimões; Orange: Amazon/Madeira/Tapajós; Pink: Branco River; Blue: Mariuá archipelago; Yellow: lower Negro islands. Birds' images were adapted from HBW Alive (http://hbw.com). **The outgroup to *H. melanopogon* is *Hypocnemoides maculicauda*

Although most of the mitochondrial genetic diversity was within islands for all species (i.e. no geographic structure), a considerable proportion of genetic diversity was attributed to comparisons between archipelagos for *M. lugubris* (24.04%) and *M. assimilis* (21.55%) and between islands for *H. melanopogon* (29.03%; Table 2). Pairwise dissimilarity index between Jaú and Anavilhanas archipelagos was significant for *M. lugubris* (Table S7), suggesting restricted gene flow.

3.3 | Historical demography at the Negro basin

Demographic analyses detected population expansion in the Negro river basin for all species (Table 3). When the archipelagos were analysed independently, demographic expansion was detected for *H. melanopogon* in both Anavilhanas and Jaú, while for the island specialists, the signal of demographic change was subtle or nonexistent (Table 3). Extended Bayesian skyline plots corroborate the trends of population expansion within the Negro river basin (Figure S4 in Appendix 3). Expansion events are not very pronounced and occurred at approximately 50 ka in *H. melanopogon* and 80 ka and 100 ka in *M. lugubris*, *M. assimilis* and *T. nigrocinereus*.

4 | DISCUSSION

4.1 | Historical connections among populations

This study is one of the first attempts to understand the spatial organization of genetic diversity in Amazonian fluvial island birds.

TABLE 1 Summary of the nuDNA data obtained for samples from the Negro river basin (Anavilhanas, Jaú, Mariuá and Branco islands)

	N	N_a	A_r	H_o	H_e	F_{is}
Hypocnemoides melanopogon						
Anavilhanas	25	7.75	7.42	0.42	0.63	0.30
Jaú	26	8.00	7.85	0.40	0.63	0.33
Total	56	11.12	10.8	0.41	0.65	0.33
Myrmoborus lugubris						
Anavilhanas	14	4.00	3.73	0.18	0.57	0.68
Jaú	28	7.23	6.78	0.24	0.62	0.57
Total	42	7.62	7.27	0.24	0.64	0.62
Myrmotherula assimilis						
Anavilhanas	23	5.40	5.33	0.48	0.57	0.16
Jaú	08	4.02	3.61	0.40	0.58	0.12
Total	35	7.42	7.18	0.46	0.60	0.20
Thamnophilus nigrocinereus						
Anavilhanas	10	4.87	4.49	0.46	0.64	0.26
Jaú	17	6.75	6.75	0.53	0.65	0.21
Total	27	7.87	7.65	0.50	0.66	0.25

N, number of individuals; N_a, number of alleles; A_r, allele richness; H_o, observed heterozygosity; H_e, expected heterozygosity; F_{is}, inbreeding coefficient.

These naturally fragmented environments represent a significant area of floodplains and harbour specialized faunal and floral communities, which exhibit mechanisms for dealing with seasonal flooding (Piedade, Junk, Adis, & Parolin, 2005; Rosenberg, 1990). Insular birds are expected to be good colonizers, dislocating horizontally (to other floodplain environments) or vertically (in vegetation strata) depending on their ecological preferences (Rosenberg, 1990). For example, *Furnarius minor* can use understorey or canopy at different periods of the year, while *Synallaxis propinqua* becomes absent in islands during flooding (Rosenberg, 1990). For this reason, different patterns recovered in species with distinct ecological characteristics are possibly related to differing strategies to use these flooded habitats.

The identification of distinct lineages within *M. lugubris*, *M. assimilis* and *T. nigrocinereus* associated to different Amazonian river basins may be an indication of more restricted gene flow in islands specialist species when compared to floodplain generalists. The discrete distribution of genetic diversity in these floodplain species contradicts the idea of river-created habitats as "corridors" to gene flow. Aleixo (2006) found a lack of population structure across the Amazon basin in two floodplain Dendrocolaptidae species, *Xiphorhynchus obsoletus* and *Dendroplex kienerii*. These patterns may be due to the use of continuous environments at the river banks in a generalist manner by these species. A similar pattern was observed in

TABLE 2 Genetic variation at three geographical scales for mtDNA and microsatellite data

	Hypocnemoides melanopogon		*Myrmoborus lugubris*		*Myrmotherula assimilis*		*Thamnophilus nigrocinereus*	
	nuDNA	mtDNA	nuDNA	mtDNA	nuDNA	mtDNA	nuDNA	mtDNA
Between archipelagos	3.12 (0.00)	5.95 (0.06)	2.85 (0.02)	24.04 **(0.24)**	7.46 **(0.07)**	21.55 **(0.22)**	5.76 (0.06)	2.68 (0.02)
Between islands	11.17 **(0.10)**	29.03 **(0.31)**	19.64 **(0.21)**	3.72 (0.05)	4.80 (0.05)	15.52 **(0.20)**	2.18 (0.02)	−2.09 (−0.21)
Within islands	85.71 **(0.10)**	65.04 **(0.35)**	77.51 **(0.22)**	72.25 **(0.28)**	87.00 **(0.12)**	62.94 **(0.37)**	92.05 (0.08)	99.42 (0.00)

Values in parenthesis refer to global dissimilarity indices FST (nuclear DNA) and Φst (mitochondrial DNA). Bold values are significant ($p \leq .05$).

TABLE 3 Mitochondrial DNA summary statistics and neutrality tests per locality and total (considering Anavilhanas, Jaú, Mariuá and Branco islands)

Species	Locality	n	H_n	H_d (±SD)	π (±SD)	D	F_s
Hypocnemoides melanopogon	Anavilhanas	18	16	0.988 (±0.021)	0.004 (±0.0012)	-2.36^{b}	-7.73^{b}
	Jaú	11	11	1.000 (±0.024)	0.007 (±0.0010)	−0.97	-6.23^{b}
	Total	33	29	0.996 (±0.007)	0.005 (±0.0004)	-2.26^{b}	-24.7^{c}
Myrmoborus lugubris	Anavilhanas	12	07	0.833 (±0.100)	0.002 (±0.0003)	−1.61	−0.34
	Jaú	20	09	0.821 (±0.073)	0.001 (±0.0002)	-2.07^{a}	−1.03
	Total	34	17	0.891 (±0.040)	0.002 (±0.0005)	-2.28^{b}	-5.50^{a}
Myrmotherula assimilis	Anavilhanas	17	10	0.882 (±0.059)	0.001 (±0.0002)	−1.51	−2.87
	Jaú	7	07	1.000 (±0.001)	0.003 (±0.0012)	−1.54	−2.13
	Total	26	18	0.938 (±0.033)	0.002 (±0.0004)	-2.32^{b}	-8.45^{b}
Thamnophilus nigrocinereus	Anavilhanas	7	07	1.000 (±0.076)	0.001 (±0.0003)	−1.36	-3.82^{b}
	Jaú	15	08	0.867 (±0.067)	0.001 (±0.0003)	−1.54	−2.12
	Total	30	19	0.908 (±0.045)	0.001 (±0.0003)	-2.39^{b}	-12.8^{c}

n, number of individuals; H_n, number of haplotypes; H_d, haplotype diversity; π, nucleotide diversity; SD, standard deviation in brackets; D, Tajima's test value; F_s, Fu's test value.

$^{a}p<.05$, $^{b}p<.01$, $^{c}p<.001$.

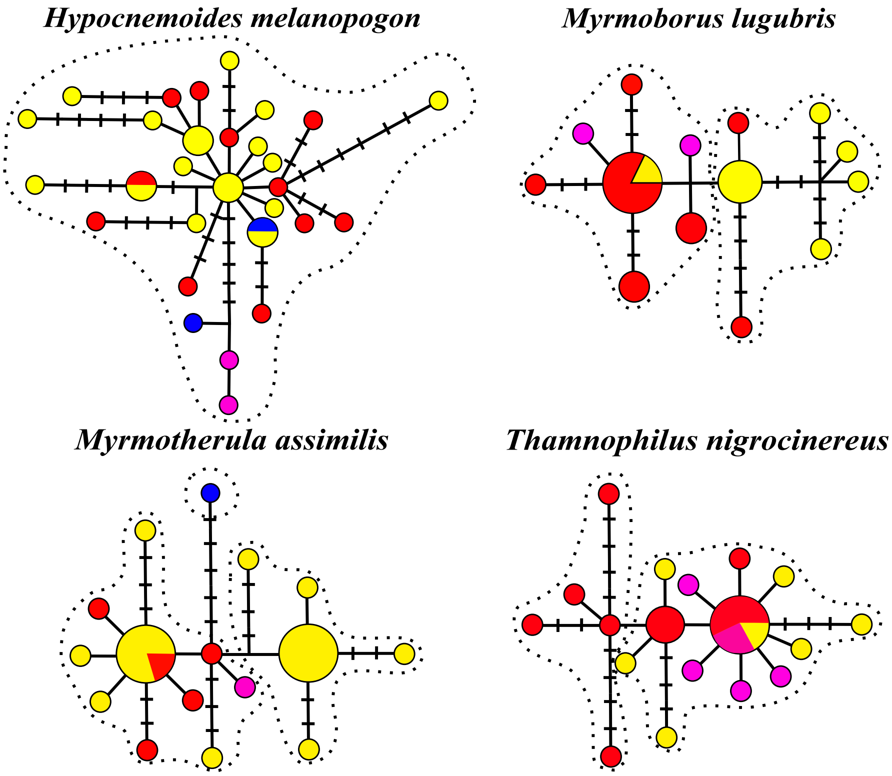

FIGURE 3 Haplotype network of Negro river basin per species. Colours refer to locality: yellow: Anavilhanas; red: Jaú; pink: Branco; blue: Mariuá. Dashed lines indicate populations inferred by the BAPS analysis

Chrysomus icterocephalus (Icteridae; Cadena et al., 2011), but in this case, besides habitat connectivity, the use of open vegetation areas by these birds may also promote gene flow (Bates, Tello, & Da Silva, 2003). Contrastingly, in a study of bird communities covering over 3,000 km of floodplain forests along the Amazonas and Solimões rivers, Cohn-Haft, Naka, and Fernandes (2007) found several closely related species to replace each other along the continuous floodplain, with some congruent replacement regions, indicating that other factors such as competitive exclusion and landscape history may promote disjunct distributions of floodplain species. Here, we show that insular birds exhibit signals of heterogeneous distribution of genetic diversity, corroborating this pattern.

Considering the high microhabitat specialization of island specialist Antbirds, limitations to dispersal may be related to regions where islands are rare or absent. The results obtained for *T. nigrocinereus* agree with the hypothesis that microhabitat continuity rules gene flow in specialist species. In the lower Negro River archipelagos, where islands occur in a high density, the genetic differentiation of nuclear DNA correlates with geographic distance, a pattern that is expected in continuous habitat conditions. Besides, AMOVA results for both markers in this species exhibited more than 90% of variation occurring without relationship to geographic structure, similar to *X. obsoletus* and *D. kienerii* (Aleixo, 2006). In contrast, distinct lineages of *T. nigrocinereus* were found in islands from other Amazonian rivers (Solimões, Madeira, Tapajós and Amazon), indicating that the absence of islands in the final stretch of lower Negro and the poorly developed floodplains in this same region (Franzinelli & Igreja, 2002), which prevent the occasional use of the river margins, may currently act as a barrier to dispersal.

4.2 | Population dynamics of Negro river basin insular birds

Most genetic variation among birds from islands and archipelagos of the Negro river basin occurred without relationship to geography. Pairwise dissimilarity indexes comparing Anavilhanas and Jaú were not significant in most cases, nuclear DNA variation indicates one single population within each species, and mtDNA haplotypes were shared between archipelagos. Despite this evidence for the lack of population structure related to the distinct archipelagos, genetic diversity is not homogeneously distributed across the landscape. The percentage of molecular variation related to geographic structure (i.e. between islands or between archipelagos) was significantly high in *H. melanopogon*, *M. assimilis* and *M. lugubris*. This last species also exhibits significant values of Φst when comparing mtDNA data for the Anavilhanas and Jaú archipelagos. MtDNA population structure analysis indicates the presence of more than one population for the three island specialists. Accordingly, for the nuDNA of all the studied species, deviations in HWE restricted to a specific geographic area indicate differences in allele frequencies as result of population substructure. These subtle patterns of intraspecific genetic diversity may be related to the recent history of the current insular environments in the lower Negro river.

The modern floodplain and islands of the Negro and Amazon rivers result from sediment accumulation during the Holocene (Latrubesse & Franzinelli, 2002, 2005). However, fluvial terraces with ages ranging from Miocene to Late Pleistocene (Cremon, Rossetti, Sawakuchi, & Cohen, 2016; Dino, Soares, Antonioli, Riccomini, & Nogueira, 2012; Nogueira, Silveira, & Guimarães, 2013; Pupim, Sawakuchi, Mineli, & Nogueira, 2016; Rossetti, Toledo, & Góes, 2005; Rossetti et al., 2015; Soares et al., 2010) are widespread in lowland Amazonia. These older fluvial terraces were formed by abandonment of older floodplains as a result of channel incision. Thus, the modern islands and floodplains are younger than the main river valleys. Fluvial islands and floodplains are dynamic landforms, which are present in Amazonia since the early phases of drainage development, but with a few thousand years lifetime due to shifts between conditions suitable for sediment accumulation and channel incision driven by base level changes. This recent dynamism is evident in the population genetic structure we found in island birds.

Stronger indication of population structure among archipelagos in the mtDNA than in the nuDNA may reflect recent secondary contact of previously isolated lineages. Historical isolation of populations may have originated the distinct mtDNA lineages, while the recent re-establishment of gene flow due to the formation and expansion of island environments in the lower Negro river during the Holocene may have resulted in the lack of structure in the microsatellite data (Latrubesse & Franzinelli, 2005; Latrubesse & Stevaux, 2015). Although this explanation agrees with the available geological information on island evolution, the alternative explanation of recent isolation with incomplete lineage sorting being stronger in the nuclear data due to larger population size cannot be ruled out with the current dataset.

The use of islands by generalist floodplain species also occurs in a different manner when compared to other floodplain environments. *Hypocnemoides melanopogon* had larger nucleotide diversity than reported for *X. obsoletus*, *D. kienerii* and *C. icterocephalus* (Aleixo, 2006; Cadena et al., 2011). Burney and Brumfield (2009) evaluated the effect of physiographic barriers on 40 Neotropical upland forest bird species and concluded that organisms that use different vegetation strata have distinct patterns of genetic variation, with canopy species exhibiting low genetic variation due to their higher dispersal ability, while understorey species were more sensitive to barriers. In fluvial islands, this pattern cannot be expected. Birds that occupy midstory or canopy are possibly less vulnerable to water level variation, while organisms that use understorey (as *H. melanopogon*) have to go through vertical or horizontal displacement in flooding periods. The pattern of genetic diversity found in *H. melanopogon* is possibly a result of several events of displacement from islands with subsequent re-colonization, due to seasonal unavailability of the islands understorey. A similar pattern was observed in small rodents that occupy lower vegetation stratum of insular habitats in the Araguaia River, Northern Brazil (Rocha et al., 2014). In contrast, fluvial island specialists remain on these environments throughout the year by having adaptive features to deal with the seasonal flooding, specifically a higher flexibility in the use of different vegetation strata (Rosenberg, 1990).

4.3 | Biogeography of Negro river basin island birds in an Amazonian context

Despite occupying the same river islands, the four species exhibit distinct phylogeographical patterns (Figure 3). *H. melanopogon* does not show geographic structure throughout its distribution, while the three island specialists show structure among different river basins. For these species, the Negro basin population diverged from western Amazonian populations during the mid-Pleistocene, and despite large confidence intervals, the estimated dates for this split overlap at about 500 ka. This period coincides with a regional retraction of flooded environments in lowland western Amazonia, especially along the Solimões main stem and its major tributaries (Nogueira et al., 2013; Rossetti et al., 2015). This environmental change is recorded by fluvial terraces of the Içá Formation, which show evidence that widespread floodplain environments converted to upland forest due to regional channel incision. This shift from a phase dominated by sediment accumulation to a phase characterized by channel incision promoted regional reorganization of flooding environments, which became more fragmented since the mid-Pleistocene, affecting the establishment of current floodplains and islands. Central Amazonia was very dynamic at this period, possibly generating current patterns of diversity and distributions found in several organisms. Variations in composition or abundance of flooded forest biological communities among eastern and western Amazonia have been described for trees, ants, birds, spiders and fishes (Albernaz, 2008), and for all of them a strong transition is seen at the confluence between Negro and Solimões rivers. Phylogeographical breaks have been detected in this same area for the parakeet *Brotogeris sanctithomae* (Canton, 2014) and for discus fishes (*Symphysodon* spp.; Farias & Hrbek, 2008). The confluence between the Negro and Solimões rivers is also the approximate boundary between western soft sedimentary substrates and eastern hard bedrock substrates, with different susceptibility to channel incision and development of flooding environments.

The dynamic history of central Amazonian riverine habitats is especially evident in the lower Negro river. A network of palaeochannels exists between the middle reach of the Negro and the Manacapuru river, a tributary of the Solimões (Almeida-Filho & Miranda, 2007). When these channels were active, the connection between populations from the middle Negro and lower Solimões could happen through small islands or riverbanks. During the Late Pleistocene to Holocene, Amazonian rivers valleys were flooded originating the modern ria lakes and interrupting these connections (Archer, 2005; Bertani, Rossetti, Hayakawa, & Cohen, 2015). Thus, current ria lakes, as the one located in the final stretch of the Negro river, would be temporary barriers for island populations.

The Anavilhanas archipelago is a result of abrupt channel widening, or fluvial ria (Archer, 2005), which traps upstream-sourced sediments and allows the development of fluvial bar complexes whose stabilization gives origin to islands. Irion et al. (2009) and Bertani et al. (2015) argued that Amazonian rias resulted from glacial/interglacial sea level variation. However, the effect of sea level changes on rivers would be minor in catchments located thousands of kilometres from the coast, and changes in hydrology and sediment yield are probably driven by climate or tectonic processes in sediment source areas (Schumm, 1993) playing a major role for channel incision and sediment accumulation. Thus, sea level would have a minor effect on the formation or degradation of fluvial islands in the Negro River. Major fluvial archipelagos are observed in black or clear water Amazonian rivers blocked by white water trunk rivers or tributaries (Archer, 2005). This suggests that changes in sediment load and water discharge play an important role for islands development or degradation. Therefore, changes in water discharge can drive channel incision or aggradation and consequently modulate the retraction or expansion of islands and floodplain habitats. Orbital (20–25 ka) and millennial variations in precipitation were recorded for Amazonia during the Quaternary (Baker et al., 2001; Cheng et al., 2013; Govin et al., 2014). Abrupt precipitation increase in western Amazonia during the Heinrich stadial 1 (18–15 ka; Zhang et al., 2016) and Younger Dryas (~12.5 ka; Baker et al., 2001) could be responsible for channel incision, provoking erosion or emergence of previous Pleistocene islands and floodplains. As a consequence, new sediment accumulation during the Holocene rebuilt the modern flooding environments under a lower base level. Thus, the origin of island specialist lineages from the Negro River basin predates the formation of the current archipelagos. This corroborates an intense dynamism of insular habitat availability in the lower Negro region, which may have created fleeting insular environments that were occupied by ancestral lineages (Cremon et al., 2016; Irion et al., 2009; Rossetti et al., 2015).

Supporting the above scenario, only slight signal of population expansion was found in the four studied species. This signal is much less pronounced than population expansions that have been reported for Amazonian upland forest species (Fernandes et al., 2012; Ribas et al., 2012). Contrary to the majority of upland species studied to date, floodplain organisms seem to have smaller populations of more constant size through recent times (Aleixo, 2006). Possibly, river-created environments suffered spatial rearrangements and changes in connectivity, but not large variations in availability during the Quaternary (Aleixo, 2006).

4.4 | Implications for Amazonian biogeography and conservation

Large Amazonian rivers are known to influence distribution and genetic diversity patterns of upland forest birds (e.g. Cracraft, 1985; Ribas et al., 2012), however, diversification patterns of species that occupy river-created habitats are still poorly known. Thus, understanding the history and diversity of lineages from floodplain or riverine habitats may offer important information on drainage evolution and, consequently, on the origins of an important component of Amazonian biodiversity. This study shows that avifauna from riverine islands exhibits a dynamic history of contact and isolation during the Quaternary, with subtle fluctuations in population sizes. This trend is in sharp contrast to the patterns of population expansion described for upland forest understorey birds (Aleixo, 2004; Thom & Aleixo, 2015).

The shallow history of populations indicates recent rearrangement of Amazonian flooded habitats that we know today, largely influenced and adapted to the annual flood pulse. Amazonian flooded habitats are currently under special pressure due to the focus on developmental projects directed to generating hydroelectric power through the construction of large dams (ANEEL, 2016). These dams will disrupt the natural flooding pulse and permanently flood several river islands. Distinct populations of species such as *T. nigrocinereus* and *M. lugubris*, are already threatened due to the possible habitat reduction in the next years (IUCN, 2015). Understanding population structure and habitat use in island specialist species is important to access and mitigate these imminent impacts to the Amazonian biota.

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AUTHOR CONTRIBUTIONS

E.L.C. conducted the research and writing as part of requirements to achieve his Master's degree; C.C.R. and S.H.B. designed the study, contributed in the discussion and writing of the manuscript; C.G. helped with laboratory procedures, data analyses and interpretation, and manuscript revision; G.T. contributed to data collection and analyses. E.A.A.S and A.O.S contributed to palaeoenvironmental interpretations. E.L.C., S.H.B. and G.T. collected most of the samples from Anavilhanas and Jaú National Park archipelagos.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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