INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA
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DO PARASITIC LICE EXHIBIT ENDEMISM IN PARALELL WITH THEIR AVIAN HOSTS? A COMPARISON ACROSS NORTHERN AMAZONIAN AREAS OF ENDEMISM

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Sinopse:

Avaliaram-se os padrões de evolução entre aves e seus piolhos entre 03 regiões biogeográficas testando os efeitos dos rios Negro e Japurá como barreira para o hospedeiro e seus parasitas através de uso de análises filogenéticas.

Palavras chave: Padrão de diversificação, Parasita-hospedeiro, Aves, Piolhos.

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RESUMO

Áreas de endemismo são as menores unidades biogeográficas e podem ser definidas como áreas biologicamente únicas compostas por táxons com limites de distribuição comum. Alta beta diversidade dentro da Amazônia é frequentemente relacionado ao turnover entre essas áreas. Por décadas, evolucionistas tentaram compreender o mecanismo que mantém e gera a estrutura espacial e alta diversidade dos organismos de vida livre da Amazônia, especialmente as aves. Porém, poucos estudos tentaram analisar esse padrão entre seus parasitos. A associação hospedeiro-parasito envolve história compartilhada que que pode permitir uma melhor compreensão da fina escala evolutiva da história do hospedeiro. Neste artigo, comparamos o padrão coevolutivo entre 2 espécies de aves hospedeiras com padrões genéticos estruturais distintos do norte da Amazônia, *Dendrocincla fuliginosa* (Aves: Dendrocolaptidae) e *Dixiphia pipra* (Aves: Pipridae) e seus piolhos ectoparasitas (Insecta: Phthiraptera), *Furnaricola* sp. *ex Dendrocincla fuliginosa*, *Myrsidea* sp. *ex Dixiphia pipra* e *Tyranniphilopterus* sp. *ex Dixiphia pipra*. Foram obtidos sequências da cytochrome oxidase subunit I (COI) do gene mitocondrial dos hospedeiros e parasitos coletados das ambas as margens do Rio Negro e do Rio Japurá, os quais delimitam 3 áreas de endemismo no norte da Amazônia: Napo, Jaú e Guiana. Os resultados demonstram que o Rio Negro é uma barreira geográfica tanto para *furnaricola* sp. e seu hospedeiro *Dendrocincla fuliginosa*. A Filogenia tanto do hopedeiro, *Dendrocincla fuliginosa*, e do seu parasito, *Furnaricola* sp., demonstram clados monofiléticos em ambas as margens do rio que não são táxons irmãs. Esse clados apresentam um distância-p de 17.8% para *Rallicola* sp. e 6.0% para *Dendrocincla fuliginosa*. Deste modo, estes clados dos parasitas constituem linhagens evolutivas distintas e podem até ser espécies diferentes. Ao contrário, *Dixiphia pipra,* apresenta nenhuma estruturação populacional associada aos rios. Conformemente, dados do piolho *Myrsidea* sp. indicam baixo suporte para a presença de clados distintos em ambas as margens do Rio Negro, e dos piolhos *Tyranniphilopterus* sp. indicam baixa estruturação através do Rio Japurá. Este estudo é o primeiro passo para a compreensão dos efeitos da história biogeográfica em ectoparasitas permanentes e sugere que a biogeografia do hospedeiro é, até certo ponto, um determinante da história do parasito. Além disso, a história evolutiva do parasito é uma fonte extra de informação sobre a evolução do hospedeiro nesta região altamente diversa do norte da Amazônia.

Palavras-chave: Piolho, coevolução, biogeografia, aves, Amazônia, Rio Negro, Endemismo.

ABSTRACT

Areas of endemism are the smallest units in biogeography and can be defined as biologically unique areas comprised of taxa with common geographic limits to their distributions. High beta diversity within Amazonia is often related to turnover among these areas. For decades, evolutionary biologists have tried to comprehend the mechanisms generating and maintaining the spatial structure and high diversity of free-living Amazonian organisms, particularly birds. However, few studies have tried to analyze these patterns among their parasites. Host and parasite associations involve shared history that may allow us to better understand the fine scale evolutionary history of the host. Here, we compare the coevolutionary patterns among 2 avian host species with distinct patterns of genetic structure in northern Amazonia, *Dendrocincla fuliginosa* (Aves: Dendrocolaptidae) and *Dixiphia pipra* (Aves: Pipridae) and their ectoparasitic lice (Insecta: Phthiraptera), *Furnaricola* sp. *ex Dendrocincla fuliginosa, Myrsidea* sp. *ex Dixiphia pipra* and *Tyranniphilopterus* sp. *ex Dixiphia pipra*. We obtained sequences of the mitochondrial gene cytochrome oxidase subunit I from hosts and parasites collected on opposite banks of the Negro and Japurá rivers, which delimit 3 areas of endemism in northern Amazonia: Napo, Jau and Guiana. Our results demonstrate that the Negro river is a geographical barrier for both *Furnaricola* sp. and its avian host, *Dendrocincla fuliginosa.* Phylogenies of both the hosts, *Dendrocincla fuliginosa*, and the parasites, *Furnaricola* sp., show monophyletic clades on opposite margins of the river that are not sister taxa. These clades have a mean uncorrected p-distance of 17.8% for *Rallicola* sp., and 6.0% for *Dendrocincla fuliginosa*. Thus, these parasite clades constitute distinct evolutionary lineages and may even be distinct species. In contrast, *Dixiphia pipra* has no population structure associated with either river. Accordingly, data from their lice *Myrsidea* sp. indicates weak support for different clades on opposite margins of the Negro river, whereas data from their lice *Tyranniphilopterus* sp. indicates weak structure across the Japurá. This study is a first step towards understanding the effects of biogeographic history on permanent ectoparasites and suggests that host biogeographic history is to some extent a determinant of the parasite's history. Furthermore, the parasite's evolutionary history is an additional source of information about their hosts evolution in this highly diverse region of Northern Amazonia.

Keywords: lice, coevolution, biogeography, birds, Amazonia, Negro River, endemism.

SUMÁRIO

Introduction

Evolutionary biologists have long been interested in the spatial structure of Neotropical biodiversity, and historically major landscape features and geological events have been used to explain biogeographic patterns in Amazonian diversity (Haffer, 1974; Cracraft, 1985; Ribas et al., 2012). Nine areas of endemism are recognized for upland forest birds in Amazonia (Cracraft, 1985, Silva et al., 2005, Borges and Silva, 2012). Ecological (e.g., environmental) and/or historical (e.g., rivers) factors may be important in driving and maintaining distributional limits for these avian taxa. Several studies have focused on understanding the processes that have generated the patterns of endemism, the timing of origin of endemic lineages, and the barriers responsible for delimiting them (Salisbury et al., 2012; Smith et al., 2014; Buckner et al., 2015). Most of these studies have focused on free living organisms (e.g., Naka et al., 2012; Boubli et al., 2015; Nazareno et al., 2017) and only a handful of studies have been aimed at understanding Amazonian diversification patterns among parasites in relation to their hosts' (Weckstein, 2004; Fecchio et al., 2018a, 2018b).

Over time, studies have shown that hosts and their parasites share a complex and intricate evolutionary relationship that makes parasites potential markers for reconstructing their hosts' evolutionary history (Whiteman and Parker, 2005; Nieberding and Morand, 2006; Nireberding and Olivieri, 2007; Poulin, 2011; Sweet and Johnson, 2016). Chewing lice (Insecta: Phthiraptera) and their hosts are among the most well-studied host/parasite systems (Page, 2003) and comprise the largest number of ectoparasitic insect species (Marshall, 1981). Several life history characteristics make lice potentially useful markers of recent host evolutionary history. First, lice complete their entire life cycle on the host and have limited dispersal capacity (Price et al., 2003). Second, chewing lice have a much shorter life cycle (~30 days) than their hosts and thus a typical avian chewing louse has 12 generations within the time period of a single avian generation (Durden, 2002). Third, the rate of mitochondrial molecular

evolution for ectoparasitic lice, is faster than that of their hosts (~2.9 times faster; Page et al., 1998; Clayton and Johnson, 2003; Johnson et al., 2014). Thus, the parasites typically stick with their hosts and their DNA will accrue differences more quickly than the hosts own DNA.

Parasite DNA diversification can exhibit concordant patterns with their hosts when they are transmitted vertically from parent to offspring (Wirth et al., 2005). For lice, many factors could influence the lack of correlation between parasites and hosts: parasites may speciate independently of their host, host switch, go extinct or may fail to speciate when the host speciates (Page, 2003). Host switching may be common among parasites found on hosts that are social, that share breeding grounds or are in large groups (Page et al., 1996; Whiteman and Parker, 2005). Also, host switching depends on the ecology of the parasites. For example, Clayton and Johnson (2003) demonstrated that 2 louse genera living on the same avian hosts may have different host defenses and vary in their ability to switch hosts. Studies have also revealed that biogeography is an important factor shaping the codiversification patterns of parasites and their hosts (Weckstein, 2004; Johnson et al., 2007; Sweet and Johnson, 2016; Fecchio et al., 2018a, and 2018b). Parasites of some avian species may act as an additional source of information about diversification, since biogeographical processes, such as isolation and migration, may determine genetic structure of parasites independently of their host associations.

To this end, we studied the cophylogeographic patterns of Plain-brown Woodcreeper (*Dendrocincla fuliginosa* Vieillot, 1818) and its louse genus *Furnaricola* sp. and White-crowned Manakin (*Dixiphia pipra* Linnaeus, 1758) and its louse genera *Myrsidea* sp. and *Tyranniphilopterus* sp., focusing on populations living in the northern portion of the Amazon Basin where three avian areas of endemism (Napo, Jau and Guiana) are delimited by two large Amazonian rivers (the Japurá and Negro rivers). The Plain-brown Woodcreeper has a widespread distribution throughout northern South America and reaches its northern limit in

Honduras. The Amazonian populations of Plain-brown Woodcreeper occur principally in upland "terra firme" forest and are obligate ant-followers that sometimes forage within mixed-species flocks (Marantz et al., 2018). Two non-sister clades of Plain-brown Woodcreeper *(D. f. fuliginosa and D. f. phaechroa)* occur on opposite margins of the Negro River (Weir and Price., 2011; Mila et al. 2012). The White-crowned Manakin also has a widespread distribution throughout northern South America, with allopatric populations in Panama-Costa Rica and in southeastern Brazil. They inhabit primary humid forests and adjacent tall secondary woodlands. They are social birds and males perform displays in leks during the mating season (Snow, 2018). Mila et al. (2012) found that there is no population structure within this species North of the Amazon River.

For this study, we used mitochondrial DNA (mtDNA) sequence data collected from lice and their avian hosts, from the three northern Amazonian areas of endemism (Napo, Jau, and Guiana), sampling on opposite margins of the Negro and Japurá rivers, which delimit these areas, to compare the evolutionary history of hosts and parasites through population structure analysis, phylogenetic reconstruction, and measures of genetic divergence. By utilizing three different louse genera from two host species that have different evolutionary histories, we aim to test whether host biogeographic history influences the genetic diversity and the patterns of connectivity in parasites populations, or whether the parasites have their own independent biogeographic histories and patterns of endemism. Also, we explore whether the parasites mitochondrial genetic structure may reveal patterns of recent host isolation, not yet detectable in the hosts DNA, because the host DNA accrues informative differences over longer periods of time than the DNA of the parasites.

MATERIALS AND METHODS

Sample collection

Lice where sampled from 2 species of birds, *Dendrocincla fuliginosa* and *Dixiphia pipra*, on both margins of the Negro and Japurá rivers. Hosts were fumigated for parasites using either the pyrethrin powder dusting or ethyl acetate fumigation and ruffling methods in the field (Clayton and Drown, 2001) and the parasites that were collected were placed in 95-100% ethanol, and stored at -20 °C or -80 °C. Blood or muscle tissue samples were also collected from the birds. All voucher bird specimens and blood samples were deposited in the Biological Collections at the National Institute for Amazonian Research (INPA).

When available, Cytochrome Oxidase I (COI) sequences for the hosts from other Amazonian areas of endemism, which we did not sample (Xingu, Belém, and Chocó), were included in the analyses to understand the regional patterns of phylogenetic relationships within each clade. We obtained these extra sequences for *Dendrocincla fuliginosa* and *Dixiphia pipra* from the GenBank submissions deposited by Mila et al. (2012) (JX487358-JX487364, JX487366, JX487367, JX487374-JX487285, JX487389, JX487391-JX487399 and JX487402).

DNA Extraction, amplification and sequencing

We used the Wizard® Promega DNA extraction kit (Wizard, Madison, Wisconsin) to extract DNA from avian muscle tissue and blood and the QIAamp DNA Micro Kit (Qiagen, Valencia, California) to extract DNA from lice. For louse extractions we used a procedure adapted from the manufacturer's protocol that allowed us to retain the louse exoskeleton as a morphological voucher. We used a sterilized syringe needle to make a partial cut between the louse head and thorax, which exposed the louse tissue to proteinase K and buffer solution and then incubated the specimen at 55°C for ~48 hr (Johnson et al., 2003; Valim and Weckstein, 2012). This DNA extraction procedure retains the exoskeleton as a voucher specimen for

morphological examination and archival preservation. Price et al. (2003) was used to identify each voucher specimen to genus level (Suppl. Table 1). All exoskeletons where slide-mounted in Canada Balsam using the Palma (1978) protocol and were deposited in the insect collection at the Academy of Natural Science of Drexel University. Remaining unextracted samples collected by MA where deposited in INPA's Zoological Collection.

For birds, we PCR amplified a fragment of COI (598 bp) using primers BirdF and BirdR (Patel et al., 2010). We purified these PCR products using PEG 8000 following the manufacturer's protocol and sequenced them using the same primers and the BigDye® Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems®, Foster City, California). We ran the sequencing reaction products on an ABI 3130/3130XL automated capillary sequencer (Applied Biosystems®).

For lice we amplified two different COI fragments using previously published protocols (Johnson and Clayton, 2000; Bush et al., 2016; Sweet et al., 2018) and primers. In addition to amplifying the short fragment of COI gene (379 bp) typically sequenced for lice, with primers L6625 and H7005 (Hafner et al., 1994), we sequenced a longer fragment (655 bp) of COI (Folmer et al., 1994) using primers LCOI4901 and HCO2198. Below we refer to these 2 different fragments of the COI gene as short COI (379 bp) and long COI (655 bp).

Louse PCR products were purified using ExoSAP-IT (Affymetrix, Santa Clara, California), sequenced using the BigDye terminator v3.1 cycle sequencing kit (Applied Biosystems®), and run on an ABI 3100 DNA sequencer (Applied Biosystems®).

All contigs of forward and reverse sequences were assembled and reconciled using Geneious (6.1.8, Biomatters LTD;http://www.geneious.com; Kearse et al., 2012). For *Furnaricola* sp. and *Myrsidea* sp., we generated consensus sequences from contigs of forward and reverse strands for both fragments of COI and concatenated them for phylogenetic analyses using Aliview. All sequences produced for this study are deposited in GenBank (#'s pending

acceptance). We checked each alignment by eye in Geneious. However, for *Tyranniphilopterus* sp. we did not concatenate the two fragments of COI because we were unable to amplify both fragments for all individuals. As a result, we have analyzed 4 different alignments, as described below.

Population structure, phylogenetic analyses and genetic divergence across rivers

Unless otherwise noted, we used the same analytical procedures for both the birds and lice. We used Bayesian Analysis of Population Structure (BAPS) (Corander et al., 2008) to check for the most likely number of populations (k) within each taxon. In the mixture analysis likelihood values for each possible number of subpopulations (K, ranging from 1 to 5), were calculated, accepting the partition with K value that maximized the likelihood. The Admixture analysis was done with 10 iterations, 3 individuals of reference for each subpopulation and 10 iterations for each individual.

For phylogenetic analyses, the 4 alignments were evaluated in PartitionFinder 2.1.1 (Lanfear et al., 2012) to test for the best substitution model under Bayesian information criterion (BIC) and Akaike information criterion (AIC). Phylogenetic trees were reconstructed using Bayesian (BI) and maximum likelihood (ML) methods.

For the Bayesian phylogenetic analysis, we used MrBayes 3.2.6 (Ronquist et al., 2012). Based on a MrBayes specific model search in PartitionFinder, we applied the GTR + G model for *Furnaricola* sp., *Myrsidea* sp. and the *Tyranniphilopterus* sp. long COI fragment. For the *Tyranniphilopterus* sp. short COI fragment the GTR + I model was selected. For the avian hosts, the GTR model was selected. We ran 20 million generations of Markov Chain Monte Carlo (MCMC) for 2 runs of 4 chains each, sampling every 1,000 trees. To assess parameter convergence, we viewed trace files in Tracer v.1.5 (Rambaut and Drummond, 2007). Based on these assessments, we discarded the first 10% of samples as a burn-in.

For the Maximum Likelihood phylogenetic analysis, we employed RAxML v 8.2.10 (Stamatakis, 2014), using the GTR + G model for *Furnaricola* sp., *Myrsidea* sp. and *Tyranniphilopterus* sp. long COI fragment and GTR + I + G model for *Tyranniphilopterus* sp. short COI fragment and for all four datasets we conducted 10,000 bootstrap replicates to assess clade support. For the hosts, we used GTR model and conducted 10,000 bootstrap replicates to assess clade support.

Finally, to measure genetic divergence between different clades in the host and parasite trees we used MEGA X (Kumar et al., 2018) to estimate mean uncorrected p-distances among clades and populations. We compared pairwise distance and mean distance between the groups using the p-distance model option.

.

RESULTS

We obtained COI sequences from 3 different bird louse genera from 2 host species: *Furnaricola* sp. (15 specimens) from Plain-brown Woodcreeper (15 specimens) and *Myrsidea* sp. (10 specimens) and *Tyranniphilopterus* sp. (11 specimens) from White-crowned Manakin (20 specimens).

Louse DNA sequences

For *Furnaricola* sp., from Plain-brown Woodcreeper, phylogenetic analyses based on concatenated mitochondrial sequences (1,034 bp) revealed a clade formed by individuals from the Napo and Jau areas of endemism and another clade formed by individuals from Guiana (Fig. 2A). BI and ML methods recovered similar topologies. Analysis of population structure in BAPS also revealed two distinct populations on either side of the Negro river (Fig. 2E). Uncorrected p-distances estimated in Mega show that lice from the eastern bank of the Negro

River were 17.8% divergent from the group formed by the individuals sampled west of this river.

The concatenated phylogenetic analysis of mitochondrial sequences (1,034pb) from *Myrsidea* sp. *ex* White-crowned Manakin revealed that the samples from Jau formed a clade sister to the single sample from Guiana (Fig. 2B). The phylogenetic trees (BI and ML) recovered basically the same topology. Population structure analysis in BAPS also found Jau and Guiana as distinct populations (Fig. 2E). However, the divergence between Jau and Guiana is only 0.6% uncorrected p-distance.

For *Tyranniphilopterus* sp. *ex* White-crowned Manakin, for which the 2 mtDNA fragments were not concatenated, separate phylogenetic analyses of both fragments showed that individuals from Guiana and Jau formed a clade, whereas individuals from Napo were grouped only in the analysis of the long fragment (Fig. 2 C and D). BAPS population structure analysis recovered similar results for both fragments: Guiana and Jau as a single population and Napo as another one (Fig. 2E). Genetic divergence (uncorrected p-distance) between (Guiana, Jau) clade and Napo clade estimated from both COI fragments were relatively low: 0.5% and a 1.5% divergence for short COI and long COI, respectively (Fig. 2B-E).

Avian Host DNA sequences

Analyses of COI from both host species revealed results concordant with those of their lice. For Plain-brown Woodcreeper, samples from Jau and Napo form a single clade that is not sister to samples from the opposite margin of the Negro river. Instead the Napo/Jau clade groups with a clade including samples from Choco (west of the Andes), and these are sister to samples from Guiana (Fig. 3A). This is supported by BAPS, which revealed 3 major groups: Guiana, (Jau, Napo) and Chocó (Fig. 3C). Estimates of uncorrected p-distance in Mega revealed 6.0% divergence between samples collected on the west and east margins of the Negro river.

For White-crowned Manakin, the phylogenetic analysis recovered samples from Northern Amazonia east of the Andes in a single clade, without structure in relation to location along the Jau and Negro rivers (Fig. 3B). This finding is corroborated by BAPS, which found only one population among samples from Guiana, Jau and Napo (Fig. 3B).

DISCUSSION

In most cases, the genetic divergence, BAPS, and both BI and ML phylogenetic analyses of mtDNA revealed concordant patterns for each louse genus and its host. *Furnaricola* sp. and its host the Plain-brown Woodcreeper, both exhibit concordant population structure and large genetic divergence across the Negro River. White-crowned Manakin does not exhibit population structure across any of the rivers (Negro or Japurá) that we studied. Instead, White-crowned Manakin is a single population across these areas, but populations of their lice (*Myrsidea* sp. and *Tyranniphilopterus* sp.) seem to have incipient differentiation across the Negro and Japurá, which is suggestive evidence of a possible recent barrier affecting populations in the region, with influence on the louse populations recorded in louse mtDNA, but not yet recorded in the avian host's mtDNA.

Plain-brown Woodcreeper and *Furnaricola* sp.

Given that phylogenetic and population analysis for *Furnaricola* sp. demonstrated that specimens sampled from opposite margins of the Negro river constituted distinct populations with genetic divergence of 17.8% uncorrected p-distance, it is possible that these are even different louse morphospecies.

Both the literature (Weir and Price 2011, Mila et al. 2012) and our own analysis of Plain-brown Woodcreeper indicate that populations on opposite margins of the Negro river are also quite distinct genetically, and are not sister groups, with the western population (*D. f.*

phaechroa) appearing as more related to populations that occur west of the Andes, whereas the eastern population (*D. f. fuliginosa*) is sister to populations from southeastern Amazonia. Our data indicates smaller genetic divergence (uncorrected p-distance) between Plain-brown Woodcreeper populations from opposite margins of the Negro river (6.0%) when compared to the divergence found for their parasitic lice (17.8%), corroborating the faster divergence rate of the parasites and a long history of independent evolution for both hosts and parasites.

An important factor to consider about *Furnaricola* sp. is that they appear to be generalist morphotypes, which occur mainly on the host body. In some studies, body lice have a lower capacity for dispersal and host switching (Clayton and Johnson, 2003; Clayton et al., 2003), and would presumably act as a strong marker of host evolutionary history as well, since they would share a concordant history. However, we do not yet know enough about the ecology of *Furnaricola* to make inferences about its capacity for dispersal and host switching. Given the shorter generation times and higher rates of molecular evolution of the lice, the relatively high divergence in *Furnaricola* sp. between both margins of the Negro river suggests that the hosts are isolated and have been diverging for a long period of time without gene flow across the river. Furthermore, our study corroborates others that demonstrate the importance of the lower Negro River as a barrier to many species such as birds, monkeys and plants (Boubli et al., 2015; Nazareno et al., 2017; Naka and Brumfield 2018) and now their associated parasites.

White-crowned Manakin and its lice (*Myrsidea* sp. and *Tyranniphilopterus* sp.)

Unlike *Furnaricola* sp., *Myrsidea* sp. and *Tyranniphilopterus* sp. (ex. White-crowned Manakin) were not highly divergent across either the Negro or Japurá rivers. The Negro seems to have some effect as a barrier for *Myrsidea*, but the lower divergence (0.6% p-distance) suggests a very recent restriction of gene flow between populations on opposite margins. The long COI fragment from *Tyranniphilopterus* sp. also revealed some genetic structure

concordant with the Japurá river, with slightly higher associated genetic divergence (1.3% p-distance).

The low and/or incipient divergence across the Negro and Japurá rivers found for lice parasitizing White-crowned Manakin is in agreement with a lack of host divergence across this barrier. Mila et al. (2012) pointed out that White-crowned Manakin lineages are divergent across the Amazon river but not across the northern Amazonian rivers such as the Negro and Japurá, and our findings for both genera of White-crowned Manakin lice corroborate this since we found only a single population across the northern Amazon and another west of the Andes. This indicates that White-crowned Manakin has higher dispersal capability than Plain-brown Woodcreeper and is, or was until very recently, able to cross the Negro River. Differences in dispersal can lead to differences in genetic structure, which in turn could potentially lead to differences in genetic divergence since the lice are closely tied to the host, which have little divergence between these populations. The incipient structure found for the parasites suggest recent restriction to gene flow across these rivers, which is not yet reflected in the hosts genetic divergence across these same geographic barriers.

Phylogeography of lice and birds

White-crowned Manakin and Plain-brown Woodcreeper are widespread species, distributed throughout the upland Terra Firme forest of Amazonia (Marantz et al., 2018) and beyond, but our analysis of their mtDNA COI sequences revealed that these avian host species have quite distinct patterns of diversification. As shown by Weir and Price (2011), we found two distinct and not closely related clades of Plain-brown Woodcreeper on opposite margins of the Negro river. However, for White-crowned Manakin we did not find divergence across the Negro river, but instead found a single population across northern Amazonia (corroborating Mila et al 2012). Accordingly, lice from each of these hosts exhibit corresponding patterns of

diversification across northern Amazonia, suggesting that the biogeography of the host influences the pattern of diversification of its louse.

Although the Negro and Japurá rivers do not separate linages for White-crowned Manakin, our analysis revealed that they may separate louse lineages, but these linages are not as highly supported or divergent across the rivers as are the ones from Plain-brown Woodcreeper. For *Tyranniphilopterus* parasitizing White-crowned Manakin, long COI divergence is 1.5% between specimens collected on opposite margins of the Japurá river. For *Myrsidea* parasitizing White-crowned Manakin, we found that specimens on either bank of the Rio Negro averaged 0.6% divergence. Thus, the low divergence and weakly supported clades in these two louse genera are perhaps suggestive that White-crowned Manakin populations from opposite margins of the Negro and Japurá rivers are very recently isolated and have not yet accumulated mtDNA divergence nor developed reciprocal monophyly.

In conclusion, data from parasites can help to corroborate or test patterns of population divergence identified in their hosts. Our results constitute important but rarely presented evidence that these parasites likely rely on host dispersal for their own dispersal, and do not seem to disperse across barriers through host switching. We found that the parasites studied here have in most cases diverged across biogeographic barriers in a similar pattern to that of their hosts. However, *Myrsidea* and *Tyranniphilopterus* from the White-crowned Manakin exhibit low level divergence and population subdivision that might also suggest recent isolation of their hosts across the rivers. Our results further underscore the importance of parasites in better understanding biogeographic history and endemism of their hosts

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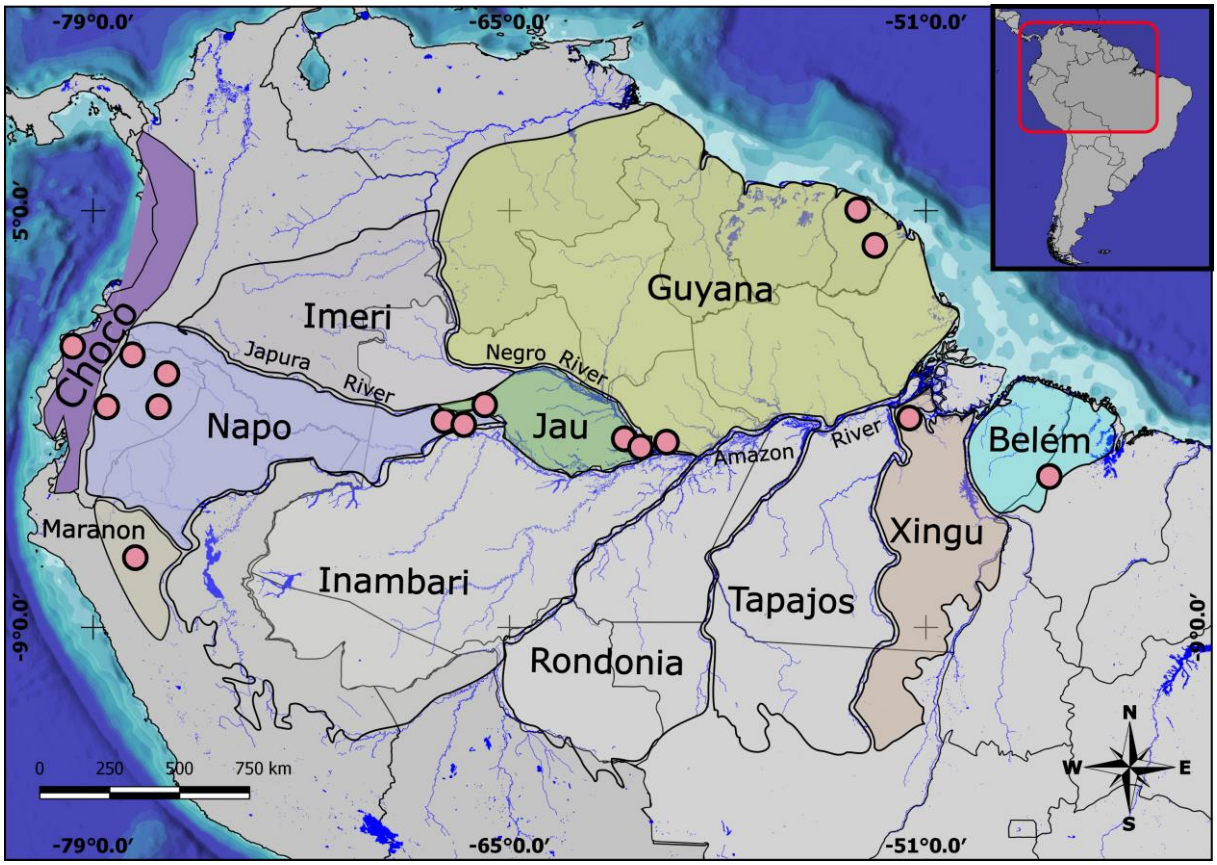

Figure 1. Map of northern South America showing the sampling localities as red dots and areas of endemism currently recognized in Amazonia**.** Detailed localities are provided in Table S1.

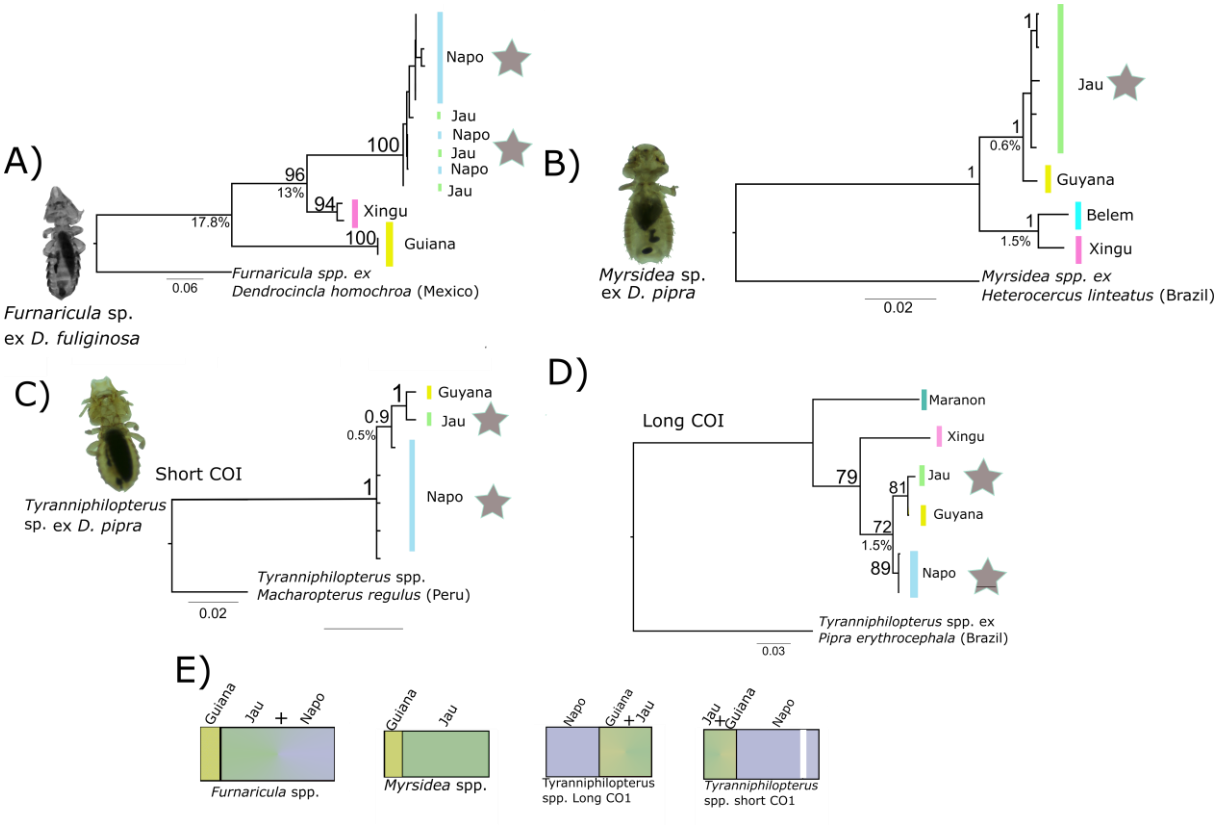

Figure 2. Louse Bayesian Inference trees and BAPS results for the 3 louse genera. The colors indicate the area of endemism. The numbers on the top of the branch indicate nodal support and below the branch are average p-distances among clades. Black stars identify specimens from the western margin of the Negro river. (**A**) *Furnaricola* sp.; (**B**) *Myrsidea* sp.; (**C**) *Tyranniphilopterus* sp. short COI; (**D**) *Tyranniphilopterus* sp. long COI; and (**E**) BAPS population structure for all 3 louse genera.

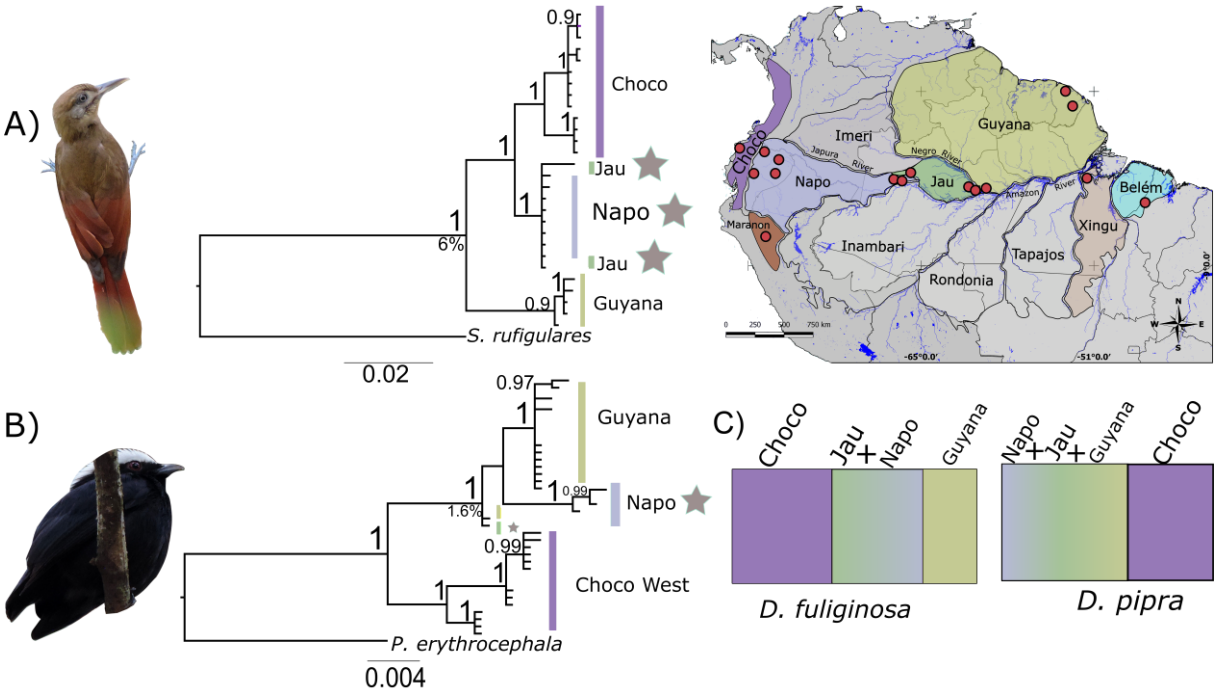

Figure 3. Host Bayesian Inference trees and BAPS results for (**A**) Plain-brown Woodcreeper (*Dendrocincla fuligionosa)* (**B**) White-crowned Manakin (*Dixiphia pipra*). The colors indicate area of endemism and the numbers on the top of the branch indicate nodal support and those below the branches indicate average p-distance among clades. Black stars identify specimens from areas of endemism that are on the western margin of the Negro river.

Table 1. Table of parasite specimens used in this study.

Louse genera	Louse Voucher	Host Tissue N°	Host	Locality	Lat/Long
Furnaricola sp.	Fusp.Defu.1.22.2018.1	INPA A 20700	*Dendrocincla fuliginosa*	Brazil, Manaus, Reserva Ducke	-2.93, -59.97
Furnaricola sp.	Fusp.Defu.1.22.2018.2	INPA A 20701	*Dendrocincla fuliginosa*	Brazil, Manaus, Reserva Ducke	-2.93, -59.97
Furnaricola sp.	Fusp.Defu.1.22.2018.3	INPA A 20716	*Dendrocincla fuliginosa*	Brazil, Amazonas, Açutuba	-3.10, -60.31
Furnaricola sp.	Fusp.Defu.1.22.2018.4	INPA A 20715	*Dendrocincla fuliginosa*	Brazil, Amazonas, Açutuba	-3.10, -60.31
Furnaricola sp.	Fusp.Defu.1.22.2018.5	INPA A 20709	*Dendrocincla fuliginosa*	Brazil, Amazonas, Açutuba	-3.10, -60.31
Tyranniphilopterus sp.	Tysp.Dipi.1.22.2018.6	INPA A 20734	*Dixiphia pipra*	Brazil, Manaus, Reserva Ducke	-2.93, -59.97
Myrsidea sp.	Mysp.Dipi.1.22.2018.7	INPA A 20735	*Dixiphia pipra*	Brazil, Manaus, Reserva Ducke	-2.93, -59.97
Myrsidea sp.	Mysp.Dipi.1.22.2018.8	INPA A 22296	*Dixiphia pipra*	Brazil, Novo Airão, RDS Rio Negro	-3.07, -60.74
Myrsidea sp.	Mysp.Dipi.1.22.2018.9	INPA A 22297	*Dixiphia pipra*	Brazil, Novo Airão, RDS Rio Negro	-3.07, -60.74
Myrsidea sp.	Mysp.Dipi.1.22.2018.10	INPA A 22312	*Dixiphia pipra*	Brazil, Novo Airão, RDS Rio Negro	-3.07, -60.74
Myrsidea sp.	Mysp.Dipi.1.22.2018.11	INPA A 22314	*Dixiphia pipra*	Brazil, Novo Airão, RDS Rio Negro	-3.07, -60.74
Tyranniphilopterus sp.	Tysp.Dipi.1.22.2018.12	INPA A 22217	*Dixiphia pipra*	Brazil, Amazonas, Açutuba	-3.10, -60.31
Myrsidea sp.	Mysp.Dipi.1.22.2018.13	INPA A 22217	*Dixiphia pipra*	Brazil, Amazonas, Açutuba	-3.10, -60.31
Furnaricola sp.	Fusp.Defu.1.22.2018.14	T19920	*Dendrocincla fuliginosa*	Brazil, Maranhão, Gurupi, REBIO Gurupi	-3.70, -46.76
Furnaricola sp.	Fusp.Defu.1.22.2018.15	T20227	*Dendrocincla fuliginosa*	Brazil, Amazonas, Japurá, Rio Mapari	-2.04 -67.28
Furnaricola sp.	Fusp.Defu.1.22.2018.16	JAP-303	*Dendrocincla fuliginosa*	Brazil, Amazonas, Japurá, Rio Mapari	-2.04 -67.28
Furnaricola sp.	Fusp.Defu.1.22.2018.17	JAP-355	*Dendrocincla fuliginosa*	Brazil, Amazonas, Japurá, Rio Acanauê	-1.93, -66.60
Furnaricola sp.	Fusp.Defu.1.22.2018.18	JAP-391	*Dendrocincla fuliginosa*	Brazil, Amazonas, Japurá, Rio Acanauê	-1.93, -66.60
Furnaricola sp.	Fusp.Defu.1.22.2018.19	JAP-536	*Dendrocincla fuliginosa*	Brazil, Amazonas, Japurá, Rio Acanauê	-1.93, -66.60
Furnaricola sp.	Fusp.Defu.1.22.2018.20	JAP-583	*Dendrocincla fuliginosa*	Brazil, Amazonas, Japurá, Rio Acanauê	-1.93, -66.60
Furnaricola sp.	Fusp.Defu.1.22.2018.21	JAP-615	*Dendrocincla fuliginosa*	Brazil, Amazonas, Japurá, Rio Acanauê	-1.93, -66.60
Furnaricola sp.	Fusp.Defu.1.22.2018.22	JAP-641	*Dendrocincla fuliginosa*	Brazil, Amazonas, Maraã, Lago Cumapi	-1.55, -65.88
Furnaricola sp.	Fusp.Defu.1.22.2018.23	JAP-858	*Dendrocincla fuliginosa*	Brazil, Amazonas, Maraã, Lago Cumapi	-1.55, -65.88

Myrsidea sp.	Mysp.Dipi.1.30.2018.1	T19891	*Dixiphia pipra*	Brazil, Maranhão, Gurupi, REBIO Gurupi	-3.70, -46.76
Tyranniphilopterus sp.	Tysp.Dipi.1.30.2018.2	JAP-844	*Dixiphia pipra*	Brazil, Amazonas, Maraã, Lago Cumapi	-1.55, -65.88
Tyranniphilopterus sp.	Tysp.Dipi.1.30.2018.3	JAP-012	*Dixiphia pipra*	Brazil, Amazonas, Japurá, Rio Acanauê	-1.93, -66.60
Tyranniphilopterus sp.	Tysp.Dipi.1.30.2018.5	JAP-029	*Dixiphia pipra*	Brazil, Amazonas, Japurá, Rio Acanauê	-1.93, -66.60
Tyranniphilopterus sp.	Tysp.Dipi.1.30.2018.6	JAP-031	*Dixiphia pipra*	Brazil, Amazonas, Japurá, Rio Acanauê	-1.93, -66.60
Tyranniphilopterus sp.	Tysp.Dipi.1.30.2018.7	JAP-037	*Dixiphia pipra*	Brazil, Amazonas, Japurá, Rio Acanauê	-1.93, -66.60
Tyranniphilopterus sp.	Tysp.Dipi.1.30.2018.8	JAP-074	*Dixiphia pipra*	Brazil, Amazonas, Japurá, Rio Acanauê	-1.93, -66.60
Tyranniphilopterus sp.	Tysp.Dipi.1.30.2018.9	P10-192	*Dixiphia pipra*	Peru, Amazonas, Quebrada 2100	-6.59, -77.55
Myrsidea sp.	Mysp.Dipi.1.30.2018.10	P10-192	*Dixiphia pipra*	Peru, Amazonas, Quebrada 2100	-6.59, -77.55
Myrsidea sp.	Mysp.Dipi.1.30.2018.11	PPBIO 063	*Dixiphia pipra*	Brazil, Pará, Potel. Flona do Caxiuanã	-1.95 -5.6
Tyranniphilopterus sp.	Tysp.Dipi.1.30.2018.12	PPBIO 063	*Dixiphia pipra*	Brazil, Pará, Potel. Flona do Caxiuanã	-1.95 -5.6
Myrsidea sp.	Mysp.Dipi.1.30.2018.13	INPA A 22301	*Dixiphia pipra*	Brazil, Novo Airão, RDS Rio Negro	-3.07, -60.74