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PROTOZOOLOGY - ORIGINAL PAPER

Mining increases the prevalence of avian haemosporidian parasites in Northeast Amazonia

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Abstract

Studies contrasting parasite prevalence and host-parasite community structure between pristine and disturbed environments will improve our understanding of how deforestation affects disease transmission and parasite extinction. To determine how infection rates of a common and diverse group of avian blood parasites (*Plasmodium* and *Haemoproteus*) respond to changes in avian host composition after mining, we surveyed 25 bird communities from pristine forests (two forest types: plateau and hillside) and reforested sites in Northeast Amazonia. Infection rates and both parasite and avian host community structure exhibited considerable variation across the deforestation gradient. In opposition to the emerging pattern of lower avian haemosporidian prevalence in disturbed tropical forests in Africa, we show that secondary forests had higher haemosporidian prevalence in one of the largest mining areas of Amazonia. The dissimilarity displayed by bird communities may explain, in part, the higher prevalence of *Haemoproteus* in reforested areas owing to the tolerance of some bird species to open-canopy forest habitat. On the other hand, deforestation may cause local extinction of *Plasmodium* parasites due to the loss of their avian hosts that depend on closed-canopy primary forest habitats. Our results demonstrate that forest loss induced by anthropogenic changes can affect a host-parasite system and disturb both parasite transmission and diversity.

Keywords Avian malaria · Bauxite mining; deforestation · Disease ecology · Parasite diversity · Reforestation

Introduction

Anthropogenic changes in land cover (e.g., agriculture, dam building, fragmentation, mining) can alter host-parasite interactions and the transmission dynamics of endemic pathogens (Patz et al. 2004, 2008; Sehgal 2015). This in turn may lead to spillover of parasitic or pathogenic organisms with subsequent emergence and outbreaks of zoonotic and human diseases (Patz et al. 2000; Keesing et al. 2010). For instance, increased infection risk and outbreaks of malaria—one of the most lethal pathogenic diseases in humans—were linked to deforestation and gold mining in the Brazilian Amazon (Barbieri et al. 2005; Olson et al. 2010). Landscape changes, such as forest clearing for human activities, can create structures (e.g.,

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mining pits, roads, craters, culverts) capable of collecting rainwater in some areas (Patz et al. 2004). This increases the availability of water sources for vector reproduction and development, thus boosting vector abundance (e.g., malaria-transmitting mosquitoes) and leading to an increase in the prevalence of vector-borne diseases (Patz et al. 2004).

Deforestation is responsible for major habitat change that can affect hosts, vectors, and parasites (Sehgal 2015). Fragmentation, tree cover loss, and edge effect can lead to changes in community composition of hosts and vectors, which could then affect parasite community composition and disease transmission dynamics (van Hoesel et al. 2019). For instance, changes in microhabitats required for hematophagous insect reproduction and larval development, such as local increase in temperature and water availability (e.g., accumulated water in pools), could potentially accelerate the development and spread of vector-transmitted parasites (Patz et al. 2004; Stresman 2010; Sehgal 2015; van Hoesel et al. 2019). Therefore, not only can deforestation lead to the loss of biodiversity, but could also disrupt a host-parasite-vector system (revision in Patz et al. 2000; Stresman 2010; Sehgal 2015), with the main outcome being an increase in disease transmission (Keesing et al. 2010). Moreover, areas harboring elevated biodiversity, such as Amazonia could serve as a source pool for new pathogens (Keesing et al. 2010).

Avian malaria parasites (*Plasmodium*) and related haemosporidians (*Haemoproteus* and *Leucocytozoon*) comprise a diverse and widespread group of vector-transmitted parasites found in avian communities across zoogeographical regions worldwide (Valkiūnas 2005; Clark et al. 2014). Due to their different degrees of avian host specificity and their dependency on sexual reproduction in different groups of hematophagous vectors, avian haemosporidians often infect several host species and exhibit variation in prevalence among host species and across avian communities (Valkiūnas 2005; Fecchio et al. 2020). Avian haemosporidian parasites (*Haemoproteus* and *Plasmodium*) and their avian hosts comprise a well-suited system for understanding the effects of disturbance and reforestation on prevalence, lineage diversity, and bird-parasite community structure. Amazonia not only harbors an astonishing diversity of avian malaria parasites, but their diversity also tracks bird host diversity (Fecchio et al. 2018a), with this megadiverse biome serving as the primary source of avian malaria biodiversity for all South American biomes (Fecchio et al. 2019). Although historical factors have played a significant role in shaping the diversity and distributions of avian malaria parasites across Amazonia (Fecchio et al. 2018b), contemporary anthropogenic changes, such as deforestation, could potentially affect local prevalence, diversity, and parasite community structure by altering the community composition of avian hosts.

Here, we used a standard barcoding approach to assess the diversity of evolutionary lineages of avian haemosporidian parasites from the genera *Plasmodium* and *Haemoproteus,* and describe their phylogenetic relationships in both disturbed and undisturbed avian communities in Northeast Brazilian Amazonia. We tested whether the diversity of haemosporidian parasites and their avian hosts differs between pristine forest and nearby disturbed areas that are now reforested. Finally, we examined spatial patterns of prevalence for each haemosporidian genus across bird communities to test whether reforested areas exhibited higher infection rates than pristine forest.

Materials and methods

Study site

We conducted this study in the Saracá-Taquera National Forest (01° 21′ S; 56° 22′ W), a sustainable use reserve within the limits of the township of Oriximiná, in northwestern Pará, Brazil (Fig. 1). The reserve is located in the Trombetas River basin, an important tributary of the Amazon River. The local vegetation is classified as typical of the dense rainforest region and Amazon low plateaus subregion (IBGE – Instituto Brasileiro de Geografia e Estatística 1992; Salomão et al. 2012). In this area, there is significant mining of bauxite on plateaus, which influences the landscape by creating a mosaic of pristine forest (undisturbed) and reforested areas. After mining, the ground is prepared and covered with native plant seedlings and fruit tree species to promote attraction of frugivorous species. Hence, reforested areas consist of native plant species in different ages of restoration (ranging from 3 to 11 years) and canopy height (ranging from 2 to 10 m). Furthermore, due to small and medium tributaries of the Trombetas River and topography (hilly landscape), there is great heterogeneity in forest vegetation of pristine forests (plateau and hillside forests), with mining zones adding further heterogeneity due to different ages of reforestation.

Bird sampling

Birds were sampled using mist nets with a sampling effort of 105 days divided between two sampling campaigns: May 2011, and February to April 2012. We sampled a total of 25 avian communities located in pristine forests (hillside and plateau) and reforestation sites (Fig. 1, Supporting Information Table S1). Approximately 30 μL of blood was collected from the brachial vein of each captured bird and stored in 95% ethanol. Captured birds were ringed and released in accordance with corresponding permits (license issued by Instituto Chico Mendes de Conservação da Biodiversidade - ICMBio number 27578-1).

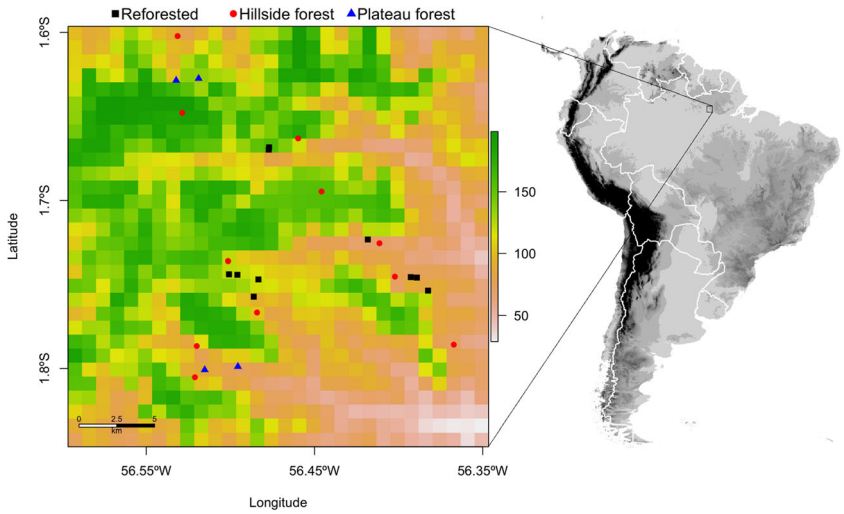

Fig. 1 Geographic location of 25 survey sites near Porto Trombetas, (Pará, Brazil) in South America. Elevation (in meters) is represented by the white to green color scale in the map inset

Parasite detection

Total DNA was extracted from avian blood samples using the Qiagen DNeasy 96 Blood and Tissue kit (Qiagen, Valencia, CA), following the Qiagen protocol for blood in 95% ethanol. DNA extractions were screened for *Plasmodium* and *Haemoproteus* using a nested PCR method developed by Hellgren et al. (2004). The first set of primers (HaemNF1 and HaemNR3; see Hellgren et al. (2004) for details) used were designed to target a conserved region of the mitochondrial cytochrome b gene of *Plasmodium*, *Haemoproteus*, and *Leucocytozoon* parasites. In the second PCR, primers (HaemF and HaemR2, see Bensch et al. (2000) for details) were used to amplify only *Plasmodium* and *Haemoproteus* mitochondrial DNA. Information on detailed laboratory methods and PCR conditions can be found in Hellgren et al. (2004). Positive controls were included in all PCR runs, with each individual host screened only once. Due to the high sensitivity of nested PCR, negative controls were also included in runs to check for possible contamination and false positives, although none was found in any PCR run. PCR products were purified using Exo-SAP-IT (Affymetrix, Santa Clara, CA, USA) and sequenced using the BigDye terminator v3.1 cycle sequencing kit (Applied Biosystems, Foster City, CA, USA). Forward and reverse sequences were visualized, assembled, and reconciled using Geneious (v8.1.8, Kearse et al. 2012) or Sequencher v.5.0.1 (Gene Codes Corp., Ann Arbor, MI). Consensus sequences were aligned using BioEdit v7.2.0 (Hall 1999). Sequence identities were verified with a local BLAST against the MalAvi database (Bensch et al. 2009). Parasite lineages were named after the host of origin following standard protocol (Bensch et al. 2009). All sequences are deposited in MalAvi and GenBank, and accession numbers can be found in the raw dataset (Supporting Information Table S1).

Phylogenetic reconstruction

Assembled lineages were used for molecular phylogenetic reconstruction using the GTR+I+G model of nucleotide substitution as determined by jModelTest (Guindon and Gascuel 2003; Darriba et al. 2012). A total of 18 lineages were included in the analysis: eight *Haemoproteus* (four subgenus *Haemoproteus*, four subgenus *Parahaemoproteus*) and 10 *Plasmodium*. *Leucocytozoon fringillarum* lineage ZOLEU02 (GenBank Accession No. FJ168564) was used as the outgroup, based on the topologies published by Galen et al. (2018).

We obtained a time-calibrated tree using the Bayesian relaxed clock model (Drummond et al. 2006) in BEAST 1.10.4 (Drummond et al. 2012). We generated two independent runs with parameters as follows: an uncorrelated lognormal relaxed clock, Yule process, 100 million generations of MCMC (Markov chain Monte Carlo), parameters sampled every 5000 generations, and 10% of generations discarded as burn-in. To obtain absolute ages for cladogenetic events in the malaria trees, we used the mutation rate of 0.006 mutations per lineage per million years estimated by Ricklefs and Outlaw (2010). Convergence and performance of runs were inspected using Tracer 1.7.1. (http://beast.bio.ed.ac.uk/Tracer), making sure that ESS (effective sample size) values were higher than 200. The maximum clade credibility (MCC) tree was generated using TreeAnnotator. Trees with divergence times were visualized in FigTree 1.4.2 (http://tree.bio.ed.ac.uk/software/figtree/).

Statistical analysis

We used generalized linear models (GLM) with a binomial error distribution to test for differences in the prevalence of haemosporidians between the different forest types. Models were fitted by pooling all lineages, considering both *Haemoproteus* lineages and *Plasmodium* lineages. We used

a likelihood ratio test to test for differences in prevalence by comparing models with and without the explanatory variable "forest types" (a three-level categorical variable: hillside forest, plateau forest, and reforested sites). Model assumptions were checked using diagnostic plots of residual distributions, and models were also checked for overdispersion. Models were consistent with GLM assumptions. We used the function "glm" implemented in the R package "MASS" (Venables and Ripley 2002) to fit models. We used the fitted response and standard error estimates of fitted GLM to visualize the fitted response of GLM, which were obtained using the "effects" R package (Fox and Weisberg 2019). To infer differences in the composition (presence and absence) of bird species and haemosporidian lineages in the different forest types, principal coordinate analysis (PCoA) was used with the Jaccard index. We used permutation tests (with 999 permutations) to test whether differences in composition were significant, and a Tukey post hoc test was applied when significant differences were found. PCoA was conducted using the function "cmdscale," and the permutation test used the "adonis2" function implemented in the "vegan" R package (Oksanen et al. 2019). All statistical analyses were conducted in the R version 3.6.2 (R Core Team 2019).

Results

We analyzed data collected from 304 individual birds surveyed across 25 avian communities in pristine forests (hillside and plateau) and reforested areas (Fig. 1). These individuals belong to 77 avian species, 21 families, and eight orders (see Supporting Information Tables S1, S2, and S3 for sample size, prevalence, and parasite lineage name found by avian host taxon, time of year, and location). Overall haemosporidian prevalence was 15.74%, with heterogeneity across sampling sites ($\bar{x} = 15.82\% \pm 16.52\%$ s.d.) and host species (Supporting Information Tables S1 and S3). When we pooled *Plasmodium* and *Haemoproteus* infections, we found that haemosporidian prevalence was significantly different among forest types (LRT: $X^2 = 16.482$, df = 2, $P = 0.0003$). This result was due to reforested areas having higher prevalence than pristine hillside and plateau forests (Fig. 2; Table 1a). Higher prevalence of *Haemoproteus* was also found for reforested areas when analyzed separately from *Plasmodium* (LRT: $X^2 = 36.492$, df = 2, $P < 0.0001$; Fig. 3; see Table 1b for model details). For *Plasmodium* infections alone, we found higher prevalence in plateau forest (Fig. 4), but differences in infection prevalence were not significant (LRT: $X^2 = 4.8141$, df = 2, $P = 0.09$; Table 1c).

We found that the three forest types had dissimilar composition of bird species (PERMANOVA: $F = 8.85$, df = 2, 22, $P = 0.02$). Pairwise comparisons showed that the plateau forest had a distinct bird community composition when

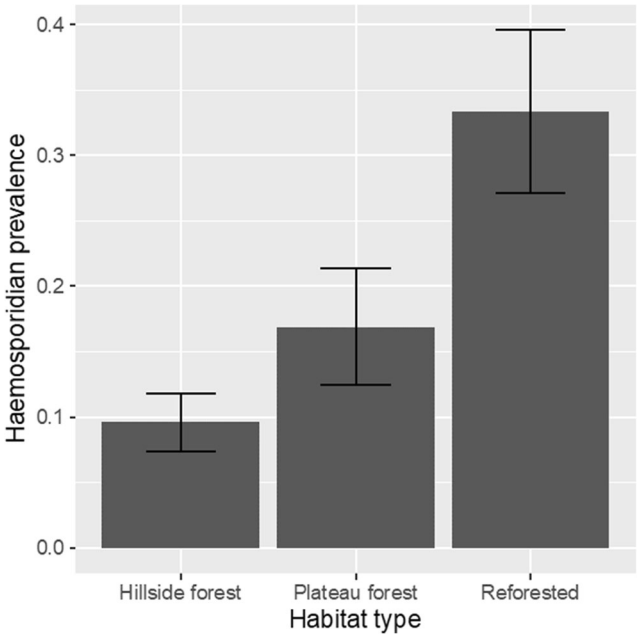

Fig. 2 Haemosporidian prevalence (and standard errors) in different forest habitat types located in the 25 survey sites near Porto Trombetas (Pará, Brazil)

compared to hillside forest (P adj. = 0.004) and reforested sites (P adj. = 0.001). However, hillside forest and reforested sites had similar avian community composition (P adj. = 0.758; see Fig. 5a). The different forest types had a tendency toward dissimilar community composition of haemosporidian parasites (PERMANOVA: $F = 1.4301$, df = 2, 13, $P = 0.06$; see Fig. 5b). The richness of *Plasmodium* lineages was higher in pristine sites, with only two lineages identified in reforested sites (Fig. 6). Also, overall haemosporidian lineage richness was higher in pristine sites and dominated by lineages of *Plasmodium*, whereas in reforested sites, there were more than twice as many *Haemoproteus* lineages than *Plasmodium* lineages (Fig. 6).

Discussion

Land cover change caused by bauxite mining disturbed a host-parasite system at a local scale in Amazonia. The effects of reforestation after mining activities were distinct for haemosporidian genera and for the composition of avian host communities. Although *Haemoproteus* prevalence was significantly higher in reforested areas, *Plasmodium* prevalence showed a tendency toward higher prevalence in plateau forests (a pristine forest type). However, it is important to note the low sample size for the pristine plateau forest sites ($n = 4$), which may account for only a tendency for higher *Plasmodium* prevalence and not a significant result. Overall, avian community composition was dissimilar between pristine and reforested sites, whereas parasite lineage composition

Table 1 Generalized linear model (GLM) for the prevalence of *Haemoproteus* and *Plasmodium* pooled (a), *Haemoproteus* prevalence only (b), and *Plasmodium* prevalence only (c) in three different forest types: (1) reforested, (2) hillside forest, and (3) plateau forest in the 25 survey sites near Porto Trombetas (Pará, Brazil). Values are in logit and a binomial error distribution was used

Model	Terms	Estimate (s.e.)	*Z*	*P*
(a) *Haemoproteus* and *Plasmodium*	Intercept	− 0.6931 (0.2810)	− 2.467	0.0136
	Hillside forest*	− 1.5488 (0.3795)	− 4.081	< 0.0001
	Plateau forest*	− 0.8995 (0.4234)	− 2.125	0.0336
(b) *Haemoproteus*	Intercept	− 0.9410 (0.2948)	− 3.192	0.0014
	Hillside forest*	− 2.8260 (0.5854)	− 4.828	< 0.0001
	Plateau forest*	− 3.3075 (1.0493)	− 3.152	0.0016
(c) *Plasmodium*	Intercept	− 2.8904 (0.5932)	− 4.873	< 0.0001
	Hillside forest*	0.3555 (0.6594)	0.539	0.5899
	Plateau forest*	− 1.1939 (0.6778)	1.761	0.0782

*Relative to reforested sites (presented as the intercept)

tended toward dissimilarity. Parasite lineage diversity was also dissimilar between sites. Pristine sites harbored more lineages and were dominated by *Plasmodium*, whereas reforested sites were less diverse and harbored more *Haemoproteus* lineages.

The effects of land use on avian malaria prevalence, diversity, and specificity at large geographic scales are yet to be evaluated. However, at a local scale, we found that *Haemoproteus* prevalence was higher in avian communities from reforested areas in Northeast Amazonia. This is in contrast with the findings reported for two Afrotropical host species. Chasar et al. (2009) showed that prevalence of *Haemoproteus* and *Leucocytozoon* was significantly higher in undisturbed rain forest in Cameroon when compared with disturbed areas (agriculture preceded by logging). Similarly, Bonneaud et al. (2009) reported a higher prevalence of *Plasmodium* from three host species in undisturbed areas in Cameroon. However, haemosporidian prevalence was higher in early (5 years) abandoned pasture when compared to later successional stages of abandoned pasture (at least 13 years) in a seasonally dry tropical forest in Brazil (Ferreira Junior et al. 2017).

Habitat fragmentation can also affect infection rates of haemosporidian parasites. In tropical rain forests of Australia, *Haemoproteus* prevalence was significantly higher in continuous forests when compared with fragmented habitats (Laurance et al. 2013). However, in the Brazilian Atlantic Forest, habitat fragmentation had no effect on the prevalence of *Haemoproteus*, *Plasmodium*, and *Trypanosoma* (Sebaio et al. 2010). A recent study contrasting prevalence of

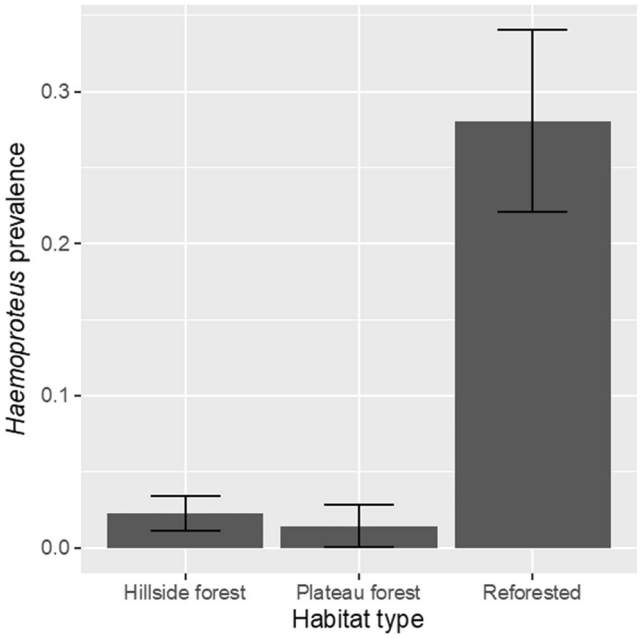

Fig. 3 *Haemoproteus* prevalence (and standard errors) in different forest habitat types located in the 25 survey sites near Porto Trombetas (Pará, Brazil)

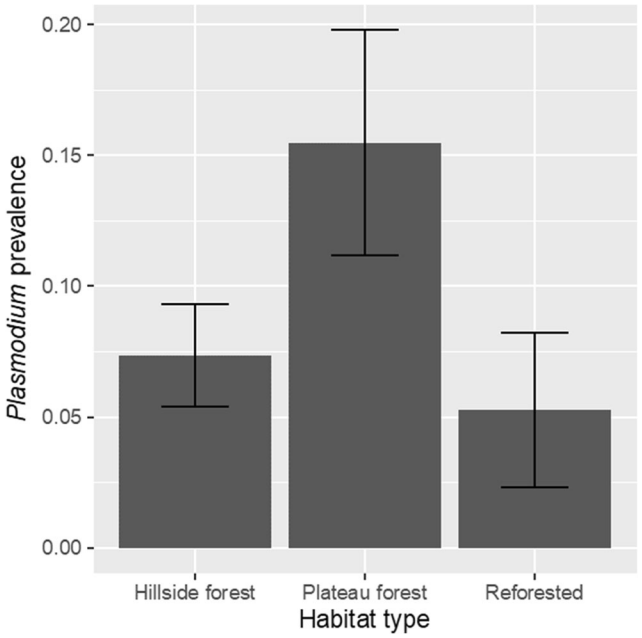

Fig. 4 *Plasmodium* prevalence (and standard errors) in different forest habitat types located in the 25 survey sites near Porto Trombetas (Pará, Brazil)

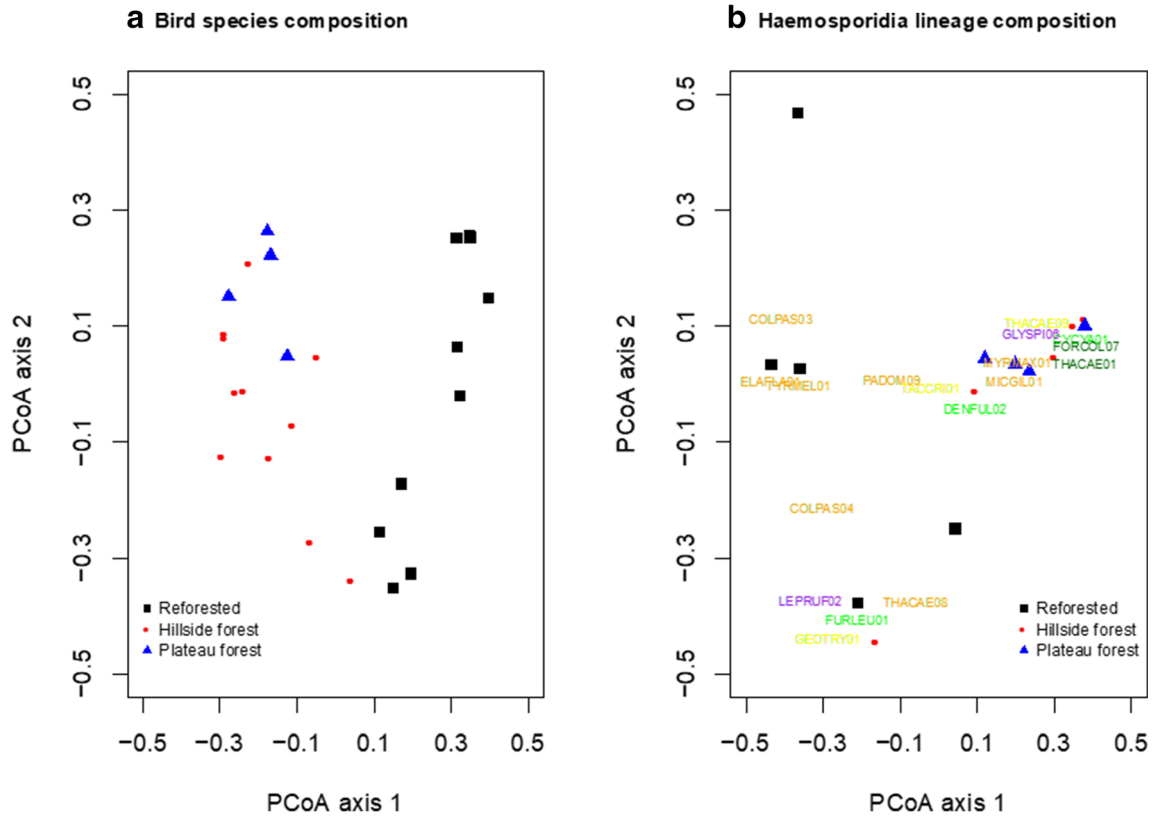

Fig. 5 Principal coordinate analysis (PCoA) of the dissimilarity of bird assemblages (**a**) and haemosporidian lineage assemblages (**b**). Black squares indicate reforested sites, red circles indicate hillside forest, and blue triangles indicate plateau forests. The Jaccard index was used to determine the dissimilarities in bird species and haemosporidian lineages. Sites with no occurrence of haemosporidian lineages were removed from the analysis, producing a lower number of sites used to determine differences in the composition of haemosporidian lineages. Colors for lineage names were used for illustrative purposes only

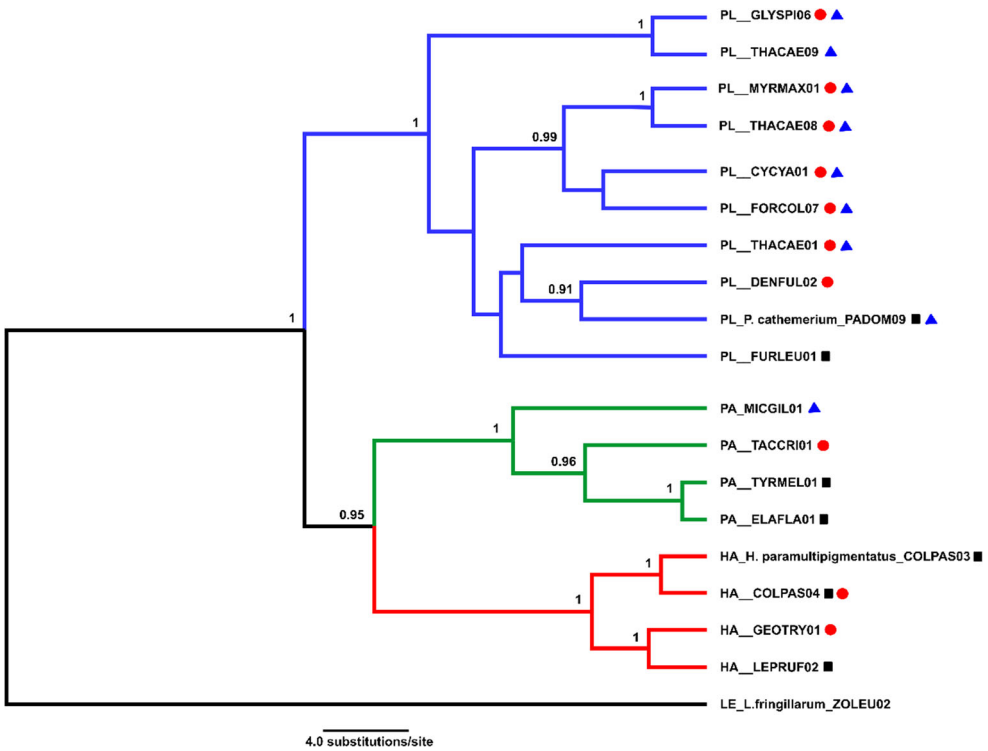

Fig. 6 Phylogenetic reconstruction of 18 haemosporidian lineages identified in 25 sampling sites based on Bayesian inference analysis of partial cytochrome b sequences. Abbreviations preceding each lineage name identify the haemosporidian genus: PL for *Plasmodium* (blue clade); PA for *Parahaemoproteus* (green clade); HA for *Haemoproteus* (red clade); and LE for *Leucocytozoon* (outgroup). Black squares indicate reforested sites, red circles indicate hillside forest, and blue triangles indicate plateau forests. Only posterior probability nodal support greater than 0.9 is shown

haemosporidian parasites and mosquito abundance among pristine forest, fragmented forest, and young palm oil plantation in Cameroon showed that pristine forest had the highest *Plasmodium* prevalence, whereas young palm oil plantation had the lowest prevalence of *Plasmodium* (Tchoumbou et al. 2020). Moreover, *Plasmodium* prevalence positively correlated with mosquito abundance in fragmented forest (Tchoumbou et al. 2020). For *Haemoproteus* infection, the highest prevalence was also recorded in pristine forest, but fragmented forest had the lowest prevalence for this parasite genus. Although there are inconsistencies, most studies cited previously have shown a higher prevalence of haemosporidian parasites in undisturbed sites. We did find a much higher diversity of *Plasmodium* lineages and a tendency toward higher *Plasmodium* prevalence in undisturbed plateau forests, corroborating this view. However, our data on *Haemoproteus* prevalence and those of Ferreira Junior et al. (2017) find higher prevalence in disturbed sites.

Spatial variation in haemosporidian infection and lineage diversity could be caused by changes in avian host community composition (Fecchio et al. 2018a), vector community composition (Ishtiaq et al. 2008), mosquito abundance (Ferreira Junior et al. 2016; Fecchio et al. 2017; Ferraguti et al. 2018), vector feeding habitats (Chasar et al. 2009; Santiago-Alarcon et al. 2012; Tchoumbou et al. 2020), and vector competence (Ishtiaq et al. 2010; van Hoesel et al. 2019). Forest loss could potentially influence all these aspects due to alteration of vegetation structure, microhabitat, and niche requirements for both avian hosts and insect vectors regardless of the geographic scale. Our analyses for one of the largest mining areas in Amazonia (Sonter et al. 2017) demonstrate a positive and significant association between forest loss and prevalence of *Haemoproteus* in the avian host communities. Such a link is expected because both subgenera of *Haemoproteus*—*H. Haemoproteus* and *H. Parahaemoproteus* (Valkiūnas 2005)—are transmitted by vectors, hippoboscidae flies and biting midges, respectively, that do not depend on clean standing water for reproduction. Moreover, these two parasite subgenera also infect frugivorous bird species, which are especially diverse in Amazonia. These birds have a high tolerance for open habitat where pioneering fruit trees are available. This host attribute could promote the occupancy of both avian hosts and *Haemoproteus* lineages in growing secondary forests (reforested sites) after mining activities, and thus may explain the higher prevalence of these parasites in reforested areas. Our work, along with that of Tchoumbou et al. (2020), demonstrates that *Plasmodium* responds differently to forest loss compared to *Haemoproteus*. *Plasmodium* infection and diversity were both higher in pristine forests, possibly because of higher diversity of habitat structure that may harbor a higher diversity of mosquito species that includes competent vectors, thus ensuring *Plasmodium* transmission (Tchoumbou et al. 2020).

Forest loss leads to biotic homogenization in Amazonia by reducing beta diversity of free-living organisms (Solar et al. 2015). We have shown that the prevalence and community structure of avian haemosporidian parasites are also altered after deforestation. Our results also offer support for biotic homogenization of avian haemosporidian parasites, as demonstrated by their avian hosts at a larger scale (Solar et al. 2015). Both processes that drive biotic homogenization (extinction of resident species and invasion of species into new areas; revision in Olden and Poff 2003) can be observed for haemosporidian lineages in Porto Trombetas. Homogenization for haemosporidian parasite lineages is likely driven by local extinction of competent vectors followed by the colonization of generalist parasite lineages with high dispersal capabilities such as PADOM09 and COLPAS04. These generalist parasites could have arrived in Amazonia through migratory bird species that forage in open forest (e.g., flycatchers and doves in reforested areas) and shifted to the resident bird species found in closed-canopy forests. Although our data do not allow for an analysis of host and habitat specificity, future studies addressing avian haemosporidian specialization across landscapes with different land use are necessary to disentangle recent anthropogenic effects from historical factors involved in host range expansion, diversity, and infection risk of these parasites across Amazonia.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00436-020-06986-9.

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Compliance with ethical standards

Both the American Ornithologist's Union and University of North Dakota Animal Care and Use Committee guidelines (Project # 1402-1) for ethically collecting avian blood and tissue samples were strictly followed.

Conflict of interest The authors declare that they have no conflict of interest.

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