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Loss of forest cover and host functional diversity increases prevalence of avian malaria parasites in the Atlantic Forest

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ABSTRACT

Host phylogenetic relatedness and ecological similarity are thought to contribute to parasite community assembly and infection rates. However, recent landscape level anthropogenic changes may disrupt host-parasite systems by impacting functional and phylogenetic diversity of host communities. We examined whether changes in host functional and phylogenetic diversity, forest cover, and minimum temperature influence the prevalence, diversity, and distributions of avian haemosporidian parasites (genera *Haemoproteus* and *Plasmodium*) across 18 avian communities in the Atlantic Forest. To explore spatial patterns in avian haemosporidian prevalence and taxonomic and phylogenetic diversity, we surveyed 2241 individuals belonging to 233 avian species across a deforestation gradient. Mean prevalence and parasite diversity varied considerably across avian communities and parasites responded differently to host attributes and anthropogenic changes. Avian malaria prevalence (termed herein as an infection caused by *Plasmodium* parasites) was higher in deforested sites, and both *Plasmodium* prevalence and taxonomic diversity were negatively related to host functional diversity. Increased diversity of avian hosts increased local taxonomic diversity of *Plasmodium* lineages but decreased phylogenetic diversity of this parasite genus. Temperature and host phylogenetic diversity did not influence prevalence and diversity of haemosporidian parasites. Variation in the diversity of avian host traits that promote parasite encounter and vector exposure (host functional diversity) partially explained the variation in avian malaria prevalence and diversity. Recent anthropogenic landscape transformation (reduced proportion of native forest cover) had a major influence on avian malaria occurrence across the Atlantic Forest. This suggests that, for *Plasmodium*, host phylogenetic diversity was not a biotic filter to parasite transmission as prevalence was

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largely explained by host ecological attributes and recent anthropogenic factors. Our results demonstrate that, similar to human malaria and other vector-transmitted pathogens, prevalence of avian malaria parasites will likely increase with deforestation.

1. Introduction

Forest loss and subsequent landscape conversion to cattle pasture and agriculture leads to biotic homogenisation through reducing the diversity of various animal taxa such as birds, beetles, bees, and ants (Solar et al., 2015). Biodiversity loss from deforestation may also impact host-parasite-vector interactions by altering vector and host abundance (Keesing et al., 2010; Sehgal, 2015). Tree cover loss can modify local microclimatic conditions needed for vector reproduction and development (e.g., increasing the water temperature while decreasing relative humidity), which impacts vector abundance and activity, thus altering local transmission and infection risk of vector-transmitted pathogens (Vittor et al., 2009; Sehgal, 2015). For instance, loss of tree cover increased vector biting frequency leading to higher human malaria infection risk in deforested sites of the Peruvian Amazon (Vittor et al., 2006). In addition, forest fragmentation was shown as the major factor driving avian malaria parasite prevalence across host populations in the Caribbean (Pérez-Rodríguez et al., 2018). Therefore, destruction of tropical forests not only leads to diminishing biodiversity of free-living organisms but also affects the transmission of pathogenic and parasitic organisms owing to changes in host distribution and diversity.

Host diversity is a key driver of parasite diversity for a multitude of host-parasite systems, regardless of spatial scale (Kamiya et al., 2014). Host evolutionary history has also been implicated in playing a critical role in parasite dispersal capability and parasite community assembly across host communities (Davies and Pedersen, 2008; Clark et al., 2018). For instance, carnivores that are phylogenetically closely related tend to harbour more similar parasite assemblages (Huang et al., 2014), and phylogenetic diversity of primate host clades is positively correlated with higher parasite species richness within individual hosts (Nunn et al., 2004). However, host ecological attributes that potentially promote exposure to parasites or enable parasite shifting are expected to impact host range expansion for parasitic organisms and thus determine parasite diversity across host communities. Therefore, host functional diversity (i.e., the diversity of host ecological attributes) ought to influence parasite richness. For instance, we expect that larger host bodies harbour a greater diversity of parasites as they have more available niches for parasite colonisation and persistence, as seen in hoofed mammals and primates (Vitone et al., 2004; Ezenwa et al., 2006). Furthermore, host foraging behaviours are also expected to influence parasite richness, especially for vector-transmitted parasites, as foraging height and the amount of time spent foraging should alter host-vector encounter rates (Svensson-Coelho et al., 2013).

Spatial heterogeneity in vector-transmitted parasite prevalence may change in response not only to host community composition changes but also to changing environmental temperature. As temperature can affect parasite development, vector distribution, and abundance, it may be the most influential factor driving infection risk with vector-transmitted pathogens (Lafferty, 2009; Cable et al., 2017). For instance, low temperature constrains the sporogony of malaria parasites in their invertebrate vectors, the critical step in the parasite's life cycle that assures transmission to their vertebrate hosts (LaPointe et al., 2010). Moreover, warming temperature facilitates vector larval development and activity of adult vectors, therefore temperature change is likely to play a major role in transmission of vector-borne diseases (Mordecai et al., 2013, 2017). Mounting theoretical and experimental evidence suggests that increases in emergence and subsequent outbreaks of pathogenic and parasitic diseases at the human-wildlife-environment interface are associated with increasing global temperatures (Patz et al., 2000; Patz et al. 2008; Mordecai et al., 2013; Garamszegi, 2011; Cable et al., 2017). For this reason, overlaying the impact of human-induced changes on land cover and climatic factors are critical for both understanding disease ecology and mitigating the impact of pathogens on biodiversity, human health, and ecosystem productivity.

The Atlantic Forest is a global hotspot of biodiversity (Mittermeier et al., 2005). This biome has lost approximately 90% of its moist evergreen forest due to the expansion of cattle pastures, croplands, and the settlement of nearly 70% of the Brazilian population (Tabarelli et al., 2010). Understanding the pervasive impact of forest loss on the biodiversity of Atlantic Forest remnants has focused on free-living organisms. For instance, Morante-Filho et al. (2018) demonstrated that avian lineages capable of inhabiting deforested patches are as important for maintaining high evolutionary diversity in Atlantic Forest remnants as avian lineages dependent on undisturbed forest. Similarly, Matuoka et al. (2020) showed that in the Atlantic Forest, avian species richness and functional diversity respond differently to forest loss. These studies, using functional and phylogenetic metrics, demonstrate that non-forest dependent birds can maintain the high diversity of bird assemblages in Atlantic Forest remnants. Therefore, spatial changes in functional and phylogenetic diversity across avian host assemblages are relevant to understanding the dynamics of avian parasite prevalence and diversity. For parasite shifting and subsequent colonisation to occur, a parasite must first be exposed to a novel host species. This parasite-host encounter will be influenced by local environmental conditions (climate), evolutionary history (host phylogenetic diversity), ecological traits (host functional diversity), and recent anthropogenic factors (e.g., forest loss), all of which impact the avian host community composition and, therefore, influence parasite community assembly.

Avian haemosporidians from the genera *Plasmodium* and *Haemoproteus* (including the subgenera *Haemoproteus* and *Parahaemoproteus*) comprise a diverse group of vector-transmitted parasites (Valkiūnas, 2005). They infect blood cells of a wide range of avian hosts across all zoogeographic regions, except for Antarctica (Valkiūnas, 2005; Clark et al., 2014). These haemosporidian parasites exhibit broad variation in prevalence among host species within and across avian communities (e.g., Ellis et al., 2015; Fecchio et al., 2019). The capacity of these parasites to shift among avian hosts has played a significant role in their diversification and distribution (Ricklefs et al., 2004; Ellis et al., 2015; Fecchio et al., 2018; Gupta et al., 2019; Ciloglu et al., 2020). Differences in infection rates may also be explained by the dependence of these parasites on different groups of hematophagous vectors for sexual reproduction. The genus *Plasmodium*, subgenus *Haemoproteus*, and subgenus *Parahaemoproteus*, are transmitted by mosquitos (Culicidae), hippoboscid flies (Hippoboscidae), and biting midges (Ceratopogonidae), respectively (Santiago-Alarcon et al., 2012). Vector life history and development of these parasites sexual stages depend on environmental temperature. Therefore, variation

in minimum temperature across avian communities might influence haemosporidian transmission due to thermal constraints in parasite and vector development and vector activity (LaPointe et al., 2010). Although historical factors have played a significant role in shaping the diversity and distribution of avian malaria parasites across South American biomes (Fecchio et al., 2019), contemporary anthropogenic changes such as deforestation could potentially affect local prevalence, diversity, and parasite community structure by altering the microclimate, diversity of host functional traits, and host phylogenetic diversity across avian communities.

We used haemosporidian parasites from the genera *Plasmodium* and *Haemoproteus* (including both subgenera) to test whether parasite prevalence, taxonomic diversity, and phylogenetic diversity in local avian host communities are influenced by metrics of landscape (proportion of native forest cover), climate (minimum temperature), and avian host attributes (functional and phylogenetic diversity). Collectively, our analyses identify the contributions of recent anthropogenic changes and historical factors, as well as climate, to the local community assemblage and infection probability of vector-transmitted parasites.

2. Materials and methods

2.1. Bird sampling

Our analyses are based on 18 bird communities surveyed between 2012 and 2019 across the Atlantic Forest in Brazil (Fig. 1). We collected 2241 blood samples from 233 bird species from different latitudes ranging from 5° 54′ 52.49″ to 29° 28′ 49.63″ S ≈ 2700 km (Supplementary Tables S1 and S2). In addition to variation in temperature, the sampling sites were chosen to encompass a gradient in land use and tree cover. All birds were caught using mist nets, and from each individual approximately 50 µL of blood were collected from the brachial vein and stored either in 95% ethanol or on FTA cards (Whatman™). We prepared two or three thin blood smears from 175 birds captured at Saint-Hilaire-Lange National Park, Serra do Mar State Park (Núcleo Curucutu), and Michelin Farm. These blood smears were air-dried and fixed in absolute methanol after collection in the field. Birds were captured in accordance with corresponding permits in Brazil (licence issued by Instituto Chico Mendes de Conservação da Biodiversidade – ICMBio, Brazil, numbers: 9054-1, 56211-1, 23405, SISBIO 59198-5, SISBIO 63785.

2.2. Parasite detection and lineage identification

All parasite lineages in our dataset were identified using PCR-based detection methods targeting a 479 bp fragment of the cytochrome-*b* (cyt-*b*) gene of the haemosporidian mitochondrial genome (Hellgren et al., 2004). The majority of parasite lineages come from field studies led by the authors during the period of 2012–2019, with additional lineages extracted from studies published by Lacorte et al. (2013) and Fecchio et al. (2019). Protocols detailing reactions, reagents, primer names, cycling conditions, and how lineages were determined, can be found in Fallon et al. (2003), Hellgren et al. (2004), Bensch et al. (2009), and Bell et al. (2015). As evidence indicates that haemosporidian lineages differing by one cyt-*b* nucleotide may be reproductively isolated entities (Bensch et al., 2004), we use the standard practise of referring to each unique cyt-*b* haplotype as a unique parasite lineage. To assure that the parasite lineages were able to reproduce within avian hosts we screened blood smears from 175 birds using traditional microcopy. Blood smears were stained with a 10% Giemsa solution for 1 h and examined for 20–25 min, viewing 100 fields at low magnification (400×) and 100 fields at high magnification

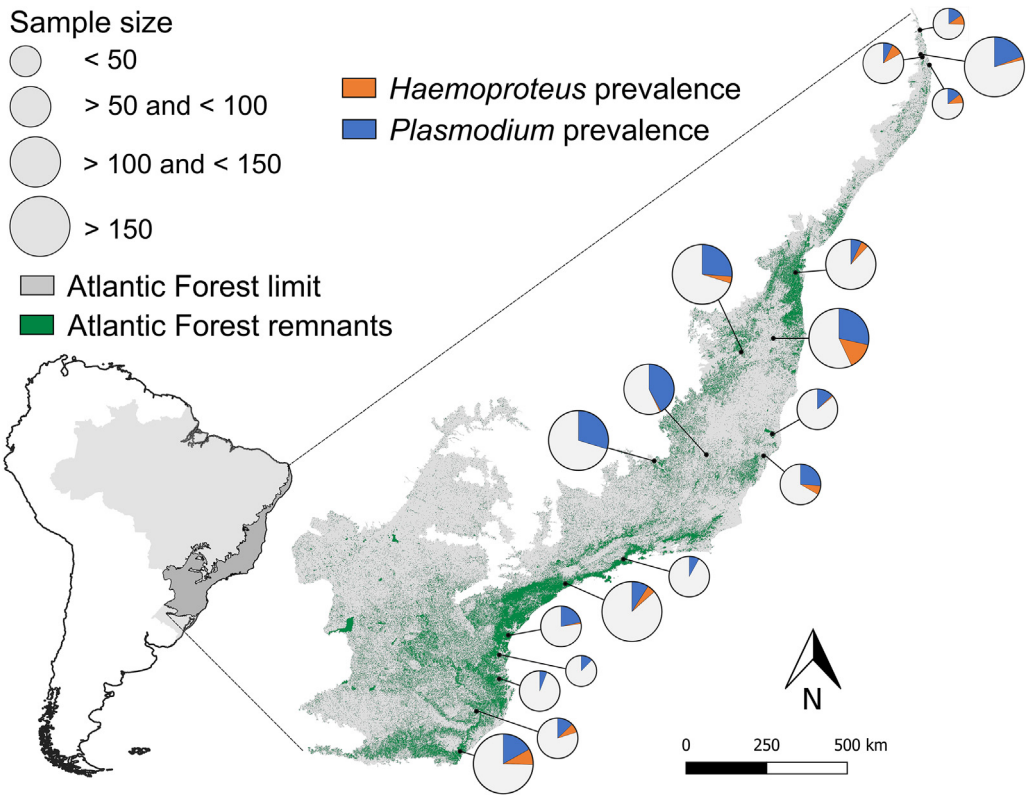

Fig. 1. Map of the 18 sampling locations across the Atlantic Forest in Brazil. Pie charts indicate the proportion of individual hosts infected by *Plasmodium* and *Haemoproteus* in each avian community. The size of each pie chart indicates the number of sampled birds at each location.

(1000×) using an Olympus BX51 light microscope. The parasites were identified morphologically according to Valkiūnas (2005).

2.3. Phylogenetic methods

We extracted 1000 bird phylogenies from the BirdTree project (tree source: Ericson all species; Jetz et al., 2012) for the avian hosts sampled and generated a consensus tree using the "consensus" function with clade representation at the highest proportion (p: 1; Felsenstein, 2004) with branch lengths computed using the "compute.brlen" function based on Grafen (1989) with a power of 0.75. For haemosporidian parasites, assembled sequences of unique haplotypes were aligned using BioEdit v7.2.0 (Hall, 1999) and then used to infer molecular phylogenies. We applied the GTR + I + G model of nucleotide substitution as determined by jModelTest (Guindon and Gascuel, 2003; Darriba et al., 2012). Lineages were labelled to identify their respective taxonomic group; HA for the subgenus *Haemoproteus*, PA for the subgenus *Parahaemoproteus*, and PL for the genus *Plasmodium*. *Theileria annulate* (GenBank accession number # KP731977) was used as the outgroup. We obtained a time-calibrated tree for the alignment using the Bayesian relaxed clock model (Drummond et al., 2006) in BEAST 1.10.4 (Drummond et al., 2012) implementing the mutation rate of 0.006 per lineage per million years as estimated by Ricklefs and Outlaw (2010). The analysis was implemented for five lineages of *Haemoproteus*, 36 lineages of *Parahaemoproteus*, and 111 lineages of *Plasmodium*. We generated two independent runs for the alignment with parameters as follows: an uncorrelated lognormal relaxed clock, Yule process, default priors, 100 million generations of Markov Chain Monte Carlo (MCMC), parameters sampled every 5000 generations, and 10% of generations discarded as burn-in. Convergence and performance of runs were inspected using Tracer 1.7.1 (http://beast.bio.ed.ac.uk/Tracer), making sure that Effective Sample Size (ESS) values were higher than 200. The maximum clade credibility (MCC) tree was generated using TreeAnnotator and visualised in FigTree 1.4.2. (http://tree.bio.ed.ac.uk/software/figtree/).

As our analysis was run at the genus level (*Haemoproteus* and *Plasmodium*), the consensus tree was pruned into two trees. We included only *Plasmodium* lineages in the first tree, whereas the second tree included *Parahaemoproteus* and *Haemoproteus* lineages, since the phylogenetic relationship between these two subgenera is still under debate (Valkiūnas, 2005; Borner et al., 2016; Galen et al., 2018). The tree manipulations were made using the Picante package (Kembel et al., 2010) and the Ape package (Paradis et al., 2004) in R 3.5.1 (R Development Core Team, 2018).

2.4. Landscape and climate metrics

We considered proportion of native forest cover as our landscape variable of interest, and minimum temperature of the coldest month as our climatic variable of interest to explain variation in parasite prevalence, diversity, and distributions. We used landcover satellite images with 30 m resolution (accessible at https://mapbiomas.org/colecoes-mapbiomas-1?cama_set_language=pt-BR) to extract the landscape variable, and GeoTiff images with 2.5 minutes/degree resolution (variable bio6, accessible at https://worldclim.org/data/bioclim.html) to assess the climatic variable. In each sampling location we created a buffer with a 2500 m radius and extracted the proportion of native forest cover within that area. We opted to use this buffer size because it comprises both the home range of most understory birds (Hansbauer et al., 2008; Marini, 2010) and the average flight distance of most potential vectors (Verdonschot and Besse-Lototskaya, 2014). As the communities were sampled in different years, we used landcover images corresponding to the sampling year of each location. We selected the minimum temperature of the coldest month due to the negative effect of low temperatures on haemosporidian development (LaPointe et al, 2010; Santiago-Alarcon et al., 2012). Further, temperature variables were highly correlated, based on a Pearsońs Correlation Test (Supplementary Table S3). We also did not use any precipitation measure as a climatic variable due to the high collinearity between precipitation and forest cover (Supplementary Table S3). In addition, all community locations receive measurable precipitation year-round, even during the driest month (mean annual precipitation among sampling locations = 1 548 mm, standard deviation = 450 mm; mean precipitation during the driest month among sampling locations = 56 mm, S. D. = 40 mm; location with the lowest precipitation during the driest month = 10 mm).

2.5. Diversity metrics

To explore the effects of host diversity on haemosporidian diversity, we used taxonomic and phylogenetic diversity of both avian host and parasite communities, and functional diversity of avian host communities. Both host and parasite taxonomic diversity were calculated using the Shannon index, which incorporates the number of species in a community and their relative abundances (represented by mist-net captures for birds and number of occurrences for parasite lineages). It returns a value taking into consideration the species richness and evenness of each community, with higher values representing richer communities and higher equitability among species (Magurran, 2004). We used body mass, foraging strata, diet, and activity (diurnal or nocturnal) as biological traits to calculate the functional diversity for avian host species. We extracted these traits for all sampled bird species using Elton Traits 1 (Wilman et al., 2014). This database provides information at the species level, where body mass is a continuous variable, activity is a binomial variable, foraging strata is the proportion of time that a bird species spends at each stratum, and diet is the feeding proportion from each diet category. We then generated a functional distance matrix using the Gower distance method, as recommended by Pavoine et al. (2009), and calculated an average distance among species for each community as described below. The distance matrix was calculated using the ade4 R package (Dray and Dufour, 2007).

We used the abundance weighted Mean Pairwise Distance (MPD_{ab}) to assess phylogenetic diversity of both the birds and the parasites. This index averages the pairwise distance among all species that comprise a community, providing information on the evolutionary history from each sampled location (Tucker et al., 2017). To avoid any correlation between MPD_{ab} and species richness (and taxonomic diversity), we calculated the Standardised Effect Size MPD_{ab} ($SES.PMPD_{ab}$) by using a null model (Miller et al., 2017). This model was generated through 1000 randomizations of the species names (tip labels) along the phylogenetic tree and calculating the MPD_{ab} of each generated tree. We then compared the observed MPD_{ab} values with the randomised MPD_{ab} by subtracting the mean random MPD_{ab} from the observed values and dividing it by the standard deviation of the randomised MPD_{ab}; zero represents the null model result and the observed values range below and above zero. The lower the value below zero, the greater the phylogenetic clustering (more closely related species in a community), whereas greater positive values signify phylogenetic overdispersion (more distantly related species in a community; Webb, 2000).

To ensure that $SES.PMPD_{ab}$ based on a consensus tree preserves its topology and comparative branch lengths, we also calculated $SES.PMPD_{ab}$ using the 1000 extracted trees from Jetz et al. (2012) and correlated the mean $SES.PMPD_{ab}$ from the extracted trees with $SES.PMPD_{ab}$ values from the consensus tree ($r = 0.98$, $P < 0.0001$).

SES.MPD_{ab} was also used to evaluate functional diversity (SES.$FMPD_{ab}$), given that the trait-based Gower distance matrix (defined for each community as described above) and the patristic distances derived from a phylogenetic tree, which is typically used in the MPD_{ab} metric, have similar structures (i.e., both give distances between pairs of species in a community). Instead of using the phylogeny in the calculation of MPD_{ab}, we included the functional data Gower distance matrix ($FMPD_{ab}$). Hence, we evaluated the proportion of the total functional information harboured by each community and compared $FMPD_{ab}$ values for trait data with null models (species identities in the Gower distance matrix were shuffled). MPD and SES.MPD were calculated using the picante R package (Kembel et al., 2010).

2.6. Statistical analyses

All predictor variables were centred and scaled (mean = 0, S.D. = 1) and tested for collinearity before running statistical analyses ($r > 0.55$). We used generalised linear models to determine whether landscape (proportion of native forest cover), climate, and host diversity (taxonomic, phylogenetic, and functional) affected haemosporidian prevalence, taxonomic diversity, and phylogenetic diversity. Before running the models, we used the Moran index (I) to test for spatial autocorrelation on our parasite metrics (Bivand and Wong, 2018). The spatial autocorrelation analyses revealed no substantial effect of space on prevalence, taxonomic diversity, and phylogenetic diversity for *Plasmodium* and *Parahaemoroteus*. Prevalence was calculated for each community ($n = 18$) as the number of infected birds divided by the total number of birds sampled in the community irrespective of bird species. This is equivalent to the mean prevalence of bird species in a community weighted by the sample sizes of those bird species. In all models, the parasitism metric (prevalence, taxonomic diversity, and phylogenetic diversity) was considered the response variable, while temperature, proportion of native forest cover, host diversity, host phylogenetic diversity (SES.$PMPD_{ab}$), and host functional diversity (SES.$FMPD_{ab}$) were predictor variables. We used beta regression for models with haemosporidian prevalence as the response variable (Ferrari and Cribari-Neto, 2004) and linear regression for the models with diversity metrics (parasite taxonomic and phylogenetic) as the response variables. We first validated the full models based on residual distribution, leverage, and Cook-distance (Zuur et al., 2009), then selected the best models using Information-Theoretic approaches. We used multi-model inference to average the importance of each variable based on the models that presented corrected Akaike Information Criteria delta values less than four ($AIC_C \Delta_i < 4.0$), this procedure avoids uncertainties commonly found when considering only one "best" model (Burnham et al., 2011).

We were unable to compare diversity metrics for the genus *Haemoproteus* from all 18 sampled communities due to the low regional prevalence of this genus. *Haemoproteus* was not identified in four locations with an additional four locations with only one individual infected by this genus. Therefore, we calculated the effect of environment and host diversity on *Haemoproteus* diversity considering only 10 communities. The results considering *Haemoproteus* and *Parahaemoproteus* separately do not significantly alter the main findings (results not shown). Therefore, we presented the results combining the two subgenera *Haemoproteus* and *Parahaemoproteus,* and hereafter refer to them as *Haemoproteus*.

2.7. Data accessibility

DNA sequences are deposited in GenBank and the MalAvi database. Accession numbers are available in the raw dataset at https://doi.org/10.6084/m9.figshare.13517264.v2 The R code required to replicate the analyses is available at https://doi.org/10.6084/m9.figshare.13523864.v1.

3. Results

3.1. General prevalence and lineage richness of Plasmodium and Haemoproteus

We analysed data collected from 2241 individual birds surveyed across a gradient of vegetation cover and climate in the Brazilian Atlantic Forest (Fig. 1). These individuals belong to 233 avian species, 42 families, and 13 orders (see raw data (DOI: 10.

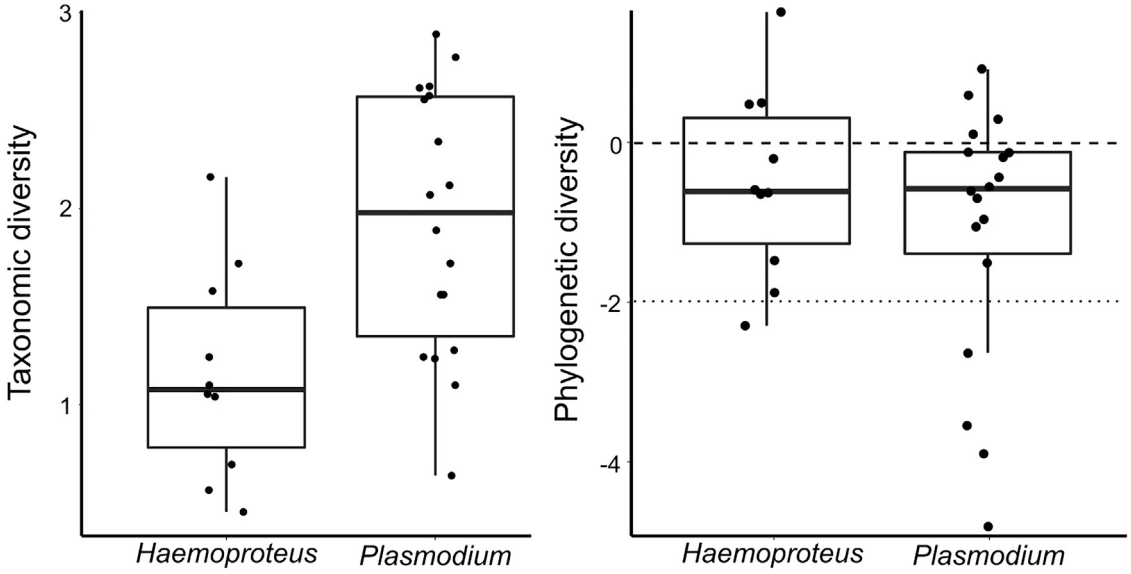

Fig. 2. Boxplots of the diversity metrics (Taxonomic diversity = Shannon diversity metric of parasite abundance; Phylogenetic diversity = Standardised Effect Size (SES) of the Phylogenetic Mean Pairwise Distance (PMPD) weighted by parasite abundance – SES.$PMPD_{ab}$) for *Haemoproteus* and *Plasmodium*, considering all sampled units (10 communities of *Haemoproteus* and 18 communities of *Plasmodium*). Black dots represent each sampling location value. Dotted lines indicate the 95% Confidence Interval (95% CI) of the null model.

6084/m9.figshare.13517264) and Supplementary Tables S1 and S2 for sample size by avian taxon, time of year, and location). The prevalence of haemosporidian parasites (pooled *Plasmodium* and *Haemoproteus*) was 23.2%, representing 521 occurrences and 152 genetic lineages, 111 *Plasmodium* and 41 *Haemoproteus* (see raw data for prevalence and lineage richness by host taxon or parasite genus). Microscopic examination of 175 slides confirmed the presence of trophozoites, meronts, and gametocytes for *Plasmodium* infection in 12 bird hosts and the presence of *Parahaemoproteus* gametocytes in nine infected individuals. Based on molecular screening the overall prevalence of *Plasmodium* was higher than *Haemoproteus* (combined *Haemoproteus* and *Parahaemoproteus* subgenera) and heterogeneous among the 18 avian communities surveyed (Fig. 1, Supplementary Table S2).

3.2. Parasite taxonomic and phylogenetic diversity

Plasmodium taxonomic diversity varied between 0.64 and 2.77 among communities (mean = 1.92, S.D. = 0.69), whereas *Haemoproteus* taxonomic diversity ranged from 0.45 to 2.16 (mean = 1.16, S.D. = 0.54). Regarding phylogenetic diversity, both haemosporidian genera had average SES of MPD below 0 (*Plasmodium*: mean = -0.96, S.D. = 1.51; *Haemoproteus*: mean = -0.53, S.D. = 1.15, Fig. 2). In addition, based on each haemosporidian regional lineage pool, 22% (n = 4) of the *Plasmodium* and 10% (n = 1) of the *Haemoproteus* communities were composed of more closely related species than expected by chance, and neither *Plasmodium* nor *Haemoproteus* community values were significantly higher than the null model. These findings suggest that community assem-

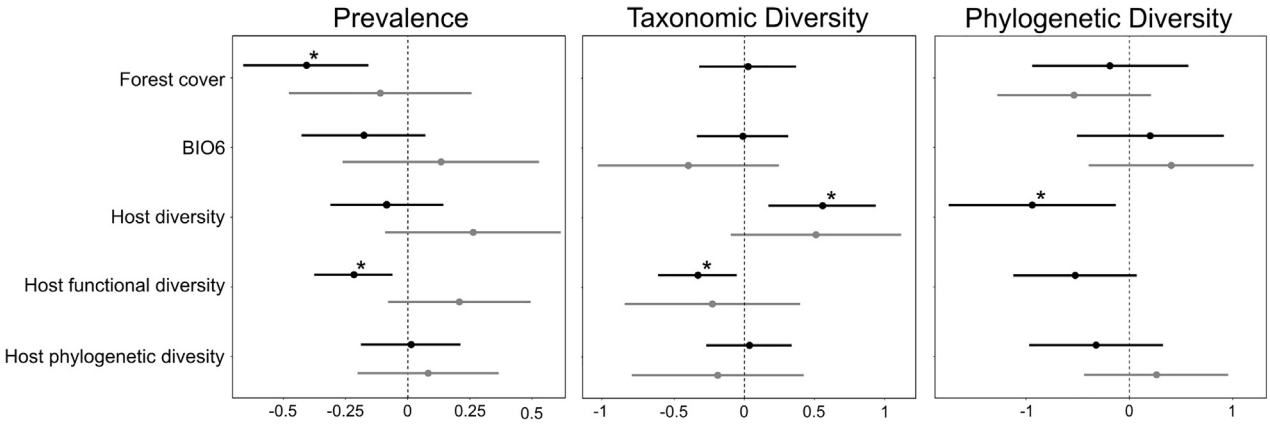

Fig. 3. Coefficient estimates and 95% Confidence Interval (95% CI) of the five predictor variables for each parasite metric (prevalence, taxonomic diversity, and phylogenetic diversity). Black bars indicate *Plasmodium* and grey bars indicate *Haemoproteus*. The estimates are based on the conditional model average (AIC_c $\Delta_i < 4$), and significant values are marked with an asterisk. Note that parasite prevalence estimates are centred and scaled in accordance with its respective model link (LOGIT). BIO6, minimum temperature of coldest month.

Table 1
Models with the best parsimony (considering ΔAIC_C equal or lower than 4.0) used to assess the effect of host and environment on *Plasmodium* prevalence, taxonomic diversity, and phylogenetic diversity. We show the number of parameters (K), the controlled Akaike Information Criteria (AIC_C), the respective distances of AIC_C values of each model from the AIC_C value of the best model (ΔAIC_C), the AIC_C weight (w_i), the cumulative AIC_C weight, and the log likelihood.

Model	Number of parameters (K)	AIC_c	Delta AIC_c (Δ_i)	AIC_c Weight (w_i)	Cumulative AIC_c Weight	Log-Likelihood
Prevalence						
For + HFun	4	−44.7	0	0.427	0.43	27.876
For + HFun + Temp	5	−42.5	2.19	0.143	0.57	28.744
For + HDiv + HFun	5	−41.2	3.44	0.076	0.65	28.116
For + Temp	4	−40.9	3.80	0.064	0.71	25.975
For + HFun + HPhy	5	−40.8	3.91	0.060	0.77	27.880
Taxonomic diversity						
HDiv + HFun	4	39.9	0	0.528	0.53	−14.432
HDiv	3	43.3	3.35	0.099	0.63	−17.788
HDiv + HFun + HPhy	5	43.8	3.85	0.077	0.70	−14.398
For + HDiv + HFun	5	43.8	3.90	0.075	0.78	−14.419
HDiv + HFun + Temp	5	43.9	3.91	0.075	0.85	−14.428
Phylogenetic diversity						
HDiv + HFun	4	67.1	0	0.265	0.27	−28.012
HDiv	3	67.9	0.83	0.175	0.44	−30.111
HDiv + HPhy	4	69.4	2.28	0.085	0.53	−29.154
~1	2	69.9	2.79	0.066	0.59	−32.545
HDiv + HFun + HPhy	5	70.3	3.17	0.054	0.65	−27.634
For + HDiv	4	70.5	3.35	0.050	0.70	−29.689
HDiv + HFun + Temp	5	70.6	3.52	0.046	0.74	−27.810
HDiv + Temp	4	70.8	3.68	0.042	0.78	−29.851
For + HDiv + HFun	5	71	3.89	0.038	0.82	−27.995

For, proportion of native forest cover; Temp, minimum temperature of coldest month; HDiv, host taxonomic diversity; HFun, host functional diversity; HPhy, host phylogenetic diversity.

Table 2
Models with the best parsimony (considering ΔAIC_C equal or lower than 4.0) used to assess the effect of host and environment on *Haemoproteus* prevalence, taxonomic diversity, and phylogenetic diversity. We show the number of parameters (K), the controlled Akaike Information Criteria (AIC_C), the respective distances of AIC_C values of each model from the AIC_C value of the best model (ΔAIC_C), the AIC_C weight (wi), the cumulative AIC_C weight, and the log likelihood.

Model	Number of parameters (K)	AIC_c	Delta AIC_c (Δ_i)	AIC_c Weight (w_i)	Cumulative AIC_c Weight	Log-Likelihood
Prevalence						
~1	2	−47.9	0	0.288	0.29	26.480
HFun	3	−46.1	1.79	0.118	0.41	27.241
HDiv	3	−45.7	2.16	0.098	0.50	27.057
HDiv + HFun	4	−45.4	2.44	0.085	0.59	28.939
Temp	3	−44.9	2.96	0.065	0.65	26.653
For	3	−44.9	2.97	0.065	0.72	26.649
HPhy	3	−44.9	2.98	0.065	0.78	26.643
Taxonomic diversity						
~1	2	33.0	0	0.329	0.33	−13.663
HDiv	3	33.5	0.45	0.262	0.59	−11.746
Temp	3	35.1	2.08	0.116	0.71	−12.557
HFun	3	36.5	3.43	0.059	0.77	−13.236
HDiv + HPhy + Temp	4	36.6	3.55	0.056	0.82	−10.297
HPhy	3	36.7	3.66	0.053	0.88	−13.351
Phylogenetic diversity						
~1	2	35.9	0	0.420	0.42	−15.093
For	3	37.3	1.38	0.211	0.63	−13.638
Temp	3	38.6	2.67	0.110	0.74	−14.286
HPhy	3	39.3	3.38	0.077	0.82	−14.640

For, proportion of native forest cover; Temp, minimum temperature of coldest month; HDiv, host taxonomic diversity; HFun, host functional diversity; HPhy, host phylogenetic diversity.

blages for both parasite genera are more likely to be phylogenetically clustered, especially for *Plasmodium* communities.

3.3. Predictors of prevalence and taxonomic and phylogenetic diversity of haemosporidian parasites

Of the five predictor variables included in the model, only three – forest cover, host functional diversity, and host taxonomic diversity – explained variance in prevalence, taxonomic diversity, and phylogenetic diversity of avian haemosporidian parasites across the Atlantic Forest, but only for *Plasmodium* (Fig. 3, Tables 1 and 2). For *Plasmodium* parasites (hereafter avian malaria), we found a negative association of prevalence with proportion of native forest cover and host functional diversity (Fig. 3). Host functional diversity was also negatively associated with *Plasmodium* taxonomic diversity, whereas host diversity had a positive association with *Plasmodium* taxonomic diversity (Fig. 3). Lastly, we found that host diversity had a negative association with *Plasmodium* phylogenetic diversity. For *Haemoproteus*, predictor variables failed to explain variation in prevalence, taxonomic diversity, and phylogenetic diversity (Fig. 3). Moreover, the null model (without any predictor variables) was the best candidate model explaining *Haemoproteus* prevalence, taxonomic diversity, and phylogenetic diversity (Table 2).

4. Discussion

Parasite diversity follows host diversity (Kamiya et al., 2014), but the underlying ecological, historical, and environmental factors causing spatial variation in parasite transmission and distributions have rarely been assessed. Our analyses of haemosporidian parasites surveyed across the threatened Brazilian Atlantic Forest demonstrated that recent anthropogenic changes to the landscape, namely a reduction in forest cover, best explained avian malaria prevalence, with higher probability of infection associated with a lower proportion of native vegetation cover at a given site. At sites with relatively low host functional diversity, both prevalence and taxonomic diversity of *Plasmodium* parasites were higher. Moreover, avian communities with higher host diversity showed a higher taxonomic diversity of *Plasmodium* lineages but harboured less phylogenetic diversity for this parasite genus.

The prevalence of avian malaria is determined by a set of factors acting at the parasite, vector, and avian host levels. Changes in microhabitat and heterogeneity in temperature affect both vector reproduction and parasite development, thus altering the transmission of avian malaria parasites (LaPointe et al., 2010; Sehgal et al., 2011; Ferraguti et al., 2018). Contrary to our expectation, minimum temperature of coldest month did not explain prevalence of haemosporidian parasites across the Atlantic Forest. Rather, we found a negative relationship between proportion of native vegetation cover and avian malaria prevalence: the higher the removal of native tree cover the higher the *Plasmodium* infection rates at a given site. The ecology of avian malaria transmission, vectoral capacity, and vector specificity are poorly documented, but it is certain that loss of tree cover can impact vector community composition (Sehgal, 2015). Changes in landscape from tree removal could increase structures capable of collecting rainwater used for vector reproduction and larval development, thus boosting local vector abundance and biting frequency leading to higher avian malaria transmission in deforested areas. Moreover, the reduction in forest cover can lead to the removal of natural breeding sites (i.e., bromeliads) for high canopy specialist mosquito species found in pristine Atlantic Forest. This in turn can promote the dispersion of mosquitoes from natural to anthropic environments, thereby changing the mosquito stratification across the modified environment (Oliveira-Christe et al., 2020). Our findings of increased avian malaria prevalence in deforested landscapes across the Atlantic Forest are in accordance with other studies linking deforestation to higher infection risk of simian malaria (Medeiros-Sousa et al., 2019), and several arboviruses (Medeiros-Sousa et al., 2017) in the Atlantic Forest and human malaria in Amazonia (Vittor et al., 2006, 2009; Olson et al., 2010; Chaves et al., 2018). This reinforces the general conclusion that recent anthropogenic transformation of natural landscapes can disrupt a host-parasite system and increase infection rates of vector-transmitted pathogens.

Host functional diversity (used here as variation in avian host traits that could promote vector exposure and parasite encounter) was negatively correlated with avian malaria prevalence and *Plasmodium* taxonomic diversity. This suggests that ecological similarity of avian hosts is an important driver of avian malaria distribution across the Atlantic Forest, whereas phylogenetic relatedness of avian hosts does not structure *Plasmodium* prevalence and diversity in our study sites. The higher prevalence and lineage richness of *Plasmodium* found in avian communities with reduced functional diversity can be explained by the high abundance of non-forest dwelling and habitat generalist avian host species such as thrushes. Thrushes are heavily infected by a diversity of avian malaria parasites and other related haemosporidians (Harl et al., 2020). Due to their high flight capability and tolerance of disturbed areas, these birds could disperse avian malaria parasites from pristine to deforested areas. The lineages found in thrushes across the Atlantic Forest have been shown to infect a broad range of unrelated host species (Lacorte et al., 2013; Fecchio et al., 2019). Host switching is the main macroevolutionary pattern in haemosporidian diversification (Ricklefs et al., 2004; Fecchio et al., 2018), but rather than a historical attribute, host shifting may rely on opportunities for parasites to infect new hosts under variable environmental conditions (Wells and Clark, 2019). The presence of thrushes harbouring lineages capable of infecting a broad range of avian hosts in disturbed landscapes with low functional diversity may impact avian malaria transmission, leading to increased prevalence and lineage richness among the several host species in the local avian host community. Whether thrushes are superspreaders of avian malaria under changing environments, or are disproportionately infected (key host species), has yet to be tested across regions, and the acquisition of more samples across both undisturbed and disturbed habitats is warranted.

Forest loss has a major impact on functional and phylogenetic diversity of avian assemblages across the fragmented Atlantic Forest (Morante-Filho et al., 2018; Matuoka et al., 2020). Therefore, we would expect that changes in functional and phylogenetic diversity of avian hosts due to disturbance would also impact the diversity and distribution of haemosporidian parasites. Our results are consistent with the pervasive feature of host parasite interactions, that host diversity drives parasite taxonomic diversity (Kamiya et al., 2014). However, variation in phylogenetic diversity of avian host communities did not explain prevalence nor diversity of haemosporidian parasites. By assessing the phylogenetic relationship of both parasite and host clades, we revealed a contrasting pattern where less diverse avian communities harboured a more phylogenetically diverse assemblage of avian malaria parasites. This indicates that more preserved remnants of Atlantic Forest sites not only harbour a more diverse bird community (Morante-Filho et al., 2018; Matuoka et al., 2020), but also higher endemism of *Plasmodium* lineages (i.e., lineages more clustered phylogenetically) as a result of local diversification. The evolutionary mechanisms underlying avian malaria-host diversification across the Atlantic Forest are possibly overshadowed by recent anthropogenic disturbance that may increase dispersion and establishment of phylogenetically distant avian malaria lineages in less diverse local avian communities after deforestation.

We found that ecological factors (e.g., forest cover and host functional diversity), together with avian diversity, best explained differences in *Plasmodium* assemblage infection rates. Phylogenetic diversity of avian communities failed to explain changes in the prevalence, taxonomic diversity, and phylogenetic diversity of *Plasmodium* lineages. Anthropogenic changes in forest cover may affect the abundance of vectors leading to higher *Plasmodium* prevalence, whereas changes in avian host diversity and host functional diversity due to anthropogenic impacts were responsible for changes in the composition and diversity of *Plasmodium* lineages. Our study demonstrates the importance of recent anthropogenic and ecological factors in influencing transmission dynamics, which can directly affect parasite assemblages.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ijpara.2021.01.001.

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