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Avian host composition, local speciation and dispersal drive the regional assembly of avian malaria parasites in South American birds

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Abstract

Identifying the ecological factors that shape parasite distributions remains a central goal in disease ecology. These factors include dispersal capability, environmental filters and geographic distance. Using 520 haemosporidian parasite genetic lineages recovered from 7,534 birds sampled across tropical and temperate South America, we tested (a) the latitudinal diversity gradient hypothesis and (b) the distance–decay relationship (decreasing proportion of shared species between communities with increasing geographic distance) for this host–parasite system. We then inferred the biogeographic processes influencing the diversity and distributions of this cosmopolitan group of parasites across South America. We found support for a latitudinal gradient in diversity for avian haemosporidian parasites, potentially mediated through higher avian host diversity towards the equator. Parasite similarity was correlated with climate similarity, geographic distance and host composition. Local diversification in Amazonian lineages followed by dispersal was the most frequent biogeographic events reconstructed for haemosporidian parasites. Combining macroecological patterns and biogeographic processes, our study reveals that haemosporidian parasites are capable of circumventing geographic barriers and dispersing across biomes, although constrained by environmental filtering. The contemporary diversity and distributions of haemosporidian parasites are mainly driven by historical (speciation) and ecological (dispersal) processes, whereas the parasite community assembly is largely governed by host composition and to a lesser extent by environmental conditions.

KEYWORDS
community assembly, disease ecology, latitudinal diversity gradient, macroecology, parasite biogeography, parasite dispersal

1 | INTRODUCTION

A pervasive feature in host–parasite associations is that host diversity drives parasite diversity (Kamiya, O'Dwyer, Nakagawa, & Poulin, 2014a). Evolutionary processes, such as shifting of parasite lineages across host species, as well as recent ecological regional processes, such as parasite dispersal, are postulated to play a critical role in governing parasite community assembly (Ricklefs, 2010; Ricklefs et al., 2014; Clark et al., 2018). While many parasites have evolved to become specialists (Poulin, 2007), multihost parasites must circumvent ecological and evolutionary barriers to infect unrelated host species, challenging ecologists and epidemiologists to predict when and where a host species is most susceptible to disease. Thus, by identifying the relative contributions of host and parasite phylogenies to regional community assembly across multiple regions, one can gain a better understanding of parasite host-switching patterns and the geographical basis for parasite diversity.

A parasite's host range can be explained as a function of the number of susceptible hosts in a given community, which in turn may be determined by historical biogeographic factors of the host clade. For example, tropical regions harbour higher bird species diversity in comparison with temperate regions (Duchêne & Cardillo, 2015), and thus, avian parasites from tropical regions will have a higher diversity of potential hosts to colonize. Furthermore, the greater diversity of host species in the tropics could lead to increased parasite diversity within host species through parasite lineage sharing and host shifting (Ricklefs et al., 2014; Clark, 2018). Parasite distributions can also be explained by the ecological fitting principle, which posits that a shared evolutionary history with a new host species is necessary for the successful invasion of parasites into new host taxa (Brooks et al., 2006). Thus, the likelihood that a parasite can successfully infect a new host species decreases continuously with increasing phylogenetic distance between its original host and potential new hosts (Davies & Pedersen, 2008; De Vienne, Hood, & Giraud, 2009; Ricklefs, 2010; Poulin, Krasnov, & Mouillot, 2011; Clark & Clegg, 2017).

Assemblage similarity is expected to decrease with increasing geographic distance (Nekola & White, 1999; Soininen, McDonald, & Hillebrand, 2007). The patterns of distance decay of parasite assemblage similarity could be caused by two mechanisms: one related to environmental differences (e.g., gradients in temperature and precipitation) and the other related to the dispersal capability of parasites (Nekola & White, 1999). Several studies, including a

diversity of host–parasite systems such as helminths of freshwater fish and terrestrial mammals (Poulin, 2003), mites and fleas of small mammals (Krasnov, Shenbrot, Mouillot, Khokhlova, & Poulin, 2005; Vinarski, Korallo, Krasnov, Shenbrot, & Poulin, 2007) and even vector-transmitted blood protozoan parasites of birds across island archipelagoes (Ishtiaq et al., 2010; Svensson-Coelho & Ricklefs, 2011), have shown a diminishing proportion of shared parasites among vertebrate host communities with increasing geographic distance. Among avian malaria parasites, dispersal capability is known to play a significant role in shaping current diversity and distributions across both Nearctic (Ellis et al., 2015) and Amazonian birds (Fecchio et al., 2018). Host–parasite systems for mainland birds may exhibit differences in parasite ecology and evolution as compared to avifauna on islands due to the differences in geographical isolation and limits to dispersal for both parasite and host lineages. For example, a study of avian malaria infecting continental manakins, a host clade endemic to the Neotropics, showed a weak association between geographic distance and parasite similarity (Fecchio et al., 2017). However, geographic proximity explained malaria parasite dispersal across Amazonian birds (Fecchio et al., 2018). One plausible explanation is that avian malaria dispersal in continental ecosystems is not as constrained as it is in insular ecosystems (Fecchio et al., 2017).

In recent decades, hundreds of studies have demonstrated the existence of an increase in species diversity towards the equator, a pattern known as the latitudinal diversity gradient (hereafter "LDG"; Pianka, 1966; Rohde, 1992; Hillebrand, 2004). Although parasites are estimated to represent the largest proportion of global biotic diversity (Dobson, Lafferty, Kuris, Hechinger, & Jetz, 2008) and can constitute a substantial part of community biomass (Kuris et al., 2008), spatial patterns of parasite species richness have received considerably less attention in comparison with that of free-living organisms (Poulin, 2007; Kamiya et al., 2014a). Metazoan parasites of marine fishes, one of the best-studied groups of parasites with regard to spatial patterns in diversity (Rohde & Rapp, 1998; Rohde, 2002; Poulin, 2007), show a strong LDG effect. However, a recent meta-analysis of other animal and plant parasites revealed that parasite diversity seems to be decoupled from latitudinal factors (Kamiya, O'Dwyer, Nakagawa, & Poulin, 2014b). The absence of an LDG for endoparasitic helminths of mammals and birds (Poulin, 1995) or primates (Nunn, Altizer, Sechrest, & Cunningham, 2005) might be explained by the relative stability of their host's internal environment, including relatively constant body temperature (Rohde & Heap, 1998). Haematozoan parasites, in contrast, are transmitted by blood-feeding insects, which are exposed to and dependent on environmental conditions (temperature and humidity) that vary with latitude. For example, Nunn et al. (2005) showed an increased risk of infection for haematozoan parasites in primates near the equator and argued that the higher diversity of protozoan parasites found in tropical primates could be caused by a greater abundance and/or diversity of biting insects closer to the equator and by associated climatic effects on vector behaviour and parasite development.

Avian malaria parasites (Order Haemospirida) of the genus *Plasmodium* and the two related genera *Parahaemoproteus* and *Haemoproteus* are vector-transmitted protozoan parasites that infect avian blood cells (Martinsen, Perkins, & Schall, 2008; Borner et al., 2016; Galen et al., 2018). These haemosporidian parasites are globally distributed and diverse in most bird families (Valkiūnas, 2005; Clark, Clegg, & Lima, 2014). The ability of these bird parasites to disperse geographically and to shift among avian hosts has played a significant role in their diversification and distribution (Ellis et al., 2015; Clark et al., 2018; Fecchio et al., 2018). However, few empirical studies have assessed how avian haemosporidian diversity and distributions differ across biogeographical regions and latitudinal gradients (Clark et al., 2014; Clark, 2018). How avian malaria parasite distributions and diversity covary with environmental conditions, ecological and historical factors across bioregions presents a substantial gap in our knowledge for this host–parasite system.

Here, we used the mitochondrial cytochrome-*b* (cyt-*b*) gene to identify haemosporidian lineages to explore macroecological and biogeographic patterns in their distributions and diversity across South America. We used this cosmopolitan and diverse group of avian parasites (Haemosporidia from the genera *Plasmodium* and *Parahaemoproteus*) to test whether parasite diversity and composition vary with avian diversity and community composition, host relatedness, climatic conditions, geographic distance and latitude. We also investigated the spatiotemporal evolution of haemosporidian parasites by inferring biogeographical processes among South American regions. Collectively, our analyses will identify the contributions of climate as well as host and parasite ancestry to regional community assembly.

2 | MATERIAL AND METHODS

2.1 | Host and parasite sampling

We collected 7,534 blood and tissue samples from 806 avian species across eight regions in South America (see raw data in Table S1). This sampling includes 41 bird communities surveyed from Amazonia to Patagonia spanning a latitudinal gradient of 4,700 kilometres (Figure 1). All tissue samples and birds were collected under appropriate permits in Argentina, Brazil and Peru.

Parasite lineages were identified from avian tissue samples using a standard molecular barcoding approach. Briefly, DNA extracted from host tissues underwent PCR-based detection targeting a 477-bp barcoding fragment of the cyt-*b* gene from the haemosporidian mitochondrial genome. Details on primers used, reaction protocols and cycling conditions can be found in Ref. (Hellgren, Waldenström, & Bensch, 2004; Bell, Weckstein, Fecchio, & Tkach, 2015). As evidence indicates that avian haemosporidian haplotypes differing by one cyt-*b* nucleotide may be reproductively isolated entities (Bensch, Pérez-Tris, Waldenström, & Hellgren, 2004), we used the conventional practice of referring to each unique cyt-*b* haplotype as a unique parasite lineage following the standard naming for these group of parasites (Bensch, Hellgren, & Pérez-Tris, 2009).

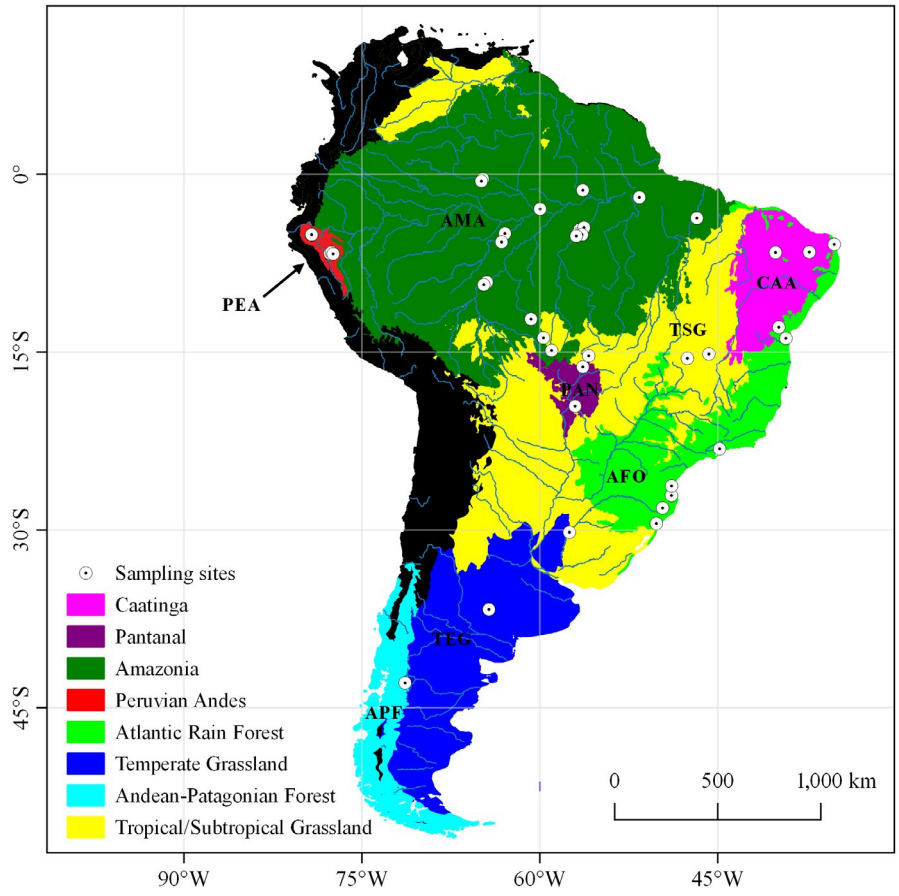

FIGURE 1 Sampling sites across South America regions. These ecoregions, used in our biogeographic analyses, are derived from the classification of Olson et al. (2010) for terrestrial biomes. Coordinates for each of the 41 avian communities, number of individuals captured, and bird and parasite richness are available in the raw data (Table S1) [Colour figure can be viewed at wileyonlinelibrary.com]

2.2 | Phylogenetic reconstruction

Assembled sequences of unique haplotypes were used to infer molecular phylogenies. We used the GTR + I + G model of nucleotide substitution as determined by jModelTest (Guindon & Gascuel, 2003; Darriba, Taboada, Doallo, & Posada, 2012). We divided avian haemosporidian parasites into two separate alignments, one for the genus *Parahaemoproteus* and one for the genus *Plasmodium*. For both alignments, *Leucocytozoon fringillarum* (GenBank accession no. FJ168564) was used as the outgroup. The genus *Haemoproteus* was excluded from the analyses because only 62 individuals were infected by 22 lineages of this genus and it was not represented in all biomes. We obtained a time-calibrated tree for each parasite lineage alignment using the Bayesian relaxed clock model (Drummond, Ho, Phillips, & Rambaut, 2006) in BEAST VER. 1.8.4 (Drummond, Suchard, Xie, & Rambaut, 2012). The analyses were conducted for 159 lineages of *Parahaemoproteus* and 339 lineages of *Plasmodium*. We generated two independent runs for each alignment with parameters as follows: an uncorrelated lognormal relaxed clock, Yule process, 100 million generations of MCMC (Markov chain Monte Carlo), parameters sampled every 10,000 generations and 10% of generations discarded as burn-in. To obtain absolute ages for cladogenetic events through parasite trees, we used a recently published substitution rate for avian malaria parasites estimated by Pacheco et al. (2018), based on whole mitochondrial genome sequences, as a uniform prior ranging from 0.00334 to 0.00487 substitutions per lineage per million years. Convergence and performance of runs were inspected using TRACER 1.6 (http://beast.bio.ed.ac.uk/Tracer), to ensure that ESS (effective sample size) values exceeded 200. The maximum clade credibility (MCC) tree for each malaria group was generated using TreeAnnotator. Time trees were visualized in FIGTREE VER. 1.4.2 (http://tree.bio.ed.ac.uk/software/figtree/).

2.3 | Biogeographic inference

To infer biogeographic process across South American regions, we reconstructed ancestral areas on internal nodes of the avian haemosporidian parasites trees using the software RASP 4.0 (Yu, Harris, Blair, & He, 2015). We used 100 trees randomly sampled from the posterior probability distribution of BEAST runs for each parasite alignment. The S-DEC (statistical dispersal, extinction and cladogenesis) method was used to infer the ancestral area distribution at each node. We considered eight geographic areas in South America: Atlantic Rain Forest, Amazonia, Andean-Patagonian Forest, Caatinga, Tropical and Subtropical Grassland, Peruvian Andes, Temperate Grassland and Pantanal. Geographic areas followed the classification of Olson et al. (2010) for terrestrial biomes (Figure 1). We also used avian compositional analyses for grouping sites into regions/biomes that are biologically meaningful at the parasite level (Figure 1). Parasite lineage distributions were coded as present or absent in each of the eight areas. We set the maximum number of areas to seven and pruned the outgroup from the parasite tree prior to analysis. Analyses were

implemented without constraints. We then computed biogeographic events (vicariance, dispersal, duplication and extinction) for each parasite alignment. Dispersal events among areas were plotted into a Chord diagram using the chorddiag package (https://github.com/mattflor/chorddiag) in R v. 3.3.3 (R Core Team, 2018).

2.4 | Distance–decay relationship

We followed the methods of Ellis et al. (2015) and used partial Mantel tests to examine whether parasite assemblages at the community level reflect differences in host communities, dispersal limitation (i.e., geographic distance) and climate. A partial Mantel test produces a coefficient that measures the strength of correlation between two dissimilarity matrices while controlling for the effect of a third (Legendre & Legendre, 1998). For example, the effect of distance on parasites might not be independent of hosts because bird species have limited geographic ranges. The correlation between parasites and distance controlling for the effect of hosts can be calculated as a partial Mantel coefficient. We used Bray–Curtis dissimilarities (Bray & Curtis, 1957; Legendre & Legendre, 1998) between sites based on their parasite assemblages (*Plasmodium* + *Parahaemoproteus*), *Plasmodium* lineages only or host communities. We partitioned the lineages by parasite genus: *Plasmodium* (867 occurrences, 339 lineages, prevalence 11.5%), *Parahaemoproteus* (392 occurrences, 159 lineages, prevalence 5.2%) and *Haemoproteus* (62 occurrences, 22 lineages, prevalence 0.3%). Therefore, we focused our analyses on *Plasmodium* and not *Parahaemoproteus* or *Haemoproteus* because of lower sample sizes in the last two groups of parasites. To construct the climate dissimilarity matrix, we used Euclidean distances based on the first five principal component (PCA) scores for 19 climatic BioClim variables (http://www.worldclim.org/) downloaded for each location, weighted by the proportion of variance explained by each PCA component. We used geographic distances between sampling sites to create the dissimilarity matrix for distance. We conducted all analyses at the community level, and we included only sites that had at least ten infections.

2.5 | Testing the latitudinal gradient hypothesis

We examined latitudinal diversity gradients at the community level. Communities differed in the number of birds collected (median, 156; range, 37–788) and in the number of infections obtained (median, 22; range, 1–136). To account for differences in sample size, we analysed only communities with at least ten infected individuals, and we used rarefaction (Hurlbert, 1971; Simberloff, 1972; Heck, van Belle, & Simberloff, 1975) to measure species diversity. Rarefaction calculates the number of species expected in a random sample of individuals from a larger collection and permits more meaningful comparisons among sites. We rarefied our samples to two and to ten infected individuals; rarefaction to two individuals equals Hurlbert's (1971) Probability of Interspecific Encounter (PIE) +1. We used linear regression to test the latitudinal diversity gradient. All statistics were conducted in R v3.5.1 (R Core Team, 2018).

We also used a PERMANOVA to test whether the composition of parasite assemblages varies with a latitudinal gradient. We used Bray–Curtis dissimilarities (Bray & Curtis, 1957; Legendre & Legendre, 1998) between sites based on their parasite assemblages and performed the PERMANOVA including the latitude and the biome of each community as explanatory variables.

3 | RESULTS

The prevalence of haemosporidian parasites (*Plasmodium*, *Parahaemoproteus* and *Haemoproteus* combined) was 17.5% representing 1,321 occurrences and 520 unique genetic lineages (see raw data for prevalence and lineage richness by host taxon or parasite genus in Table S1).

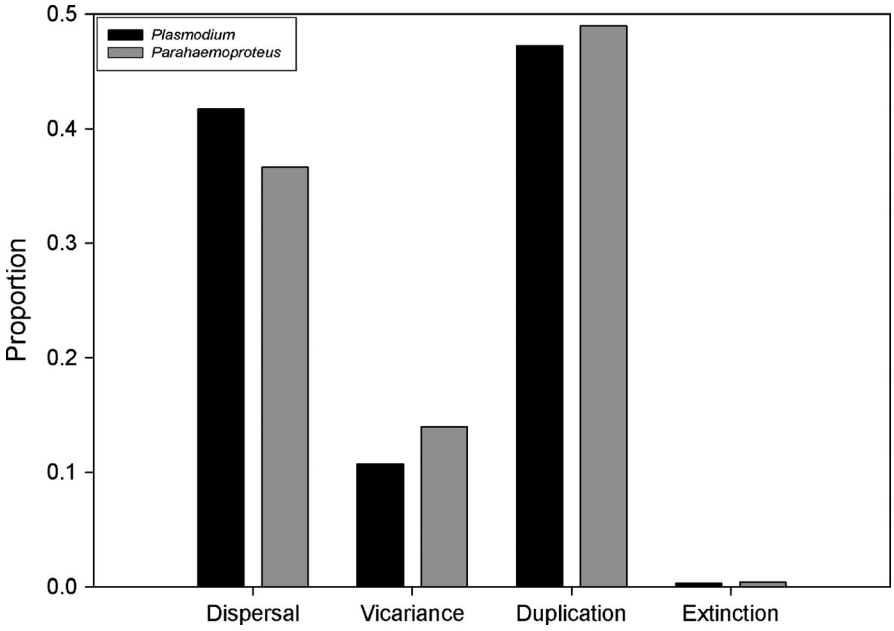

FIGURE 2 Frequency of occurrence for the four biogeographic events inferred by S-DEC in South American bioregions

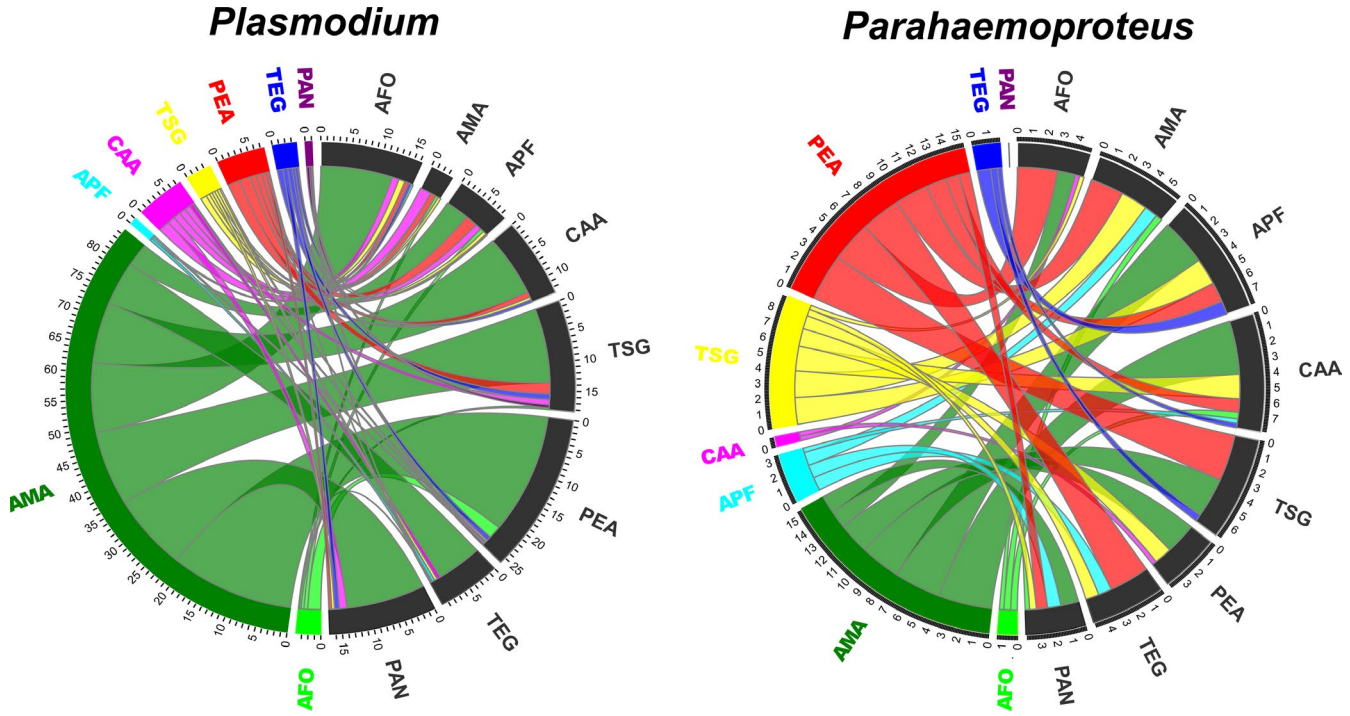

FIGURE 3 Chord diagram depicting connectivity among South American regions. Chord thickness indicates the frequency of dispersal events, and chord colours indicate the region of origin for the dispersal events inferred for *Plasmodium* and *Parahaemoproteus*. Abbreviated region names and colour scheme correspond to those regions in Figure 1. Source regions are on the left (coloured names), and sink regions are on the right (dark grey names). Dispersal events were inferred by the S-DEC algorithm in RASP [Colour figure can be viewed at wileyonlinelibrary.com]

3.1 | Biogeographic processes

Duplication and dispersal were the most important events at ancestral nodes for *Plasmodium* (duplication: 47.3%; dispersal: 41.7%) and *Parahaemoproteus* (duplication: 49.0%; dispersal: 36.6%) (Figure 2). Most duplication events for these genera occurred in Amazonia (*Plasmodium*: 87.9%; *Parahaemoproteus*: 38.7%), with an impressive dominance for *Plasmodium*. Through dispersal events, Amazonia was the most important region for the radiation of *Plasmodium*, acting as the primary source of lineage dispersal across South America and Peruvian Andes as the most important sink region (Figure 3). Yet, the Peruvian Andes was as important as Amazonia as the primary source of diversity for *Parahaemoproteus* (Figure 3). In contrast, the Andean-Patagonian Forest and Caatinga received the highest number of *Parahaemoproteus* lineages followed by Tropical and Subtropical Grassland and Temperate Grassland.

3.2 | Parasite and host assemblage similarity

For most analyses, patterns for *Plasmodium* assemblages were qualitatively similar to those for all parasites (*Plasmodium* + *Parahaemoproteus*). When patterns differed, however, both patterns are described, and all results are provided in Table 1. Mantel tests showed significant correlations between parasite and host community dissimilarities (r = 0.41, p < 0.001; Table 1, Figure 4a). Mantel tests also revealed significant correlations between parasite and climatic dissimilarities (r = 0.26, p < 0.001; Table 1, Figure 4a) and parasite and geographic distance (r = 0.30, p < 0.001; Table 1, Figure 4a).

We used partial Mantel tests to separate the direct effects of climate and distance on parasite assemblages from indirect effects that occur through their effects on the avian hosts. When controlling for the effect of avian host communities, *Plasmodium* dissimilarity was related to climate (r = 0.17, p = 0.01; Table 1) and to geographic distance (r = 0.15, p = 0.03; Table 1). When all parasites were examined, dissimilarities were significantly related to geographic distance (r = 0.12, p = 0.04; Table 1, Figure 4b), but not to climate (r = 0.10, p = 0.07; Table 1, Figure 4b) when controlling for the effect of avian host communities. In contrast, parasite and avian host community dissimilarities remained significant even when controlling for geographic distance (r = 0.31, p < 0.001; Table 1, Figure 4c) or climate (r = 0.34, p < 0.001; Table 1, Figure 4d).

3.3 | Latitudinal diversity gradient in parasite and avian hosts

When parasite diversity was measured by rarefying communities to ten infections, parasite diversity decreased with latitude (β = −0.053, R^2 = 0.260, p = 0.001; Figure 5). Diversity patterns did not depend on the size to which communities were rarefied (i.e., rarefaction to two and to ten infected individuals produced similar results); thus, we present only the results from communities

TABLE 1 Results of Mantel and partial Mantel tests comparing hypothesized relationships between parasites (i.e., parasite assemblage dissimilarity), *Plasmodium* (i.e., *Plasmodium* assemblage dissimilarity), geographic distance (i.e., distance between sites), climate (i.e., climatic differences between sites) and bird community (i.e., host community dissimilarity between sites). We report the partial Mantel correlation coefficient (r_p) and associated *p* value

Relationship between		Controlling for	r_p	*p*
Parasites	Distance	None	0.300	0.001
Parasites	Climate	None	0.256	0.001
Parasites	Birds	None	0.406	0.001
Parasites	Birds	Distance	0.308	0.001
Parasites	Birds	Climate	0.339	0.001
Parasites	Distance	Birds	0.117	0.040
Parasites	Distance	Climate	0.190	0.001
Parasites	Climate	Birds	0.100	0.067
Parasites	Climate	Distance	0.100	0.040
Plasmodium	Distance	None	0.298	0.001
Plasmodium	Climate	None	0.287	0.001
Plasmodium	Birds	None	0.334	0.001
Plasmodium	Birds	Distance	0.215	0.003
Plasmodium	Birds	Climate	0.240	0.003
Plasmodium	Distance	Birds	0.149	0.025
Plasmodium	Distance	Climate	0.156	0.012
Plasmodium	Climate	Birds	0.165	0.008
Plasmodium	Climate	Distance	0.131	0.021

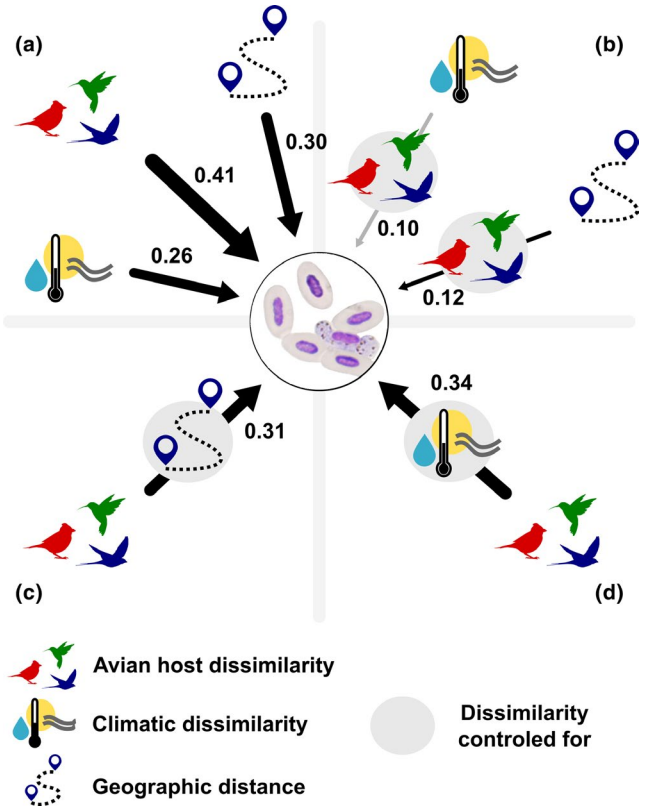

FIGURE 4 Host community dissimilarity, geographic distance and climatic dissimilarity on parasite dissimilarity. The thickness of the arrows is proportional to the correlation coefficient. Grey arrow indicates nonsignificant (α = 0.05). Quadrant (a) summarizes the results of the Mantel tests from Table 1, whereas the remaining quadrants summarize the results of partial Mantel tests controlling for (b) avian host dissimilarity; (c) geographic distance; and (d) climatic dissimilarity [Colour figure can be viewed at wileyonlinelibrary.com]

rarefied to ten samples. Bird diversity also decreased with latitude (β = −0.042, R^2 = 0.290, p < 0.001; Figure 6), but this pattern was driven by a single community with low bird diversity that occurs at 42°S. Parasite diversity increased with host diversity (β = 0.683, R^2 = 0.261, p = 0.002; Figure 7). *Plasmodium* diversity showed a decreasing significant trend with latitude (β = −0.052, R^2 = 0.157, p = 0.03) and did not vary significantly with host diversity (β = 0.40, R^2 = 0.112, p = 0.07).

The PERMANOVA indicated that the composition of parasite assemblages follows a latitudinal gradient (F = 1.3, R^2 = 0.03, p = 0.018), but biome is a stronger determinant for the occurrence of parasite lineages in each community (F = 1.5, R^2 = 0.27, p = <0.001) than latitude.

4 | DISCUSSION

One biogeographical and two macroecological patterns emerge as the dominant events in the diversification and distribution of haemosporidian parasites across South American biomes. First, local diversification followed by dispersal between regions was the most common biogeographic processes reconstructed within both the *Plasmodium* and *Parahaemoproteus* phylogenies, with Amazonia as the primary source of haemosporidian diversity. Second, similarity of parasite assemblages decreases with geographic distance and climatic dissimilarity, suggesting that parasite lineages are dispersal-limited. The correlation between parasite and host dissimilarities remains highly significant when controlling for geographic distance or climate. These findings suggest that parasite assemblages obey the distance–decay relationship, but that parasite similarity is most strongly influenced by the host community rather than climate similarity or geographic distance. Third, haemosporidian parasites increased in diversity from Patagonia to Amazonia supporting the latitudinal gradient hypothesis.

4.1 | Amazonia is the primary source of haemosporidian diversity in South America

Our biogeographic analyses indicate that Amazonia is the greatest contributor of *Plasmodium* and *Parahaemoproteus* lineages to other regions in South America. For *Parahaemoproteus*, the Peruvian Andes were as important as Amazonia in contributing lineages to other regions in South America. Our results for two clades of avian protozoan parasites are consistent with those of a recent analysis in which Amazonia was identified as the primary source of Neotropical biodiversity in four groups of vertebrates (birds, frogs, mammals

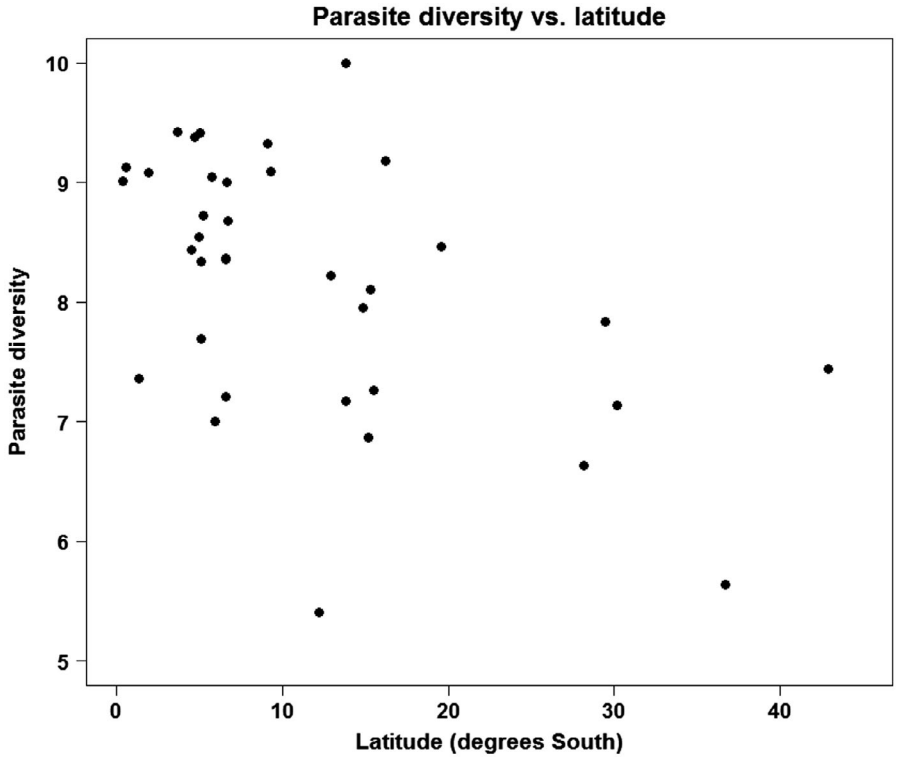

FIGURE 5 Parasite diversity, measured as the expected number of lineages in a random sample of ten infections, decreases with latitude (β = −0.053; R^2 = 0.260; p = 0.001)

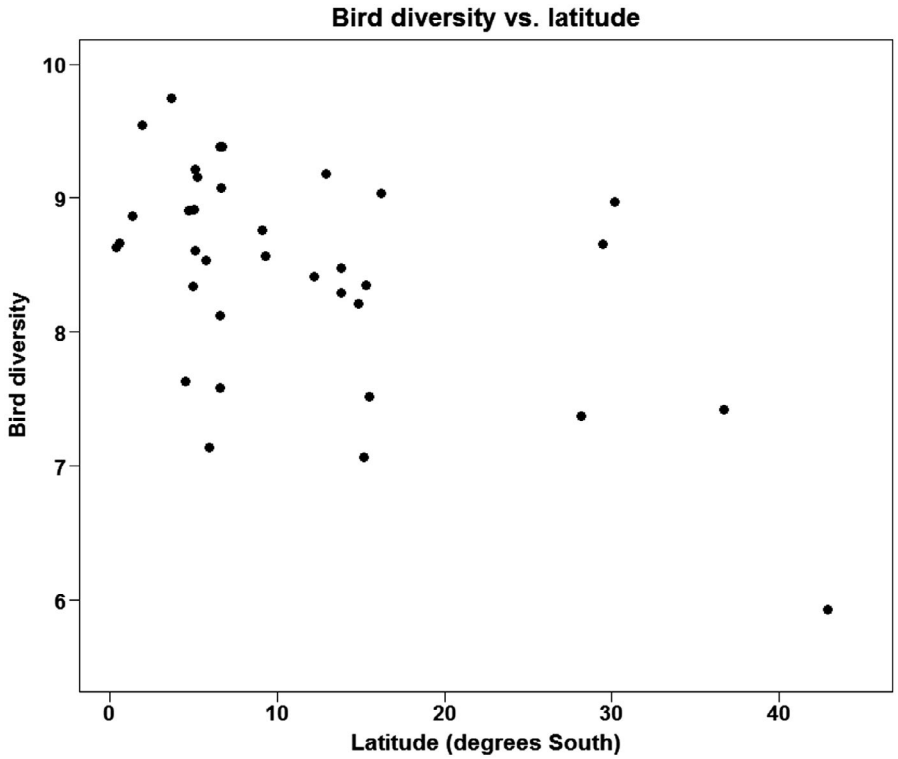

FIGURE 6 Bird diversity, measured as the expected number of lineages in a random sample of ten infected individuals, decreases with latitude (β = −0.042; R^2 = 0.290; p < 0.001). Removing the community with the lowest bird diversity located at 42°S renders a marginally significant trend (β = −0.028; R^2 = 0.128; p = 0.038)

and squamates) and two groups of plants (angiosperms and ferns) (Antonelli et al., 2018). Amazonia was recovered as the main source of parasite lineage dispersal into the Caatinga (the driest region) and Andean-Patagonian Forest as well, despite a lack of current connection between Amazonia and these two regions. A high level of *Plasmodium* dispersal from Amazonia into the Atlantic Rain Forest was observed, which concurs with several studies on vertebrates that suggest periodic contact between these biomes since the Miocene (Costa, 2003; Batalha-Filho, Fjeldså, Fabre, & Miyaki, 2013; Ledo & Colli, 2017). The high level of *Plasmodium* lineage dispersal from the

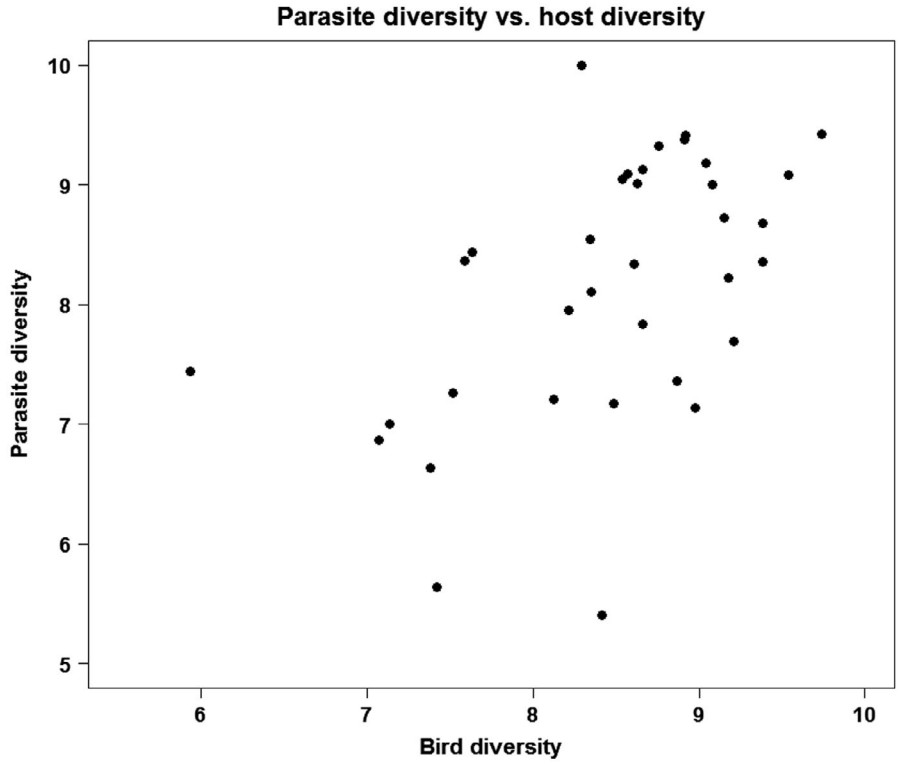

FIGURE 7 Parasite diversity increases with host diversity (β = 0.683; R^2 = 0.261; p = 0.002). Diversity was measured as the expected number of species in a random sample of ten infected individuals and decreases with latitude (see Figure 5)

Atlantic Rain Forest to the Peruvian Andes is remarkable considering the geographical distance and isolation between these two regions. At the same time, the lack of *Parahaemoproteus* dispersal from the Atlantic Rain Forest to Tropical and Subtropical Grassland is surprising considering their spatial connectivity, which would be expected to allow the highest number of lineage interchanges (Donoghue & Edwards, 2014). Here, we show that despite having high ecological and geographic dispersal capabilities (Ellis et al., 2015, 2019; Clark et al., 2018; Fecchio et al., 2018), *Plasmodium* and *Parahaemoproteus* differ with respect to interchange frequency across regions in South America, possibly due to differential host specificity of parasite lineages or differential mobility of avian hosts across biomes with subsequent parasite host range expansion, two hypotheses that warrant future investigation.

4.2 | The distance–decay relationship

Avian haemosporidian parasite assemblage similarity would be expected to decrease with climate dissimilarity (Nekola & White, 1999; Soininen et al., 2007; Clark et al., 2018) and with geographic distance (Ishtiaq et al., 2010; Svensson-Coelho & Ricklefs, 2011; Clark et al., 2018). Climatic factors are especially expected to influence the diversity and distributions of vector-transmitted parasites, such as those that cause avian malaria (Fecchio et al., 2019). Our findings across South America suggest that the influence of climate and geographic distance is driven largely but not entirely by their effects on birds, thereby indirectly influencing parasite similarity on a regional scale. It is therefore plausible to infer that the vertebrate host may play the main role in haemosporidian diversity, distributions and dispersal for three reasons. First, the avian host provides a constant environment for the protozoan parasite throughout the year where it is often maintained as a chronic infection in avian tissues even when the vectors are not active. Second, in comparison with the ephemeral invertebrate hosts (vectors), the longer lifespan of the vertebrate host may also select for haemosporidian specialization towards this predictable and conditionally stable resource. It is worth mentioning that locally stochastic climatic events will likely have a larger effect on the ectothermic invertebrate hosts, thus increasing the risk of local parasite extinction at this life stage. Lastly, the few studies of vector specificity in avian malaria parasites suggest that the invertebrate hosts are not important in structuring parasite communities (Gager, Del Rosario Loaiza, Dearborn, & Bermingham, 2008; Njabo et al., 2010), either because they feed widely across host species in a bird community (Medeiros, Ricklefs, Brawn, & Hamer, 2015) promoting invertebrate host sharing and subsequent lack of cospeciation (Ishtiaq et al., 2008) or because host compatibility rather than vector encounter rates plays a major role in the range expansion of *Plasmodium* (Medeiros, Hamer, & Ricklefs, 2013). Thus, at present, there is not strong evidence to support vectors as the driving factor in avian haemosporidian parasite community assembly. How climatic conditions affect vector distribution, specialization and vectorial capacity across environmental gradients or regions warrants further study and will contribute greatly to understanding the complexity of this host–parasite–vector system.

4.3 | Haemosporidian diversity decreases from Amazonia to Patagonia

Avian malaria parasites show a prominent latitudinal diversity gradient in South America bird communities, contrasting with two previous studies that showed no effect of latitude on haemosporidian diversity in temperate Chile (Merino et al., 2008) or even on a global scale (Clark, 2018). Our finding of increasing diversity from Patagonia towards Amazonia was robust for both the parasites and their avian hosts and is consistent with the pattern of elevated richness of most animal and plant taxa towards the equator (Pianka, 1966; Rohde, 1992; Hillebrand, 2004). The LDG has been observed in some micro- and macroparasite–host systems, such as ectoparasites of marine fishes (Rohde & Heap, 1998), vector-transmitted protozoan parasites of primates (Nunn et al., 2005), directly transmitted viruses of rodents (Bordes, Guégan, & Morand, 2011) and helminths in several vertebrate host taxa (Dallas et al., 2018). However, many other studies have failed to show an effect of latitude on parasite diversity (Poulin, 1995; Bordes, Morand, Krasnov, & Poulin, 2010; see Kamiya et al., 2014b for a meta-analysis; Clark, 2018; Krasnov et al., 2019). These contradictory results in latitudinal patterns of diversity among host–parasite systems could be explained by differences in parasite life cycle and modes of transmission (Bordes et al., 2011). Specifically, for avian *Plasmodium* parasites, both richness of mosquito vectors (Foley, Rueda, & Wilkerson, 2007) and diversity of avian hosts (Duchêne & Cardillo, 2015) increase towards the equator, making it difficult to decouple any effect related to parasite reproduction within the intermediate or definitive host. To our knowledge, no study has tested whether avian haemosporidian parasite diversity follows the diversity of vectors or avian hosts when controlling for the other. Here, we show that haemosporidian parasites and avian host diversity covary across a latitudinal gradient of nearly 5,000 km. At least three hypotheses may explain the LDG pattern found in this host–parasite system across temperate and tropical regions of South America. First, a latitudinal gradient in opportunities for parasite diversification through host switching may exist because haemosporidian parasites will have more opportunities to colonize available hosts in richer, tropical bird communities. This hypothesis is supported by the number of duplication events observed within Amazonia for *Plasmodium* and *Parahaemoproteus* (Figure 3). Second, in tropical bird communities with high parasite and pathogen diversity, avian hosts might be overwhelmed and incapable of coping with such pathogen diversity (e.g., possibly being unable to mount immune responses to all types of pathogens), thereby causing a latitudinal gradient in avian host resistance to malarial parasitism (Svensson-Coelho, Ellis, Loiselle, Blake, & Ricklefs, 2014). Third, a latitudinal gradient in host specificity might influence patterns of parasite community assembly (Clark, 2018).

5 | CONCLUSION

Our study confirms that local diversification and dispersal are the main biogeographic processes shaping the diversity and distributions of haemosporidian parasites. Moreover, we found that community assembly of haemosporidian parasites is governed by host community composition and to a lesser extent by climatic similarity and geographic distance. This finding is not surprising considering that the avian host provides a constant environment during the longest phase of the parasite's life cycle. Our results also provide one hypothesis to explain the latitudinal diversity gradient found in this host–parasite system, where parasite diversity mirrors host diversity and increases towards the equator. Increased sampling of avian haemosporidians will improve our understanding of phylogenetic relationships within this diverse group of parasites and combining these data with information about avian host radiations will allow for further testing of this hypothesis.

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AUTHOR CONTRIBUTIONS

AF conceived the original idea. AF, HBF, RBPP and MDC designed the research and performed the analyses. The remaining authors conducted the fieldwork, collected samples or performed the laboratory work. AF wrote the manuscript with significant contributions from JAB, HBF and MDC. All other authors contributed with the revision of the final version of the manuscript.

DATA AVAILABILITY

The raw data set will be uploaded as Supporting Information. All DNA sequences are available in Genbank (Accession numbers

KU562119–KU562810, KY924307–KY924317, MG192486–MG192534 and MK695213–MK695499) and can be found in Supporting Information.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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