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Research

Migrant birds disperse haemosporidian parasites and affect their transmission in avian communities

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Migration has an important impact on the transmission of pathogens. Migratory birds disperse parasites through their routes and may consequently introduce them to new areas and hosts. Hence, haemosporidian parasites, which are among the most prevalent, diverse and important bird pathogens, are potentially dispersed when infecting migrant hosts. Further, migrant hosts could enhance local parasite prevalence and richness by transporting new parasite strains to new areas. Here, we hypothesize and aim to evaluate if 1) migratory birds spread parasite lineages along their routes, and 2) localities crossed by more migratory birds have greater prevalence and richness of haemosporidians. For the first hypothesis, we tested whether parasite lineages found 1) in both migrants and residents, and 2) only in residents, differ in their frequencies of occurrence among localities. For the second hypothesis, we tested for a relationship among localities between the overall local haemosporidian parasite richness and prevalence, and the proportion of migratory bird individuals present in a locality. We combined a dataset on 13 200 bird samples with additional data from the MalAvi database (total: ~2800 sequenced parasites comprising 675 distinct lineages, from 506 host species and 156 localities) from South America, and used Bayesian multi-level models to test our hypotheses. We demonstrate that parasites shared between resident and migratory species are the most spatially widespread, highlighting the potential of migrants to carry and transmit haemosporidians. Further, the presence of migrants in a locality was negatively related to local parasite richness, but not associated with local prevalence. Here, we confirm that migrants can contribute to parasite dispersal and visiting migrants are present in regions with lower *Plasmodium* prevalence. Also, we observed their presence might raise *Haemoproteus* community prevalence. Therefore, we demonstrate migrants enhance pathogens spread and their presence may influence parasite community transmission.

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Introduction

Migration has an important impact on the transmission of disease across the world as migrant species disperse pathogens and parasites between localities, while also being exposed to more infectious agents (Bartel et al. 2011, Bauer and Hoye 2014, Teitelbaum et al. 2018). Migrant species might play an important role in the evolution and distribution of parasites and promote the spread of pathogens to new areas and new hosts species. The introduction of pathogens by migrants to new localities might lead to changes to the local community structure or richness, depending on the susceptibility of resident species to infection (Altizer et al. 2011). Indeed, recent studies have demonstrated that migratory birds harbor a greater diversity of parasites than resident species (Koprivnikar and Leung 2015, Gutiérrez et al. 2019) and documented the influence of migratory birds on the spread of important pathogens (Morshed et al. 2005, Hellgren et al. 2007, Ricklefs et al. 2017) with some of these able to infect humans (Morshed et al. 2005, Poupon et al. 2006, Lindeborg et al. 2012). Thus, the migratory behavior of birds may directly influence host local richness and community structure, as well as the local richness of parasite species.

The metabolic demands of migration can decrease the amount of resources available to mount an immune response, which could lead to higher susceptibility to infections (Wikelski et al. 2003, Altizer et al. 2011). For this reason, it might also be expected that migratory birds harbor a more diverse range of parasites and might be more susceptible to parasite infections. Conversely, migration may also have a protective effect since migratory behavior allows hosts to escape environments presenting a high risk of infection (Altizer et al. 2011, Poulin et al. 2012). Avian haemosporidians, which include the genera *Plasmodium*, *Haemoproteus* and *Leucocytozoon*, are vector-borne protozoan parasites and are among the most prevalent, diverse and well-studied avian parasites, being widely distributed and able to infect many avian clades (Valkiūnas 2005, Fecchio et al. 2020). Due to the high abundance and diversity of both birds and haemosporidians, and the relevance of vector-borne diseases to human health, these parasites are frequently used as ecological models of host–parasite interactions (Marzal 2012).

Since most haemosporidians cause life-long infections (Valkiūnas 2005), parasites may travel across long distances with their bird host during migration, allowing them to infect new vectors and new avian hosts in novel environments. Indeed, migratory species are known for their potential to connect distant habitats and transfer large amounts of biomass, nutrients and other organisms between ecosystems (Bauer and Hoye 2014). However, previous research has demonstrated differences in the timing of the main occurrence of haemosporidian infection in migrating birds. These studies have suggested that differences in haemosporidian lineages harbored could indicate whether birds had become infected in different areas (Marzal 2012). Other factors such as environmental conditions, and the richness and phylogenetic diversity of the local host community can also impact the susceptibility of avian hosts to haemosporidian parasites (Barrow et al. 2019, Fecchio et al. 2019a, 2021, Clark et al. 2020).

South America comprises different types of biomes, which hold a great richness of resident and migratory bird species, thus making it an ideal system to investigate such questions. Moreover, prevalence of *Plasmodium*, which is the most prevalent haemosporidian in this region, can be markedly different among South American regions (Braga et al. 2011). *Plasmodium* parasites present higher host-shifting rates than other bird haemosporidians (Hellgren et al. 2007), which could certainly result in their increased dissemination by migratory birds into new areas. Indeed, host-shifting of a *Plasmodium* species from domestic chicken to wild and native birds has already been reported in South America (Ferreira-Junior et al. 2018).

Furthermore, the great avian richness (~3500 species) and abundance in South America (Remsen et al. in press) could also enhance the probability of parasite host-shifting between migratory and resident birds, given the likely presence of susceptible birds in any particular area. Besides that, the great richness and abundance of vectors (Consoli and Oliveira 1994, Santiago-Alarcon et al. 2012a) could also increase the chances of host-shifting between migratory and resident birds as it increases the chances of compatible vectors being present in any given locality. These features make the South American avian haemosporidians a great model system to investigate the putative transmission of pathogens via host migration in nature.

Studying the potential of migrant hosts to spread pathogens and their impact on local community transmission is fundamental to understand patterns of pathogen dispersal, prevalence and diversity. In this context, the main goal of this study is to evaluate the influence of migratory birds on the spread and community transmission of haemosporidian parasites in South America. Specifically, we evaluated the hypothesis that 1) migratory birds spread parasite lineages along their migratory routes, and 2) localities crossed by more migratory routes have greater prevalence and richness of haemosporidian lineages. For the first hypothesis, we tested whether parasite lineages found 1) in both migrants and residents and 2) only in residents differ in their geographical range. Due to the fact migrants can carry parasites from many sites and potentially infect resident birds, we predicted that, all else being equal, parasite lineages using migratory birds should occur across a greater spatial range than those infecting only resident birds. Moreover, migratory behavior increases the exposure of birds to more parasite lineages and hence their contact with different parasites as migrants are present in regions that harbor different parasite communities. Therefore, we expect higher haemosporidian richness and prevalence in regions with more migratory birds. For the second hypothesis, we tested for a relationship among localities between the overall local haemosporidian parasite richness and prevalence, and the proportion of migratory birds present in a locality. Our analysis also takes into account other potential drivers of haemosporidian prevalence and species

richness, such as temperature and precipitation, which influence the local abundance of vectors.

Methods

Dataset

All analyses were performed using a dataset comprising ~13 200 bird blood samples accounting for 896 species from 63 different localities sampled from 2005 to 2018 in South America, with a subset of those samples previously used in Lacorte et al. (2013), Ferreira et al. (2017), Ferreira-Junior et al. (2018), Fecchio et al. (2019); and supplemented with new, previously unpublished data (Supporting information). In addition to this dataset, we mined further data on haemosporidian lineages from the MalAvi database (<http://130.235.244.92/Malavi/>, Bensch et al. 2009) including data from the South American region, and extracting information from the Grand Lineage Summary after filtering out the data contained in our first dataset (Fig. 1). Combining both datasets, we obtained a total of ~2800 sequenced parasites representing 675 distinct lineages collected from 506 different host species and 156 localities (all lineages belonging to *Plasmodium* or *Haemoproteus*). Each locality was assigned to a biome based on the classification of Turchetto-Zolet et al. (2013). The parasite prevalence per bird species and locality was estimated using PCR diagnostic protocols described by Fallon et al. (2003), Hellgren et al. (2004) and Bell et al. (2015). The parasite lineages were sequenced by the PCR protocol described by Hellgren et al. (2004) and identified by comparing the sequences with the ones deposited in MalAvi and GenBank (<www.ncbi.nlm.nih.gov/genbank/>). This protocol produces a *cyt b* fragment of 478 bp. The birds present in each locality were classified into three ecological classes: 1) resident; 2) partial migrant and 3) full migrant (Supporting information), according to the Brazilian Committee of Ornithology Records – CRBO

(2014), Somenzari et al. (2018) and BirdLife International (<www.birdlife.org/>).

Statistical analyses

All analyses were conducted in R ver. 4.02 (<www.r-project.org>). Aiming to evaluate the potential impact of locality, avian phylogenetic relationships and climate in our models, we calculated spatial autocorrelation, phylogenetic signal and extracted climate data from Worldclim (Supporting information, <https://worldclim.org/version2>). The spatial autocorrelation analyses revealed there was no substantial effect of space on parasite richness (Moran index = −0.0007), however, for prevalence, we observed a Moran index of 0.15 which differed from the null expectation. For this reason, biome and locality ID were used as random effects in our second and third Bayesian models to control for idiosyncratic characteristics of localities. Likewise, considerable phylogenetic signals were observed among birds for prevalence (Pagel's lambda = 0.49) and parasite richness (0.17) and, therefore, we incorporated avian phylogeny in the second Bayesian model. All Bayesian models were checked for chain convergence using 'plot' function in R.

Bayesian models

To determine whether migratory birds spread parasite lineages along their migratory routes and to evaluate the parasite connectivity among localities due to migratory behavior, we used multi-level modeling (MLM) with the 'brms' package (Bürkner 2017) to evaluate the geographical range in which each haemosporidian lineage occurred depending on whether they were found only in resident birds or in both residents and migrants. We used Bayesian modelling as it allows to statistically estimate the geographical range among which lineages are distributed according to their host migratory status. Naturally, for parasites to be dispersed by migrant hosts, they need not only to be moved around by migratory hosts,
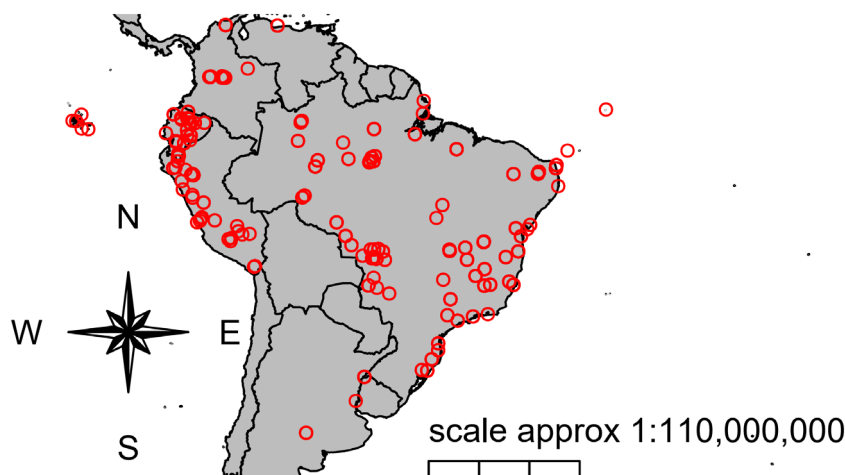

Figure 1. Bird collection localities. Collection localities comprise a total of 156 localities (including offshore islands) by combining our dataset and the MalAvi database.

but also infect the resident community. Hence, we compared the geographic range of parasites found in resident birds only with that of parasites shared by resident and migratory host species. However, for this last group, we discarded all localities where lineages were found infecting only migrant hosts since only when the parasite is also present in the resident community would there be real evidence of parasite dispersal.

To understand the variation of geographical range (estimated by minimum spanning tree distance – i.e. shortest total distance of all lines connecting each locality where a lineage was found, Supporting information) among haemosporidian lineages, we built a model including the migratory status of hosts used by a lineage. We ran a model comparing lineages present in resident birds only and lineages present in residents plus also birds of any migratory category. Our reference category in this models was lineages present only in resident bird species. We also controlled for sample size (i.e. number of birds positive for that lineage) and number of host species used by a lineage by including them as fixed factors.

Geographical range was the response variable and migratory status of hosts used by a lineage was the independent variable. We chose our priors using the 'get_prior' function. As our response variable had a continuous positive but skewed distribution, we applied the Gamma distribution family, using four chains with MCMC 4000 total iterations per chain (2000 for warmup, 2000 for sampling). The model results were plotted using the 'conditional_effects' function to visualize the predicted geographical range as a function of the host migratory status. We ran three models per analyses: one for two parasite genera combined, one for *Plasmodium* lineages only and one for *Haemoproteus* lineages only which are the most frequent and abundant haemosporidian genera in our dataset.

Next, we analysed the prevalence of infection in each bird individual among localities to test whether haemosporidian prevalence is generally higher in localities with more migratory birds. For this, we considered the local number of infections out of the total sample for each locality as our dependent variable using the total number of birds as our offset, and local proportion of migratory individuals (i.e. proportion of migratory individuals, including both partial and full migrants, out of all individual birds sampled in a locality) as our independent variable. In this model we used only our original dataset and excluded the data from the MalAvi database, since the latter includes only positive and sequenced samples. Thus, our analyses were based on 142 bird species distributed among 63 localities. Also, in this model, we filtered our data in order to include only species with 10 or more bird individuals analysed per species in each locality where that bird species occurred. Further, we calculated the proportion of migrant individuals in an area based on the data on captured birds in our dataset, and calculated local parasite richness across all birds in an area independently of their migratory category.

We initially evaluated if host richness (i.e. number of bird species sampled per locality), local parasite richness, proportion of migratory species, number of migrant individuals,

temperature and precipitation had significant effects on prevalence. Following these analyses, only parasite richness was retained as fixed factors since we did not detect any influence of the other factors on parasite infections. The negative binomial distribution was applied in this model to account for the overdispersion of prevalence data, thus avoiding production of biased estimates. We used four chains with MCMC 4000 total iterations per chain (2000 for warmup interactions, 2000 for sampling). Further, we considered biome and locality ID as random variables. Also, we created a matrix with phylogenetic distances between species and added as random variable in the model to account for possible phylogenetic influence on parasite infections. The model results were plotted using the 'conditional_effects' function to visualize the predictions based on the independent variable. Moran's I value was checked for model residuals. Again, we ran three models: one for all two parasite genera combined, one for *Plasmodium* lineages only and one for *Haemoproteus* lineages only; in these last two models we fitted the data to a zero inflated negative binomial distribution.

Another Bayesian model was performed to estimate whether localities with more migratory birds have greater richness of haemosporidian lineages. We considered parasite richness as our dependent variable and proportion of migratory individuals per locality (n = 63 localities) as the independent variable using total local number of bird individuals as our offset. Here, we also used only our original dataset, not data from the MalAvi database, because our dataset provides more information regarding the localities, such as prevalence data and host richness. We firstly evaluated whether local prevalence, host richness (i.e. number of bird species sampled per locality), number of migrant individuals (log-transformed scaled value), temperature (log-transformed scaled value) and precipitation had significant effects on prevalence. Following these analyses, only prevalence and host richness were retained as fixed factors since we did not detect any influence of the other factors on parasite infections. The negative binomial distribution was also applied in this model to account for the overdispersion of prevalence data, thus avoiding production of biased estimates. We used four chains with MCMC 4000 total iterations per chain (2000 for warmup interactions, 2000 for sampling). Further, we considered proportion of migratory species (i.e. proportion of migratory species, including both partial and full migrants, out of all bird species sampled in a locality) as fixed factor and biome and locality ID as random variables. We ran three models: one for all two parasite genera combined, one for *Plasmodium* lineages only and one for *Haemoproteus* lineages only; in these last two models we fitted the data to a zero inflated negative binomial distribution. Again, Moran's I value was checked for model residuals.

Results

Out of the 896 bird species considered in the analyses, 852 were classified as residents and 32 as partial, 12 as full

migrants. Most species (86%) were passerines, with the remaining mostly belonging to the orders Columbiformes, Piciformes and Apodiformes. Haemosporidian lineages occurred in anywhere from one to 38 localities, with many of them (15%) occurring in multiple biomes. Only 175 out of 675 lineages were observed in two or more localities and were used to estimate lineage spread in our analyses, besides, 426 linages were singletons. All models presented well converged chains.

Our first Bayesian model analyses revealed that lineages shared by migrants and residents showed the broadest geographical range (Fig. 2, Table 1). Lineages shared by resident and any type of migrant species presented a geographical range almost 50% greater than that of lineages occurring only in resident species. More specifically, we observed distinct patterns of distribution for *Plasmodium* and *Haemoproteus* lineages. For *Plasmodium* linages shared by residents and migrants were also more spatially widespread, whereas for *Haemoproteus* no difference in geographical range was observed between lineages found in residents only and those shared by residents and migrants (Supporting information). It is important to notice that similar patterns regarding parasite geographical range was also observed when plotting data from our raw dataset (Supporting information).

Our next Bayesian model analysed the relationship between local number of infected birds and the proportion of migratory bird individuals in the local avian community. We observed no correlation between the relative occurrence of migrants and number of infected hosts (Supporting information). However, when we repeated the analysis separately for only *Plasmodium* or *Haemoproteus* lineages, we observed negative and positive relationships between the number of infections per locality and local proportion of migrants in an area, respectively (Fig. 3, Table 2, 3). Parasite richness had

a significant positive association with the local number of infected birds, whether when considering all haemosporidian lineages (Supporting information), or only *Haemoproteus* lineages (Table 3).

Our last Bayesian model examining the influence of migrants on parasite richness revealed a negative effect of the proportion of individual migrants in the local community considering both haemosporidian genera together (Table 4, Fig. 4). We observed also no relationship between the proportion of migratory species and parasite richness. Further, we observed no effect for the proportion of migratory bird individuals or species on local parasite richness for *Plasmodium* and *Haemoproteus* infections when the two genera were treated separately (Supporting information). We observed positive effects on parasite richness of two other predictors in all models: local host richness and overall local prevalence.

Discussion

Animal migrations can play important roles in both the geographical dispersal of disease agents, and in the local epidemiology of diseases for both resident and migratory species (Bradley and Altizer 2005, Bauer and Hoye 2014, Teitelbaum et al. 2018). Our results indicate that haemosporidian lineages (both *Plasmodium* and *Haemoproteus*) infecting both migrants and residents are more widespread than those restricted to residents, possibly due to dispersal through migrants. Despite migration leading to lineages dispersing across South America, we did not observe higher prevalence of infection in localities with higher proportions of migratory individual birds. Nevertheless, we observed different patterns for *Plasmodium* and *Haemoproteus* parasites, such that *Plasmodium* prevalence negatively correlated with

Figure 2. Mean (±confidence intervals) geographical range in kilometers in which haemosporidian lineages are detected according to the type of birds in which they are found. Number of lineages in each of the two categories are shown on the graph.

Table 1. Parameter estimates, standard errors and confidence intervals for the Bayesian model testing the differences in the geographical range of haemosporidian lineages among those that occur in migratory and/or resident avian host species. (Residents only = reference category).

	Estimate	SE	CI (95%)	
Intercept	7.10	0.11	6.88	7.32
Resident and any migrant	0.40	0.19	0.05	0.79
Number of bird individuals	0.00	0.01	−0.02	0.03
Number of host species per lineage	0.05	0.03	−0.01	0.11

an increasing proportion of migrants, whereas *Haemoproteus* prevalence was higher in the presence of migrants. Moreover, the proportion of migratory individuals might have a negative effect on parasite richness. However, parasite richness seems to be positively related to local host richness and prevalence. Thus, migrant birds could potentially influence the ecology and evolution of haemosporidian dispersal in South America leading to an increase in parasite spread and influencing parasite prevalence and composition. In addition, we also demonstrate that generalist parasites may be more successful in colonizing new regions since parasites that infected both residents and migrant hosts had broader geographic distributions.
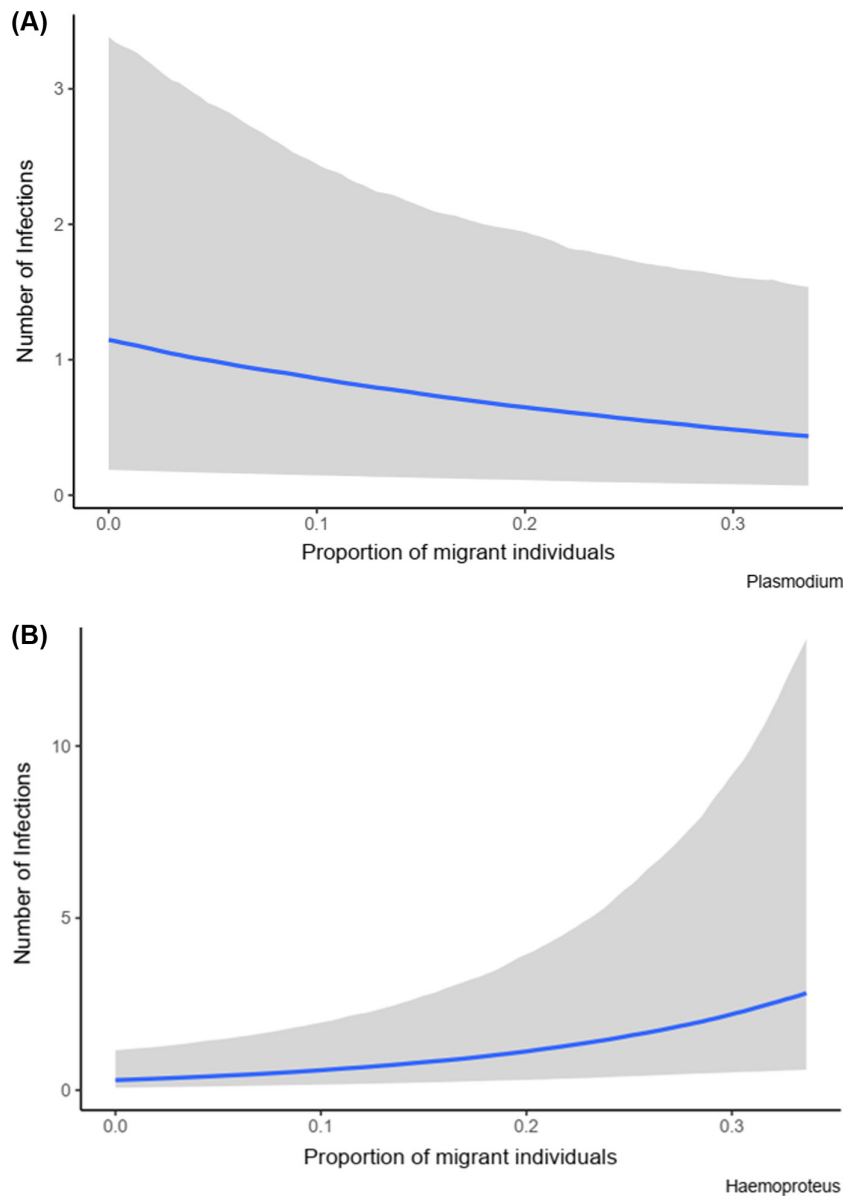

Figure 3. (A) Predicted model relationship (±95% confidence intervals) between local number of infections of *Plasmodium* parasites and proportion of migrants in an area. (B) Predicted model relationship (±95% confidence intervals) between local number of infections of *Haemoproteus* parasites and proportion of proportion of migrants in an area.

Table 2. Parameter estimates, standard errors and confidence intervals for the Bayesian model testing the variation of local number of birds infected by *Plasmodium* as a function of the proportion of migratory individuals out of all individual birds sampled per locality and parasite richness. Residual Moran value = 0.0015.

	Estimate	SE	CI (95%)	
Intercept	−0.47	0.77	−2.07	0.87
Proportion of migrant individuals	−2.78	1.40	−5.58	0.07
Parasite richness	0.02	0.01	−0.01	0.04

Dispersal of haemoporidians might be an important step toward parasite diversification for local community composition since parasites, after establishing in new regions, can evolve into new and distinct parasite lineages (Ellis et al. 2019, Fecchio et al. 2019a). Indeed, Ellis et al. (2019) found that South America presents high rates of parasite diversification, with the greatest proportion of sympatric nodes for *Plasmodium* spp. and one of the greatest *Haemoproteus* diversification rates. Hence, considering the potential contribution of migrant birds toward parasite dispersal, these hosts might play a fundamental role in parasite evolution and diversification in South America. Indeed, many species migrate in between the breeding season and relapses (increases in parasite intensity circulating in the host) mainly occur after this period (Valkiūnas 2005), thus facilitating parasite dispersal to new regions. However, we did not observe a clear relation between the presence of migrant birds and local haemosporidian prevalence since our data suggest that *Plasmodium* and *Haemoproteus* parasites respond differently to the presence of migrant hosts. The fact that most of our lineages were observed only in resident birds could explain the lack of a relationship between avian migrants and general haemosporidian prevalence, since the greatest haemosporidian diversity occurs in resident avian species. However, Hellgren et al. (2007) also suggest that new haemosporidian introductions into resident bird faunas are not common evolutionary events.

It is worth mentioning that distinct parasite taxa can respond differently to the presence of migrant hosts. As we reported in this study, despite the fact no relation was observed for general haemosporidian prevalence, *Plasmodium* and *Haemoproteus* showed contrasting responses to an increase in the local proportion of migrant individuals. Whereas *Plasmodium* prevalence was negatively correlated with an increase of migrants in the local bird community, we observed a raise in *Haemoproteus* infections.

Table 3. Parameter estimates, standard errors and confidence intervals for the Bayesian model testing the variation of local number of birds infected by *Haemoproteus* as a function of the proportion of migratory individuals out of all individual birds sampled per locality and parasite richness. Residual Moran value = −0.005.

	Estimate	SE	CI (95%)	
Intercept	−2.37	0.84	−4.07	−0.76
Proportion of migrant individuals	6.78	2.30	2.40	11.37
Parasite richness	0.04	0.02	0.01	0.07

Table 4. Parameter estimates, standard errors and confidence intervals for the Bayesian model testing the variation of local parasite richness by haemosporidian parasites as a function of the proportion of migratory individuals out of all individual birds sampled per locality, prevalence and host richness. Residual Moran value = 0.017.

	Estimate	SE	CI (95%)	
Intercept	1.30	0.22	0.86	1.73
Proportion of migrant individuals	−0.04	0.02	−0.08	0.00
Proportion of migrant species	0.04	0.02	−0.01	0.08
Prevalence	0.03	0.00	0.02	0.04
Host richness	0.01	0.00	0.01	0.02

This demonstrates that different groups of pathogens respond differentially to host migratory behavior. Besides, migration can work either as a mechanism that reduces parasite prevalence through migratory escape, or that increases prevalence due to higher host exposure and associated costs (Altizer et al. 2011). Indeed, previous research has documented different effects of host migration on parasite–host dynamics (Hellgren et al. 2007, Koprivnikar and Leung 2015, Teitelbaum et al. 2018). This distinct pattern for haemosporidians can occur due to the fact that haemosporidians are vector-borne parasites whose vectors differ between parasite genera. Thus, the broad host preferences of *Haemoproteus* vectors (Santiago-Alarcon et al. 2012b) could explain the increase in parasite prevalence observed for this genus as the chance of parasite transmission between hosts should increase for parasites vectored by highly generalist hosts. At the same time, it is possible that migratory behavior could had evolved as a mechanism of escaping *Plasmodium* infections.

Our findings also may suggest that where the proportion of migrant individuals in a community is higher, local haemosporidian richness is lower. In fact, migration often allows species to escape environments that present higher risks of infection, a mechanism that could decrease infection levels and favor the evolution of less-virulent pathogens (Altizer et al. 2011, Krasnov et al. 2012, Satterfield et al. 2015). This could lead to reduced haemosporidian richness in localities with higher proportions of migrant individuals since long-distance migratory behavior can remove infected individuals from bird communities, as diseased animals are less likely to successfully migrate because of the physiological requirements of migration and the energetic costs of disease (Bradley and Altizer 2005, Altizer et al. 2011). However, Hahn et al. (2018) experimentally verified that low intensity haemosporidian infections do not affect the capacity of birds to migrate, thus, most infected birds could still migrate and potentially spread their parasites into new areas. Meanwhile, the fact that migration filters out highly and moderately infected birds, which are the most likely to infect new vectors (Pigeault et al. 2015), allows community prevalence and parasite richness to remain low. At the same time, it is also possible migrant birds select localities with lower parasite richness. Certainly, further research will be required to
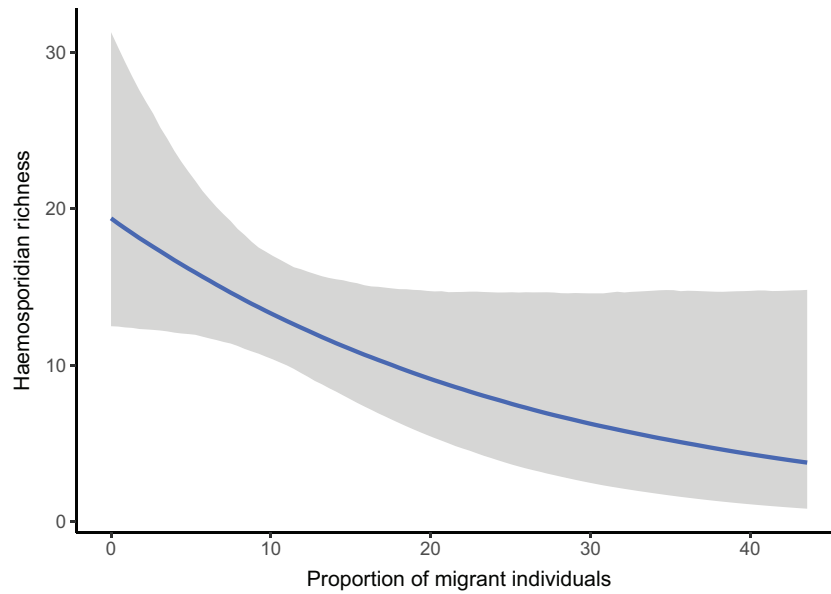
Figure 4. Predicted model relationship (±95% confidence intervals) between local haemosporidian richness and proportion of migrants in an area.

confirm the importance of migratory behavior in modulating haemosporidian community richness.

Previous studies have tried to explain parasite species assembly patterns globally and also specifically in South America (Clark et al. 2014, Fecchio et al. 2019a). These authors have reported that South America presents the greatest diversity of *Plasmodium* and *Haemoproteus* parasites on the globe. Indeed, Fecchio et al. (2019a) have proposed parasite dispersal as one of the main processes driving parasite diversity in this region. In contrast, we detected a negative association of parasite richness in regions with greater proportions of migrant individuals, while host richness and prevalence seem to be the main factors that positively drive parasite diversity. Also, we did not observe a clear relationship between migratory behavior and prevalence. Recently, Barrow et al. (2019) suggested that susceptibility to haemosporidian infection is partially driven by conserved, latent aspects of anti-parasite defense, and that prevalence of infection is strongly linked to avian phylogeny in Tropical Andes birds. Further, Fecchio et al. (2019a) also suggested that historical processes, such as host speciation, are also key drivers of haemosporidian diversity in South America. However, present-day environmental factors, mainly precipitation patterns, may be important for host range expansion across regions in haemosporidian parasites, as these vector-transmitted parasites exhibit greater host specificity in localities with pronounced seasonality and wetter dry seasons (Fecchio et al. 2019b). Thus, it seems other processes (apart from parasite dispersal through migrants) might also be important in determining parasite richness and prevalence in South America.

In summary, our results indicate that South American migrant birds play a moderate role in parasite dispersal and, consequently, in their evolution and diversity. Further, as observed by Ricklefs et al. (2017), most haemosporidian lineages are not shared between resident and migrant species, indeed, most of our parasite lineages were observed only in resident birds. We also demonstrated that, despite the fact that migrants might carry haemosporidians to new localities, migration by itself may not affect general parasite prevalence, possibly because parasite spread among local bird communities relies on the capability of haemosporidians to reproduce and develop in their ectothermic vector hosts. In addition, migrants might tend to concentrate or stay longer in communities with lower parasite prevalence and richness in our study system, as their presence seems to be related to lower community-wide haemosporidian richness and *Plasmodium* prevalence. By comparing the distribution of different pathogen lineages, our analyses demonstrate that migrant hosts may disperse haemosporidians and possibly other pathogens throughout their migration routes and, most importantly, their presence can impact transmission within the general avian community.

Data availability statement

A part of the data that support the findings of this study is openly available at <https://onlinelibrary.wiley.com/doi/10.1111/mec.15094> and <http://130.235.244.92/Malavi/> (Bensch et al. 2009). The other portion of the data that support our findings can be shared by Prof. Érika Martins Braga under reasonable request. R scripts are available as Supporting information.

Author contributions

Daniela de Angeli Dutra: Conceptualization (lead); Data curation (supporting); Formal analysis (lead); Investigation (lead); Writing – original draft (lead); Writing – review and editing (lead). **Antoine Filion**: Data curation (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Writing – review and editing (supporting). **Alan Fecchio**: Data curation (equal); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Resources (supporting); Supervision (supporting); Writing – review and editing (supporting). **Érika M. Braga**: Data curation (equal); Investigation (supporting); Methodology (supporting); Resources (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Robert Poulin**: Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Investigation (supporting); Methodology (supporting); Project administration (lead); Resources (lead); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (equal).

References

Altizer, S. et al. 2011. Animal migration and infectious disease risk. – Science 331: 296–302.

Barrow, L. N. et al. 2019. Deeply conserved susceptibility in a multi-host, multi-parasite system. – Ecol. Lett. 22: 987–998.

Bartel, R. A. et al. 2011. Monarch butterfly migration and parasite transmission in eastern North America. – Ecology 92: 342–351.

Bauer, S. and Hoye, B. J. 2014. Migratory animals couple biodiversity and ecosystem functioning worldwide. – Science 344: 1242552.

Bell, J. A. et al. 2015. A new real-time PCR protocol for detection of avian haemosporidians. – Paras. Vect. 8: 1–9.

Bensch, S. et al. 2009. MalAvi: a public database of malaria parasites and related haemosporidians in avian hosts based on mitochondrial cytochrome b lineages. – Mol. Ecol. Resour. 9: 1353–1358.

Bradley, C. A. and Altizer, S. 2005. Parasites hinder monarch butterfly flight: implications for disease spread in migratory hosts. – Ecol. Lett. 8: 290–300.

Braga, É. M. et al. 2011. Recent advances in the study of avian malaria: an overview with an emphasis on the distribution of *Plasmodium* spp. in Brazil. – Mem. Inst. Oswaldo Cruz 106: 3–11.

Bürkner, P. C. 2017. brms: an R package for Bayesian multilevel models using Stan. – J. Stat. Softw. 80: 27239.

Clark, N. J. et al. 2014. A review of global diversity in avian haemosporidians (*Plasmodium* and *Haemoproteus*: Haemosporida): new insights from molecular data. – Int. J. Parasitol. 44: 329–338.

Clark, N. J. et al. 2020. Robust geographical determinants of infection prevalence and a contrasting latitudinal diversity gradient for haemosporidian parasites in Western Palearctic birds. – Mol. Ecol.: 0–1.

Comitê Brasileiro de Registros Ornitológicos – CRBO. 2014. Listas das aves do brasil. – Com. Bras. Regist. Ornitol.: 1–38.

Consoli, R. A. G. B. and Oliveira, R. L. de 1994. Principais mosquitos de importância sanitária no Brasil. – Fiocruz.

Ellis, V. A. et al. 2019. The global biogeography of avian haemosporidian parasites is characterized by local diversification and intercontinental dispersal. – Parasitology 146: 213–219.

Fallon, A. S. M. et al. 2003. Detecting avian malaria : an improved polymerase chain reaction diagnostic. – 89: 1044–1047.

Fecchio, A. et al. 2019a. Avian host composition, local speciation and dispersal drive the regional assembly of avian malaria parasites in South American birds. – Mol. Ecol. 28: 2681–2693.

Fecchio, A. et al. 2019b. Climate variation influences host specificity in avian malaria parasites. – Ecol. Lett. 22: 547–557.

Fecchio, A. et al. 2020. Evolutionary ecology, taxonomy and systematics of avian malaria and related parasites. – Acta Trop.: 105364.

Fecchio, A. et al. 2021. Higher infection probability of haemosporidian parasites in blue-black grassquits *Volatinia jacarina* inhabiting native vegetation across Brazil. – Parasitol. Int. 80: 102204.

Ferreira, F. C. et al. 2017. Habitat modification and seasonality influence avian haemosporidian parasite distributions in southeastern Brazil. – PLoS One 12: e0178791.

Ferreira-Junior, F. C. et al. 2018. A new pathogen spillover from domestic to wild animals: *Plasmodium juxtanucleare* infects free-living passerines in Brazil. – Parasitology: 1–10.

Gutiérrez, J. S. et al. 2019. Micro- and macroparasite species richness in birds: the role of host life history and ecology. – J. Anim. Ecol. 88: 1226–1239.

Hahn, S. et al. 2018. Low intensity blood parasite infections do not reduce the aerobic performance of migratory birds. – Proc. R. Soc. B 285: 20172307.

Hellgren, O. et al. 2004. A new PCR assay for simultaneous studies of leucocytozoon, *Plasmodium* and *Haemoproteus* from avian blood. – J. Parasitol. 90: 797–802.

Hellgren, O. et al. 2007. Detecting shifts of transmission areas in avian blood parasites – a phylogenetic approach. – Mol. Ecol. 16: 1281–1290.

Koprivnikar, J. and Leung, T. L. F. 2015. Flying with diverse passengers: greater richness of parasitic nematodes in migratory birds. – Oikos 124: 399–405.

Krasnov, B. R. et al. 2012. Phylogenetic signal in module composition and species connectivity in compartmentalized host–parasite networks. – Am. Nat. 179: 501–511.

Lacorte, G. A. et al. 2013. Exploring the diversity and distribution of neotropical avian malaria parasites – a molecular survey from southeast Brazil. – PLoS One 8: 1–9.

Lindeborg, M. et al. 2012. Migratory birds, ticks and crimean-congo hemorrhagic fever virus. – Emerg. Infect. Dis. 18: 2095–2097.

Marzal, A. 2012. Recent advances in studies on avian malaria parasites. – Malar. Paras.: 135–158.

Morshed, M. G. et al. 2005. Migratory songbirds disperse ticks across Canada, and first isolation of the Lyme disease spirochete, *Borrelia burgdorferi*, from the avian tick, *Ixodes auritulus*. – J. Parasitol. 91: 780–790.

Pigeault, R. et al. 2015. Avian malaria: a new lease of life for an old experimental model to study the evolutionary ecology of *Plasmodium*. – Phil. Trans. R. Soc. B 370: 323–330.

Poulin, R. et al. 2012. Migration as an escape from parasitism in New Zealand galaxiid fishes. – Oecologia 169: 955–963.

Poupon, M. et al. 2006. Prevalence of *Borrelia burgdorferi* sensu lato in ticks collected from migratory birds in Switzerland. – Appl. Environ. Microbiol. 72: 976–979.

Remsen, J. V. J. et al. in press. A classification of the bird species of South America. – Am. Ornithol. Soc.

Ricklefs, R. E. et al. 2017. Avian migration and the distribution of malaria parasites in New World passerine birds. – J. Biogeogr. 44: 1113–1123.

Santiago-Alarcon, D. et al. 2012a. Diptera vectors of avian Haemosporidian parasites: untangling parasite life cycles and their taxonomy. – Biol. Rev. 87: 928–964.

Santiago-Alarcon, D. et al. 2012b. Bloodmeal analysis reveals avian plasmodium infections and broad host preferences of culicoides (diptera: Ceratopogonidae) vectors. – PLoS One 7: e31098.

Satterfield, D. A. et al. 2015. Loss of migratory behaviour increases infection risk for a butterfly host. – Proc. R. Soc. B 282: 20141734.

Somenzari, M. et al. 2018. An overview of migratory birds in Brazil. – Pap. Avulsos Zool. 58: 3.

Teitelbaum, C. S. et al. 2018. Migratory behaviour predicts greater parasite diversity in ungulates. – Proc. R. Soc. B 285: 20180089.

Turchetto-Zolet, A. C. et al. 2013. Phylogeographical patterns shed light on evolutionary process in South America. – Mol. Ecol. 22: 1193–1213.

Valkiūnas, G. 2005. Avian malaria parasites and other Haemosporidia.

Wikelski, M. et al. 2003. Costs of migration in free-flying songbirds. – Nature 423: 704.