**Abstract:**

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. 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 (i) only in migratory birds, (ii) in both migrants and residents, and (iii) 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 13200 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 and mixed 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. Indeed, migrants may decrease the richness of avian haemosporidians, probably due to local constraints on transmission. Therefore, we demonstrate migrants enhance pathogens spread and their presence may influence parasite community transmission.

1.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). Further, 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). Conversely, migration may have a protective effect since migratory behaviour allows hosts to escape environments presenting a high risk of infection (Altizer et al. 2011, Poulin et al. 2012). Moreover, 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. At the same time, human-introduced pathogens and host species can decrease the fitness and survival of resident and native host species, compromising the population abundance of local species and reducing community richness (Callaway and Ridenour 2004, Prenter et al. 2004).

Nevertheless, the spread of pathogens might increase host richness by reducing local competition pressures and, consequently, preventing competitive exclusion. Hence, pathogens might act as an environmental filter to new species colonization as they can reduce survival and fitness of infected individuals and affect general population growth. Recent studies have demonstrated that migratory birds harbor a greater diversity of parasites than resident species (Koprivnikar and Leung 2015, Gutiérrez et al. 2019). In addition, several studies have 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 population size, as well as the local richness of parasite species.

Avian malaria parasites and related haemosporidians could be used as geographical markers for migratory birds (Marzal 2012). 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). 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). Furthermore, O’Connor et al. 2020 have demonstrated that migratory birds do not possess higher immune gene richness in wetter areas, which jointly with temperature is one of the main climatic factors that influence haemosporidian prevalence (Illera et al. 2017). Therefore, migratory birds may be more susceptible to pathogens in those regions. 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.

South America comprises different types of biomes, which hold a great richness of native 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 between 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 from 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.

In this context, the main goal of this study is to evaluate the influence of migratory birds on the spread 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 (i) in both migrants and residents and (ii) 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 parasite lineages using migratory birds should occur across a greater spatial range than those infecting only resident birds. Moreover, migration 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.

2. Methods

2.1 Dataset

All analyses were performed using a dataset comprising ~13200 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 Fecchio, Bell, et al., 2019a; Ferreira-Junior et al., 2018; Ferreira et al., 2017; Lacorte et al., 2013, and supplemented with new, previously unpublished data (See Supplementary Table 1). 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 (Figure 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 one of these three genera: *Plasmodium*, *Haemoproteus* and *Leucocytozoon*). 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 Hellgren et al. 2004, Fallon et al. 2003, 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 (https://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 (see Supplementary Table 2), according to the Brazilian Committee of Ornithology Records - CRBO 2014, Somenzari et al. 2018 and BirdLife International (<https://www.birdlife.org/>).

2.2 Statistical Analyses

All analyses were conducted in R version 4.02 (R Core Team, 2019). 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 (see supplementary material, <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 nested random effects in our second Bayesian and mixed 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.

*Bayesian models*

In order 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, 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, see supplementary material) among haemosporidian lineages, we built two models including the migratory status of hosts used by a lineage. We first ran a model comparing lineages present in resident birds only and lineages present in residents plus also birds of any migratory category. In addition, we built a second model comprising four categorical variable levels: lineages present only in resident species, lineages present only in partial migratory and resident species, lineages present only full migratory and resident species, and lineages present in species from all three migratory status: partial, full migratory and resident. Our reference category in both 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 but skewed distribution, we applied the Gamma distribution family, using 4 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 all three parasite genera combined, one for *Plasmodium* lineages only, and one for *Haemoproteus* lineages only.

Next, we analysed the prevalence of infection in each bird species 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, 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 grouped the dataset per bird species and localities and 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, log-transformed scaled value), local parasite richness (log-transformed scaled value), proportion of migratory species (log-transformed scaled value), number of migrant individuals (log-transformed scaled value), temperature (log-transformed scaled value) and precipitation had significant effects on prevalence. Following these analyses, only parasite 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 applied in this model to account for the overdispersion of prevalence data, thus avoiding production of biased estimates. We used 4 chains with MCMC 4000 total iterations per chain (2000 for warmup interactions, 2000 for sampling). Further, we considered biome and locality ID as nested random variables. Also, we created a matrix with phylogenetic distances between species and used the function “cov\_ranef” 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. Again, we ran three models: one for all three 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.

*Mixed model*

A mixed model was performed to estimate whether localities with more migratory birds have greater prevalence and 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. 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 tested our variables for normal distribution and created models including variables that presented an effect on our dependent variable, and then selected the best model among them using the Akaike information criterion (AIC). We ran a generalized linear mixed model applying the “glmer” function from the “lme4” package (Bates et al. 2015) with a Poisson distribution. We considered local host richness (log-transformed scaled value), prevalence across all birds sampled (log-transformed scaled value), proportion of migratory species (log-transformed scaled value), number of migrant individuals (log-transformed scaled value), temperature (log-transformed scaled value) and precipitation as fixed variables. Biome and locality ID were set as random intercept. We ran three models: one for all three parasite genera combined, one for *Plasmodium* lineages only, and one for *Haemoproteus* lineages only.

3. 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 rest 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.

Our first Bayesian model analyses revealed that lineages shared by migrants and residents showed the broadest geographical range (Figure 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 *Haemoproteus*, no difference in geographical range was observed between lineages found in residents only and those shared by residents and migrants, while for *Plasmodium* linages shared by residents and migrants were also more spatially widespread (Figure S1, Figure S2, Table S2 and Table S3).

Nevertheless, when repeating these analyses after separating each distinct migrant category that a lineage can infect, we observed that only lineages shared by resident and full migratory species are more widespread spatially, as they occupy a broader geographical range. Further, we observed that lineages shared among residents and other type of migrants (partial migrant and partial plus full migrant) are as widely distributed as the lineages present in only resident hosts (Figure 3, Table 2). However, when analysing both parasite genera separately no difference was observed in the geographical range of lineages with different types of bird hosts (Figure S3, Figure S4, Table S4 and Table S5).

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 (Figure S5, Table S6). However, when we repeated the analysis separately for only *Plasmodium* or *Haemoproteus* lineages, we observed negative and positive relationships between the local proportion of migrants in an area and number of infections per locality, respectively (Figure 4, Table 3 and 4). Parasite richness had a significant positive effect on local number of infected birds, whether when considering all haemosporidian lineages (Table S6), or only *Haemoproteus* lineages (Table 4).

Our mixed model examining the influence of migrants on parasite richness revealed no effect of the proportion of individual migrants in the local community considering both haemosporidian genera together (Figure 5, Table 5). The Akaike information criterion revealed that the best model set considered only local host richness, prevalence across all birds sampled, proportion of migratory species, number of migrant individuals and temperature as fixed factors (Table S7). However, we observed a negative relation between the proportion of migratory species and parasite richness. Further, we also observed no effect of the proportion of migratory bird individuals on local parasite richness for *Plasmodium* and *Haemoproteus* infections when the two genera were treated separately (Figure S6 and S7, Table S8 and S9). Further, the proportion of migratory species was also negatively correlated to *Haemoproteus* lineage richness, with the total number of migrants showing the opposite pattern. Moreover, we observed positive effects on parasite richness of two other predictors in all models: local host richness and overall local prevalence.

**4. 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 lineages 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 birds. Nevertheless, we observed different patterns for *Plasmodium* and *Haemoproteus* parasites, such that *Plasmodium* prevalence negatively correlated with an increasing proportion of migrants, whereas *Haemoproteus* prevalence was higher in the presence of migrants. Moreover, haemosporidian richness decreased as the proportion of migratory species rose across localities. However, parasite richness also 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, composition and richness.

Further, parasites infecting only resident and partial migrant or full and partial migrant birds occurred across a similar geographical range as those infecting only resident avian hosts. We believe insufficient sampling of certain migrant avian species in many areas could have led to the limited geographical range in which lineages infecting only resident and partial and full and partial migrant birds were found. 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.

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 after 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 migration and general haemosporidian prevalence, since the greatest haemosporidian diversity occurs in resident avian species. In addition, Hellgren et al. (2007) also suggest that new haemosporidian introductions into resident bird faunas are not common evolutionary events. Moreover, we observed that other factors such as host richness and overall local prevalence also influence parasite richness. Therefore, it seems environmental and host features could be more important in determining local parasite richness than dispersal patterns.

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 rise in *Haemoproteus* infections. Such behavior illustrates that different pathogens do not respond identically 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 suggest that where the proportion of migrant species 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 species 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 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 *Plamodium* 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 effect on parasite richness in regions with greater proportions of migrant species, 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 suggest 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 rainfall 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.

References

Altizer, S. et al. 2011. Animal migration and infectious disease risk. - Science (80-. ). 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.

Bates, D. et al. 2015. Fitting linear mixed-effects models using lme4. - Stat. Softw. 67: 1–48.

Bauer, S. and Hoye, B. J. 2014. Migratory animals couple biodiversity and ecosystem functioning worldwide. - Science (80-. ). 344: 1242552.

Bell, J. A. et al. 2015. A new real-time PCR protocol for detection of avian haemosporidians. - Parasites and Vectors 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.

Callaway, R. M. and Ridenour, W. M. 2004. Novel weapons: Invasive success and the evolution of increased competitive ability. - Front. Ecol. Environ. 2: 436–443.

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.

Comitê Brasileiro de Registros Ornitológicos - CRBO 2014. Listas das aves do brasil. - Com. Bras. Regist. Ornitológicos: 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 Detecting Avian Malaria : an Improved Polymerase Chain. 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.

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.

Ferreira, F. C. et al. 2017. Habitat modification and seasonality influence avian haemosporidian parasite distributions in southeastern Brazil. - PLoS One 12: 0178791.

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 Biol. Sci. 285: 20172307.

Hellgren, O. et al. 2004. A New Pcr Assay For Simultaneous Studies Of Leucocytozoon, Plasmodium, And Haemoproteusfrom 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.

Illera, J. C. et al. 2017. Factors governing the prevalence and richness of avian haemosporidian communities within and between temperate mountains. - PLoS One 12: 1–22.

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. Parasites: 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.

O’Connor, E. A. et al. 2020. Wetter climates select for higher immune gene diversity in resident, but not migratory, songbirds. - Proceedings. Biol. Sci. 287: 20192675.

Pigeault, R. et al. 2015. Avian malaria: a new lease of life for an old experimental model to study the evolutionary ecology of Plasmodium. - Philos. Trans. R. Soc. Lond. B. Biol. Sci. 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 Prevalence of Borrelia burgdorferi Sensu Lato in Ticks Collected from Migratory Birds in Switzerland. - Appl. Environ. Microbiol. 72: 976–979.

Prenter, J. et al. 2004. Roles of parasites in animal invasions. - Trends Ecol. Evol. 19: 385–390.

Remsen, J. V. J. et al. 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: 31098.

Satterfield, D. A. et al. 2015. Loss of migratory behaviour increases infection risk for a butterfly host. - Proc. R. Soc. B Biol. Sci. 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 Biol. Sci. 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.

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

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.

Figure 3: Mean (±confidence intervals) geographical range in kilometers in which haemosporidian lineages are detected according to the type of birds in which they are found. R = resident, R\_M = resident and full migratory, R\_PM = resident and partial migratory and R\_PM\_M = resident, partial migratory and full migratory. Number of lineages in each of the four categories are shown on the graph.

Figure 4: 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.

Figure 5: Parameter estimates illustrating the influence of all fixed variables on parasite richness.

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** | **Std. error** | **Conf. Inter (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 |

Table 2: 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** | **Std. error** | **Conf. Inter (95%)** | |
| Intercept | 7.20 | 0.12 | 6.87 | 7.33 |
| Resident and full migrant | 0.54 | 0.29 | 0.00 | 1.13 |
| Resident and partial migrant | 0.29 | 0.24 | -0.17 | 0.79 |
| Resident, partial and full migrant | 0.53 | 0.41 | -0.21 | 1.41 |
| 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 |

Table 3: 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.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | **Estimate** | **Std. error** | **Conf. Inter (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 |

Table 4: 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.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | **Estimate** | **Std. error** | **Conf. Inter (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 5: Parameter estimates, standard errors, z and p values for the mixed model testing the variation of local haemosporidian richness as a function of the proportion of migratory individuals out of all individual birds sampled per locality, as well as other predictors.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | **Estimate** | **Std. error** | **Z** | **P** |
| Intercept | -6.16 | 1.71 | -3.60 | <0.001 |
| Proportion of migrant individuals | 0.57 | 1.07 | 0.53 | 0.59 |
| Host richness | 0.92 | 0.12 | 7.87 | <0.001 |
| Prevalence | 0.70 | 0.10 | 6.97 | <0.001 |
| Proportion of migrant species | -0.26 | 0.13 | -2.03 | 0.04 |
| Number of migrants | 0.11 | 0.10 | 1.04 | 0.30 |
| Temperature | 0.62 | 0.32 | 1.95 | 0.05 |