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

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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. 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 (i) in both migrants and residents, and (ii) 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 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.

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. 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 (i) in both migrants and residents, and (ii) 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 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.

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). 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 (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, 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.

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 et al., 2019; 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 *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 Bell et al. 2015, Fallon et al. 2003 and Hellgren et al. 2004. 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 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, 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 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 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 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 4 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 4 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.

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 remaining mostly belonging to the orders Columbiformes, Piciformes and Apodiformes. Haemosporidian lineages occurred in anywhere from one to 38 localities, with many of them

231 (15%) occurring in multiple biomes. Only 175 out of 675 lineages were observed in two or
232 more localities and were used to estimate lineage spread in our analyses, besides, 426 linages
233 were singletons. All models presented well converged chains.

234 Our first Bayesian model analyses revealed that lineages shared by migrants and
235 residents showed the broadest geographical range (Figure 2, Table 1). Lineages shared by
236 resident and any type of migrant species presented a geographical range almost 50% greater
237 than that of lineages occurring only in resident species. More specifically, we observed
238 distinct patterns of distribution for *Plasmodium* and *Haemoproteus* lineages. For
239 *Plasmodium* linages shared by residents and migrants were also more spatially widespread,
240 whereas for *Haemoproteus* no difference in geographical range was observed between
241 lineages found in residents only and those shared by residents and migrants (Figure S1,
242 Figure S2, Table S2 and Table S3). It is important to notice that similar patterns regarding
243 parasite geographical range was also observed when plotting data from our raw dataset
244 (Figure S3-5).

245 Our next Bayesian model analysed the relationship between local number of infected
246 birds and the proportion of migratory bird individuals in the local avian community. We
247 observed no correlation between the relative occurrence of migrants and number of infected
248 hosts (Figure S6, Table S4). However, when we repeated the analysis separately for only
249 *Plasmodium* or *Haemoproteus* lineages, we observed negative and positive relationships
250 between the number of infections per locality and local proportion of migrants in an area,
251 respectively (Figure 3, Table 2 and 3). Parasite richness had a significant positive association
252 with the local number of infected birds, whether when considering all haemosporidian
253 lineages (Table S4), 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, Figure 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 (Table S6 and S7). 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 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 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

277 the ecology and evolution of haemosporidian dispersal in South America leading to an
278 increase in parasite spread and influencing parasite prevalence and composition. In addition,
279 we also demonstrate that generalist parasites may be more successful in colonizing new
280 regions since parasites that infected both residents and migrant hosts had broader geographic
281 distributions.

282 Dispersal of haemoporidians might be an important step toward parasite
283 diversification for local community composition since parasites, after establishing in new
284 regions, can evolve into new and distinct parasite lineages (Ellis et al. 2019, Fecchio et al.
285 2019a). Indeed, Ellis et al. (2019) found that South America presents high rates of parasite
286 diversification, with the greatest proportion of sympatric nodes for *Plasmodium* spp. and one
287 of the greatest *Haemoproteus* diversification rates. Hence, considering the potential
288 contribution of migrant birds toward parasite dispersal, these hosts might play a fundamental
289 role in parasite evolution and diversification in South America. Indeed, many species migrate
290 in between the breeding season and relapses (increases in parasite intensity circulating in the
291 host) mainly occur after this period (Valkiūnas 2005), thus facilitating parasite dispersal to
292 new regions. However, we did not observe a clear relation between the presence of migrant
293 birds and local haemosporidian prevalence since our data suggest that *Plasmodium* and
294 *Haemoproteus* parasites respond differently to the presence of migrant hosts. The fact that
295 most of our lineages were observed only in resident birds could explain the lack of a
296 relationship between avian migrants and general haemosporidian prevalence, since the
297 greatest haemosporidian diversity occurs in resident avian species. However, Hellgren et al.
298 (2007) also suggest that new haemosporidian introductions into resident bird faunas are not
299 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. 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 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

346 in Tropical Andes birds. Further, Fecchio et al. (2019a) also suggested that historical
347 processes, such as host speciation, are also key drivers of haemosporidian diversity in South
348 America. However, present-day environmental factors, mainly precipitation patterns, may be
349 important for host range expansion across regions in haemosporidian parasites, as these
350 vector-transmitted parasites exhibit greater host specificity in localities with pronounced
351 seasonality and wetter dry seasons (Fecchio et al. 2019b). Thus, it seems other processes
352 (apart from parasite dispersal through migrants) might also be important in determining
353 parasite richness and prevalence in South America.

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

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471

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: 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 4: Predicted model relationship (±95% confidence intervals) between local haemosporidian richness and proportion of migrants in an area.

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

491

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

	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

496

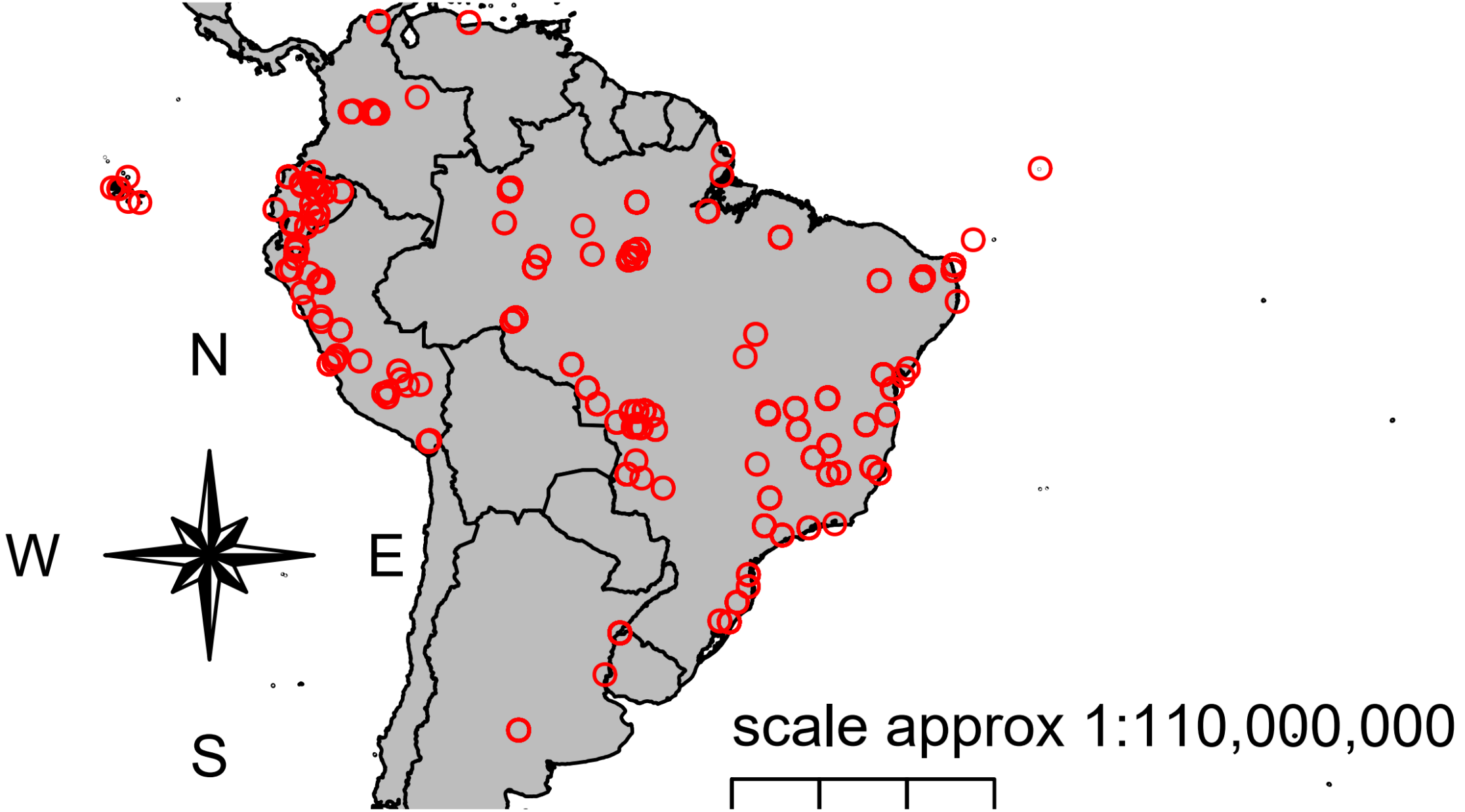
497 Table 3: Parameter estimates, standard errors, and confidence intervals for the Bayesian
498 model testing the variation of local number of birds infected by *Haemoproteus* as a function
499 of the proportion of migratory individuals out of all individual birds sampled per locality and
500 parasite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

	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

501

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	**Std. error**	**Conf. Inter (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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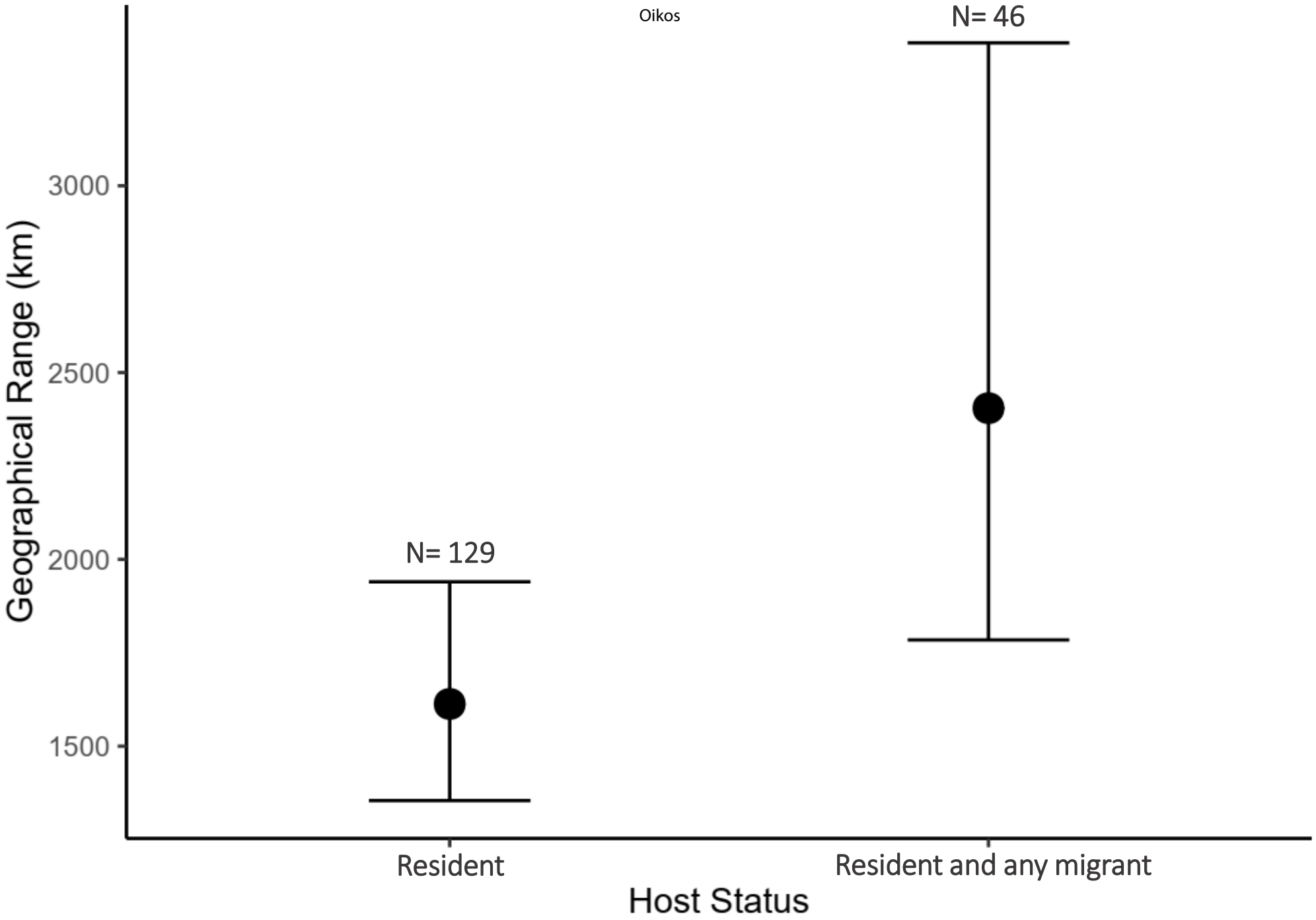
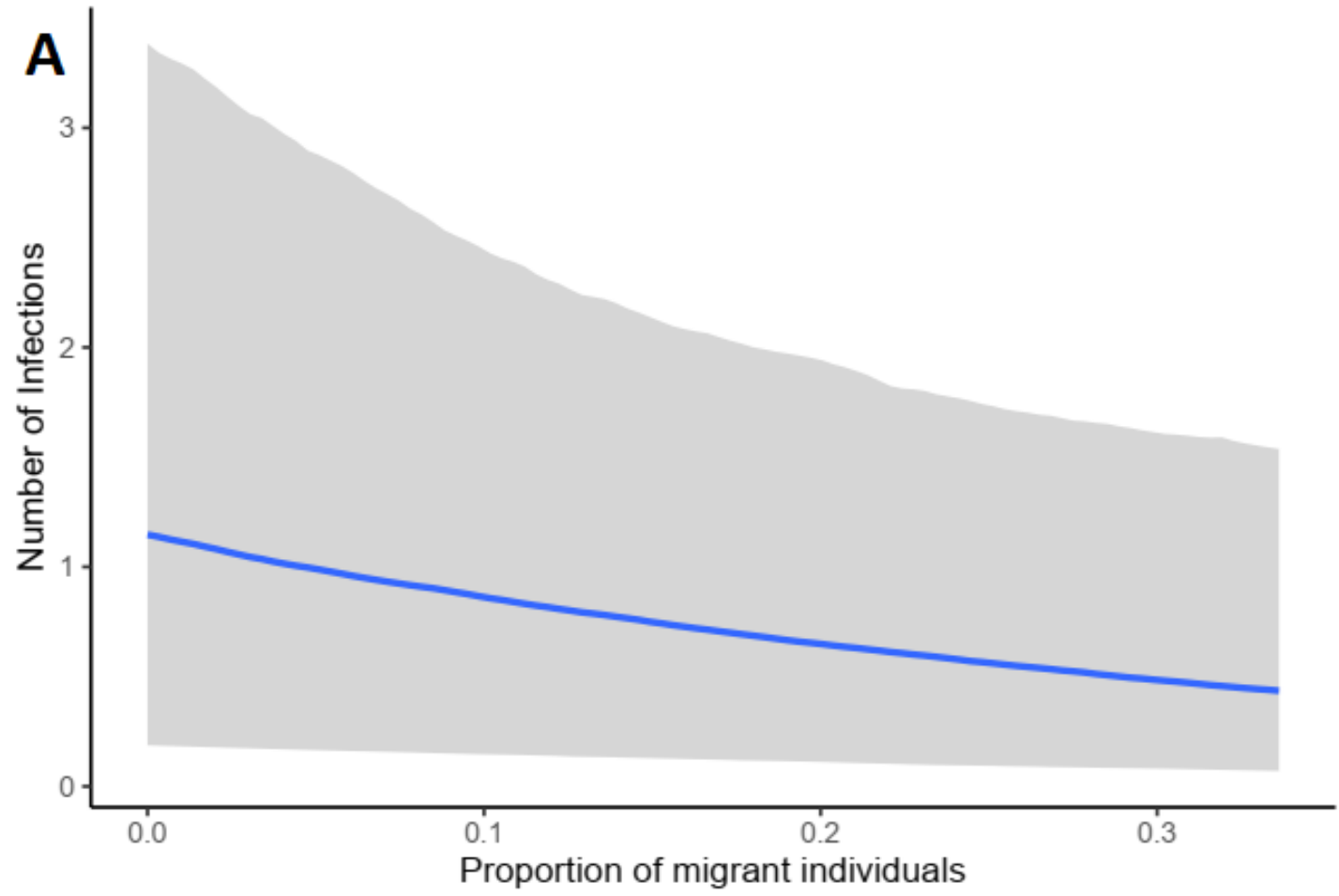
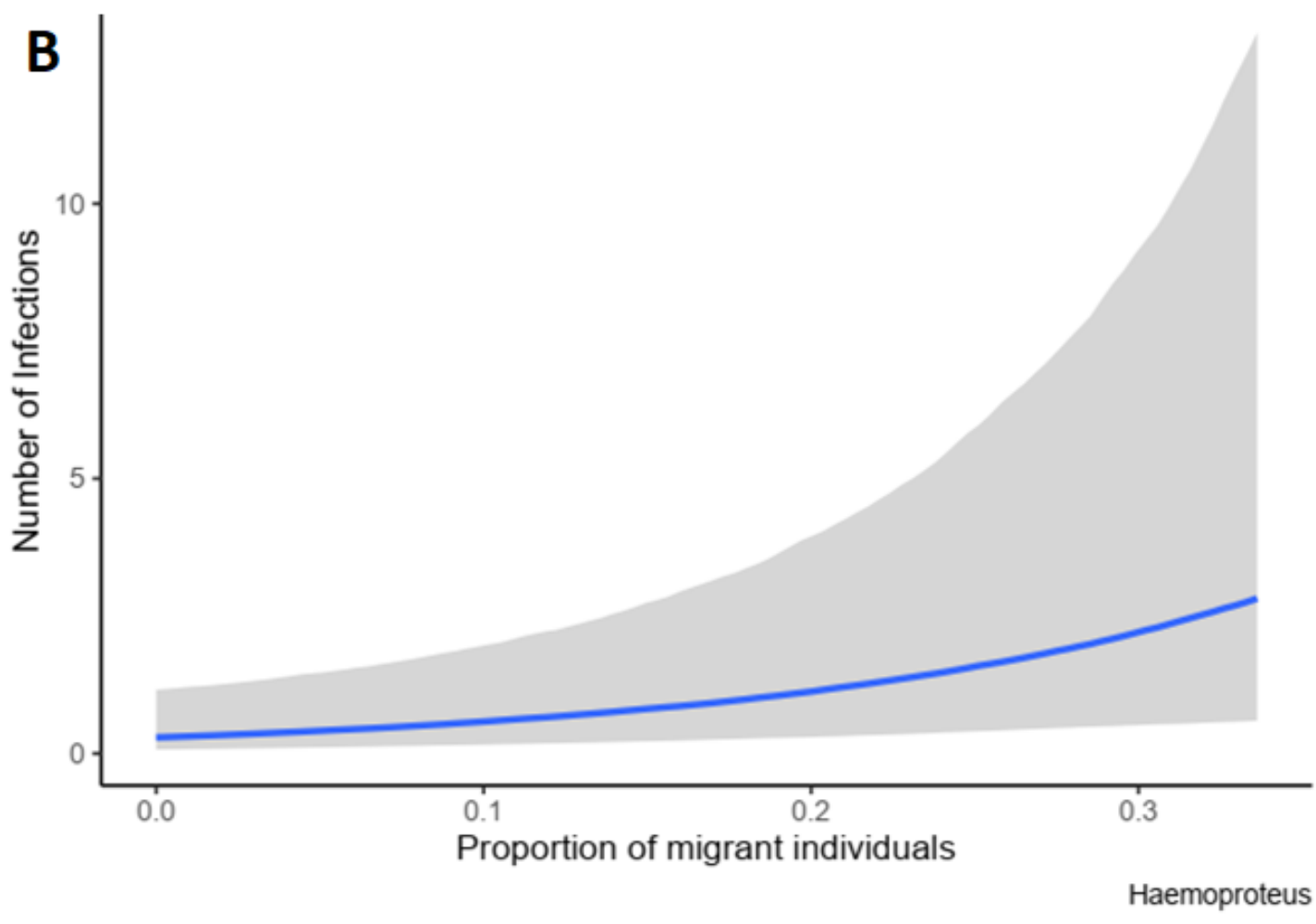
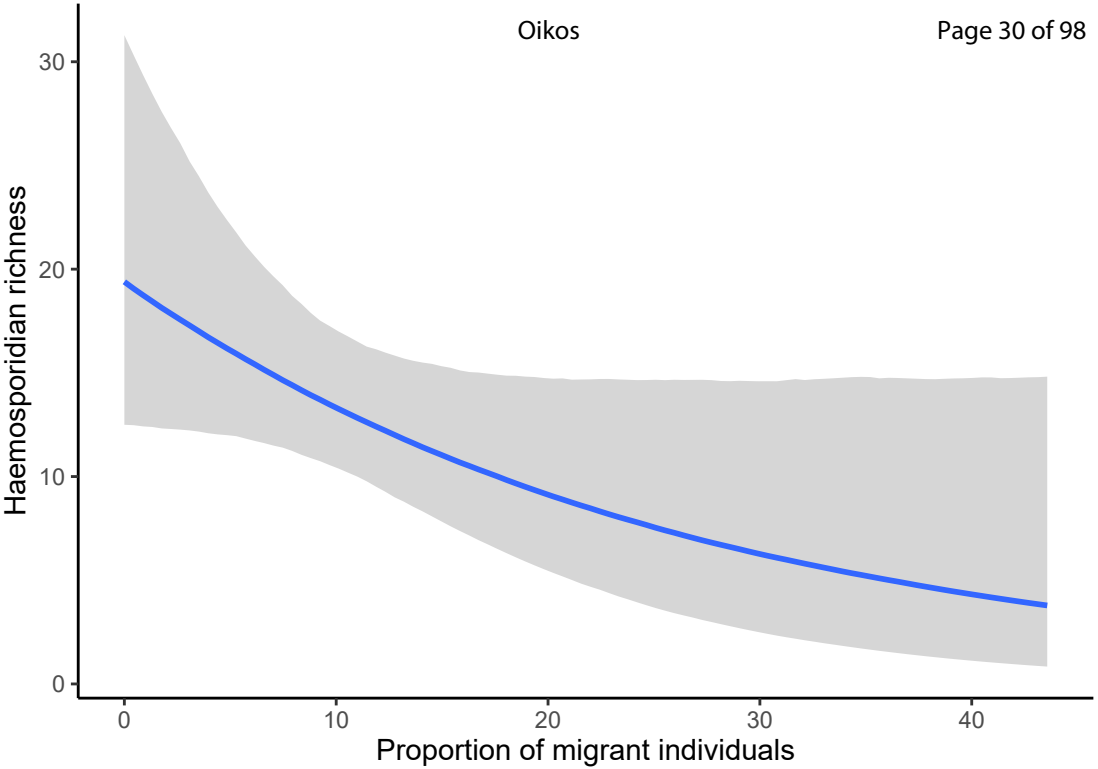
W
E
S
scale approx 1:110,000,000


N= 46
N= 129
3000
2500
2000
1500
Geographical Range (km)
Resident
Resident and any migrant
Host Status


A
Number of Infections
3
2
1
0
0.0
0.1
0.2
0.3
Proportion of migrant individuals
Plasmodium


B
Number of Infections
10
5
0
0.0
0.1
0.2
0.3
Proportion of migrant individuals
Haemoproteus


Haemosporidian richness
30
20
10
0
0
10
20
30
40
Proportion of migrant individuals

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

Daniela de Angeli Dutra[1]*, Antoine Filion[1], Alan Fecchio[2], Érika Martins Braga[3], Robert Poulin[1]

SUPPLEMENTARY MATERIAL

Supplementary Table 1: Dataset summary detailing information regarding locality ID, total number of birds individuals and host richness per locality, biome, latitude, longitude and data source.

LOCALITY ID	TOTAL OF BIRDS	HOST RICHNESS	BIOME	LATITUDE	LONGITUDE	YEAR OF COLLECTION	SOURCE
BSB	242	50	Brazilian Savanna	-15.5211053	-47.552045	2014/2015	unpublished
SALVADOR	161	28	Atlantic Rain Forest	-12.5450889	-38.207439	2015/2016	unpublished
VIRACOPOS	150	24	Brazilian Savanna	-23.029538	-47.815246	2014	unpublished
AIU1	62	24	Caatinga	-6.6	-40.116667	2012/2013	Fecchio et al. 2019
ARACRUZ	84	26	Atlantic Rain Forest	-19.4910125	-40.1206373	2011/2012	Lacorte et al. 2013
BASE UFMT	94	53	Pantanal	-15.3633507	-56.355506	2011/2012	unpublished
BEL1	320	157	Amazonia	-3.7	-46.75	2013	Fecchio et al. 2019
BOCAIUVA	295	59	Brazilian Savanna	-17.657674	-43.4844164	2011/2012	Lacorte et al. 2013
BRA1	788	52	Brazilian Savanna	-15.533333	-47.55	2005 a 2009	Fecchio et al. 2019
BRASILANDIA DE MINAS	133	56	Brazilian Savanna	-16.5630651	-45.5308804	2011/2012	Lacorte et al. 2013
BRU1	53	25	Atlantic Rain Forest	-27.098611	-48.8925	2016	Fecchio et al. 2019
BUSCA VIDA	169	37	Atlantic Rain Forest	-12.5143471	-38.1715148	2015/2016	unpublished
CARATINGA	126	33	Atlantic Rain Forest	-19.4724319	-42.825918	2011/2012	Lacorte et al. 2013
CHA1	90	36	Brazilian Savanna	-15.316667	-55.866667	2011/2014/2015	Fecchio et al. 2019
CHAP GUIM	101	32	Brazilian Savanna	-15.61953	-55.327475	2011/2012	Ferreira et al. 2018
CLBI	1800	70	Atlantic Rain Forest	-5.5524107	-35.103905	2014/2015	unpublished
ESEC	933	56	Caatinga	-6.344364	-37.152527	2013/2014	unpublished
ESP1	244	63	Grassland	-30.205564	-57.495736	2014	Fecchio et al. 2019
FAZ ST. MARIA	131	35	Brazilian Savanna	-21.1658279	-47.45862	2014	unpublished
FELIXLANDIA	175	40	Brazilian Savanna	-18.4526633	-44.5356927	2011/2012	unpublished
GRA1	127	26	Brazilian Savanna	-15.166667	-45.733333	2013	Fecchio et al. 2019
GUI1	178	53	Amazonia	-0.4	-64.8	2012	Fecchio et al. 2019
GUI2	304	77	Amazonia	-1.35	-56.366667	2011/2012	Fecchio et al. 2019

GUI3	39	15	Amazonia	-2.932778	-59.972533	2014	Fecchio et al. 2019
HUAL1	80	42	Peruvian Andes	-6.583333	-77.55	2010	Fecchio et al. 2019
HUAL2	167	55	Peruvian Andes	-6.683333	-77.683333	2010/2011	Fecchio et al. 2019
HUAL3	157	60	Peruvian Andes	-5.1	-79.233333	2010/2011	Fecchio et al. 2019
HUAL4	352	101	Peruvian Andes	-6.583333	-77.55	2010	Fecchio et al. 2019
HUAL5	400	114	Peruvian Andes	-6.716667	-77.416667	2010	Fecchio et al. 2019
IME1	164	51	Amazonia	-0.583333	-64.916667	2010	Fecchio et al. 2019
INA1	211	40	Amazonia	-4.998	-62.935	2012	Fecchio et al. 2019
INA2	208	53	Amazonia	-5.72	-63.217	2012	Fecchio et al. 2019
INA3	297	65	Amazonia	-9.1	-64.466667	2010/2011	Fecchio et al. 2019
JAU1	116	37	Brazilian Savanna	-14.866667	-59	2011	Fecchio et al. 2019
JEQUITINHONHA	166	50	Brazilian Savanna	-16.2559998	-41.011001	2011/2012	Lacorte et al. 2013
JOI1	49	18	Atlantic Rain Forest	-26.3	-48.883333	2014	Fecchio et al. 2019
MANGA	120	42	Brazilian Savanna	-14.4510092	-43.5630135	2011/2012	Lacorte et al. 2013
MATA SECA	461	64	Brazilian Savanna	-14.50911	-43.59298	2013/2014	Ferreira et al. 2016
MIC1	106	34	Atlantic Rain Forest	-13.84	-39.241	2017	Fecchio et al. 2019
MIL1	214	64	Caatinga	-12.90198	-39.841985	2015/2017	Fecchio et al. 2019
NAT1	37	16	Atlantic Rain Forest	-5.916667	-35.166667	2012/2015	Fecchio et al. 2019
NOVA LIMA	164	46	Atlantic Rain Forest	-19.5907472	-43.5049448	2011/2012	Lacorte et al. 2013
PAN1	110	10	Pantanal	-19.566667	-57.016667	2009/2012	Fecchio et al. 2019
PAN2	122	57	Pantanal	-16.25	-56.366667	2009/2017	Fecchio et al. 2019
PARNA BSB	258	41	Brazilian Savanna	-15.4018485	-47.5852374	2014/2015	unpublished
ROND1	429	86	Amazonia	-4.683333	-56.633333	2012	Fecchio et al. 2019
ROND2	60	35	Amazonia	-5.066667	-56.85	2012	Fecchio et al. 2019
ROND3	176	53	Amazonia	-9.316667	-64.716667	2010/2011	Fecchio et al. 2019
ROND4	117	40	Amazonia	-12.216667	-60.733333	2011	Fecchio et al. 2019
ROND5	136	42	Amazonia	-13.8	-59.683333	2011	Fecchio et al. 2019
RONDIL	85	18	Amazonia	-4.5	-56.266667	2012	Fecchio et al. 2019
SAJ1	55	21	Atlantic Rain Forest	-28.153369	-49.641754	2014/2015	Fecchio et al. 2019
SALTO DA DIVISA	196	56	Brazilian Savanna	-15.5954324	-39.5655673	2011/2012	Lacorte et al. 2013
SEB1	76	30	Atlantic Rain Forest	-23.166667	-44.833333	2015	Fecchio et al. 2019
SER1	178	38	Caatinga	-6.566667	-37.266667	2012/2013	Fecchio et al. 2019
SFR1	179	57	Atlantic Rain Forest	-29.466667	-50.166667	2017	Fecchio et al. 2019
SOORETAMA	86	21	Atlantic Rain Forest	-19.1130526	-40.613344	2011/2012	Lacorte et al. 2013
STA1	156	30	Grassland	-36.716667	-64.283333	2015	Fecchio et al. 2019
TAIAMA	44	22	Pantanal	-16.577528	-55.1027227	2011/2012	unpublished
TAP1	39	22	Amazonia	-5.1	-56.433333	2012	Fecchio et al. 2019
TAP2	61	36	Amazonia	-5.216667	-56.916667	2012	Fecchio et al. 2019
VARZ GRANDE	38	13	Brazilian Savanna	-15.3846493	-56.757767	2011/2012	unpublished
XING1	322	104	Amazonia	-1.95	-51.6	2007	Fecchio et al. 2019
TOTAL	13191	896					

Potential correlates of prevalence and richness

Spatial autocorrelation

All analyses were conducted in R version 4.0 (R Core Team, 2019). To evaluate the potential impact of locality on our variables, we determined whether there was significant spatial autocorrelation among localities for total prevalence (i.e., number of infected hosts/total number of hosts) and parasite richness (total number of parasites lineages) in our dataset by calculating the Moran Index value. Index values vary between -1.0 and +1.0, with 0 indicating no spatial autocorrelation and -1.0 or +1.0 high spatial autocorrelation. In order to estimate this index, we combined the coordinates data into a matrix and employed the function "Moran.I" from the "Ape" package (Paradis and Schliep 2018).

Phylogenetic Signal

In order to estimate the phylogenetic signal (i.e., tendency for phylogenetically closely-related species to resemble each other more than random species of the same tree) among prevalence and richness estimates for the bird species in our dataset, we downloaded the file AllBirdsHackett1.tre from https://birdtree.org/ website. Using the "treeman" package (Bennett et al. 2017), we created a treeman file containing all trees from the original file. Then, we randomly selected 100 trees. This new file was converted from treeman to a phylo file, from which we extracted a consensus tree to account for phylogenetic uncertainty. We grouped our data per species and eliminated all bird species from the phylo tree which were not present in our dataset. Using the "match" function from the "picante" package (Kembel et al. 2010), we matched the species between the tree and our dataset. Then, we calculated

Pagel's lambda (λ) to evaluate the phylogenetic signal among bird species in our dataset, for haemosporidian (all three genera) prevalence and parasite richness (Mark Pagel 1999). Values of λ can range between 0 and 1, being 1 when the trait has evolved consistently with a Brownian motion. In order to estimate lambda (λ), we applied the "phylosig" function from the "phytools" package (Revell 2012).

Climate variables

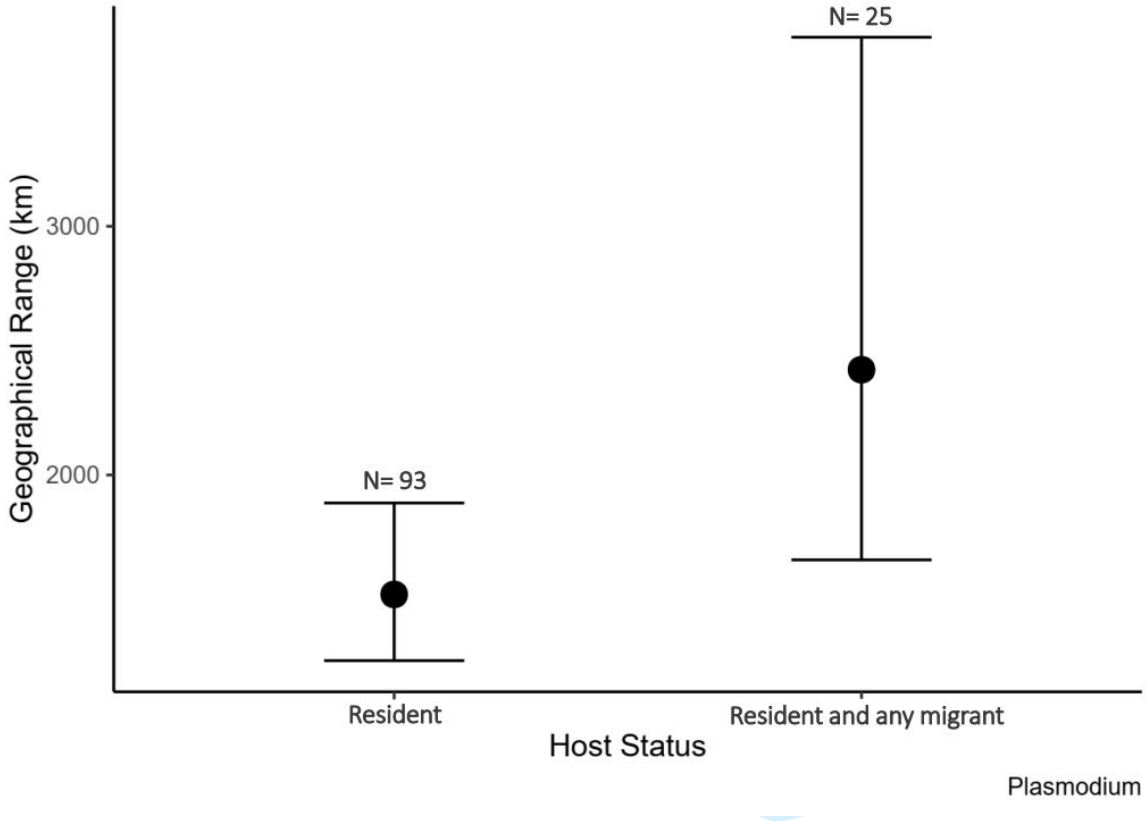
We used annual mean precipitation (variable BIO15) and annual mean temperature (variable BIO1, ºC) as predictors in the Bayesian and mixed models since temperature and precipitation are known to impact haemosporidian infections (Illera et al. 2017, Clark et al. 2020). We used R to extract these climate variables from the Worlclim database (https://worldclim.org/version2). Using the package "raster", we extracted the data using the "getData" function, then we selected the data from the 63 localities included in our original dataset (10 minute resolution) since climate variables were applied only in the mixed model and the second Bayesian analyses, for which the MalAvi data were not employed.

Geographical Range

In order to estimate the geographical range of each parasite lineage, we used the R package "GeoRange" and chose the variable minimum spanning tree distance (i.e. shortest total distance of all lines connecting each locality). Initially, using the function "create.matrix" from the "fossil" package in R, we created a matrix of species and localities. After generating the occurrence matrix, we filtered our data to account only for the parasites

present in two or more localities and used the function "GeoRange_MultiTaxa" to calculate the minimum spanning tree distance for each parasite lineage.

Supplementary Results

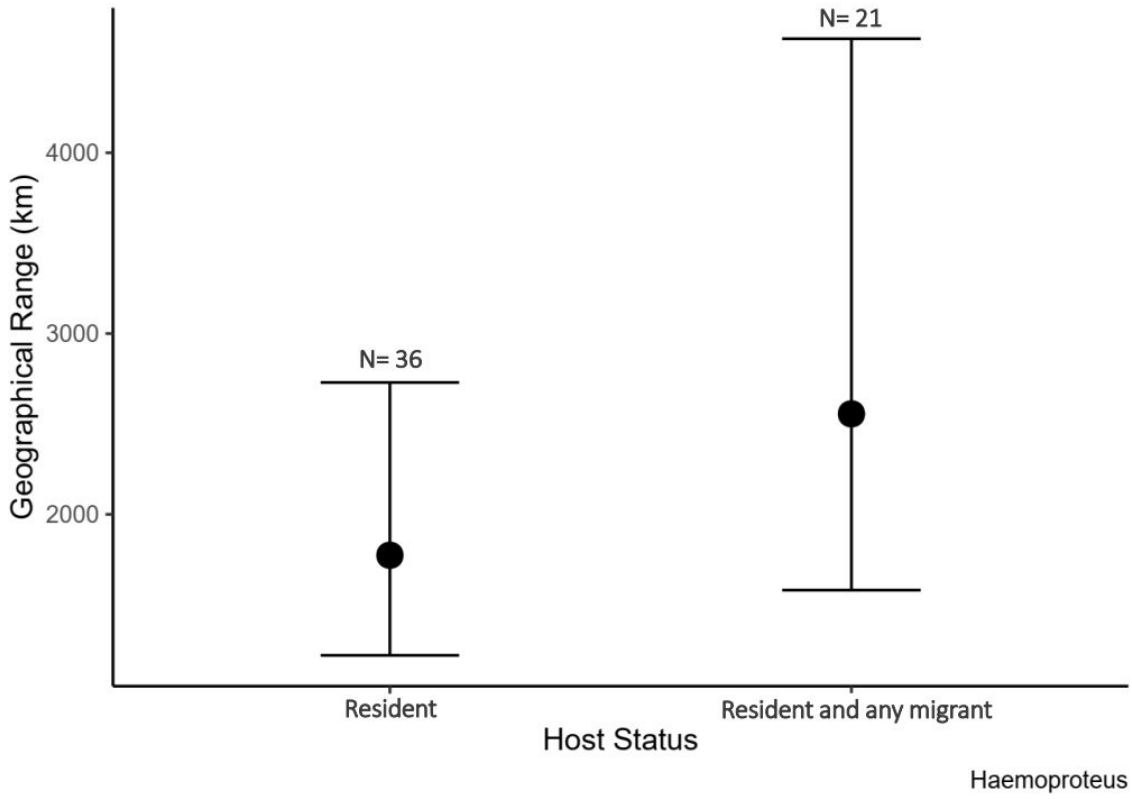


Supplementary Figure 1: Mean (±confidence intervals) geographical range in kilometers in which *Plasmodium* lineages are detected according to the type of birds in which they are found. Number of lineages in each of the two categories are shown on the graph.

Supplementary Table 3: Parameter estimates, standard errors, and confidence intervals for the Bayesian model testing the differences in the geographical range of *Plasmodium* lineages

among those that occur in migratory and/or resident avian host species. (Residents only = reference category)

	Estimate	Std. error	Conf. Inter (95%)	
Intercept	6.95	0.13	6.71	7.21
Resident and any migrant	0.47	0.24	0.01	0.95
Number of bird individuals	-0.02	0.02	-0.06	0.03
Number of host species per lineage	0.11	0.04	0.02	0.19



Supplementary Figure 2: Mean (±confidence intervals) geographical range in kilometers in which *Haemoproteus* 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.

Supplementary Table 4: Parameter estimates, standard errors, and confidence intervals for the Bayesian model testing the differences in the geographical range of *Haemoproteus* lineages among those that occur in migratory and/or resident avian host species. (Residents only = reference category)

	Estimate	**Std. error**	**Conf. Inter (95%)**	
Intercept	7.35	0.22	6.92	7.80
Resident and any migrant	0.37	0.36	-0.33	1.08
Number of bird individuals	0.01	0.02	-0.03	0.06
Number of host species per lineage	0.01	0.04	-0.06	0.10

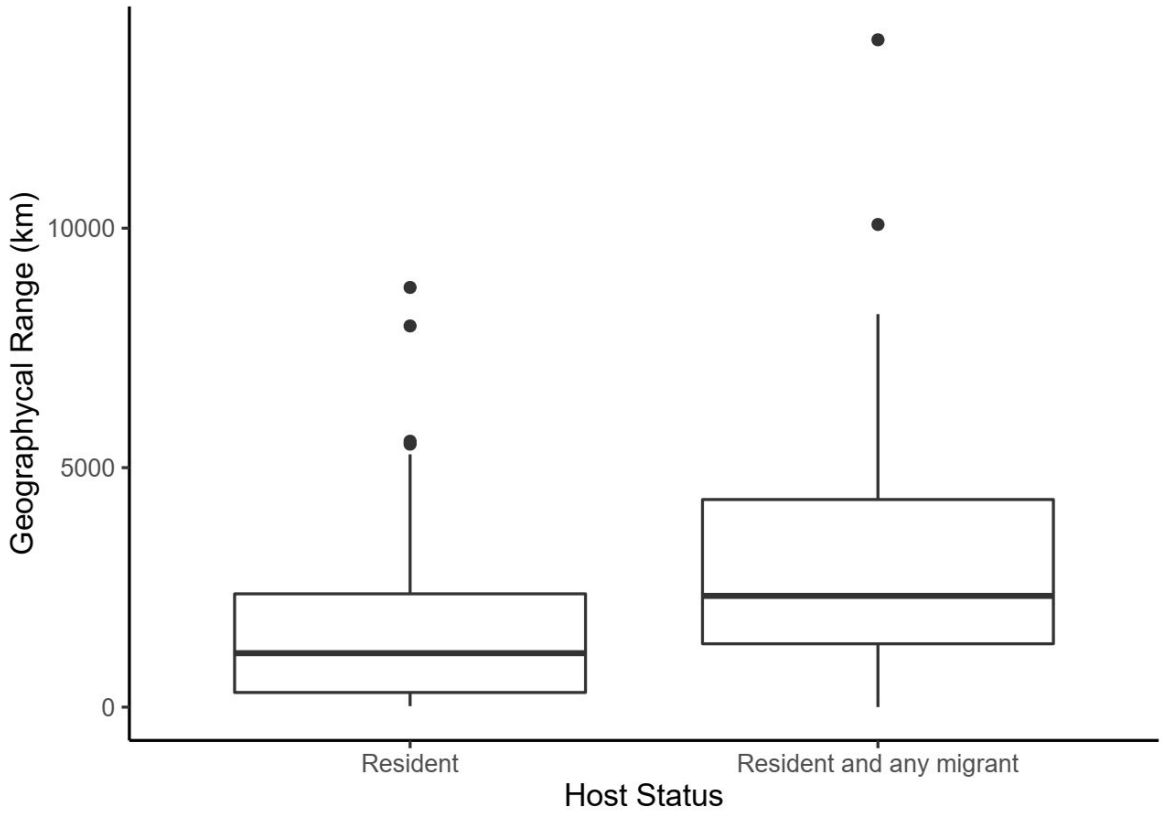


Figure S3: Median geographical range in kilometers in which haemosporidian lineages are detected according to the type of birds they are found plotted from our raw dataset.

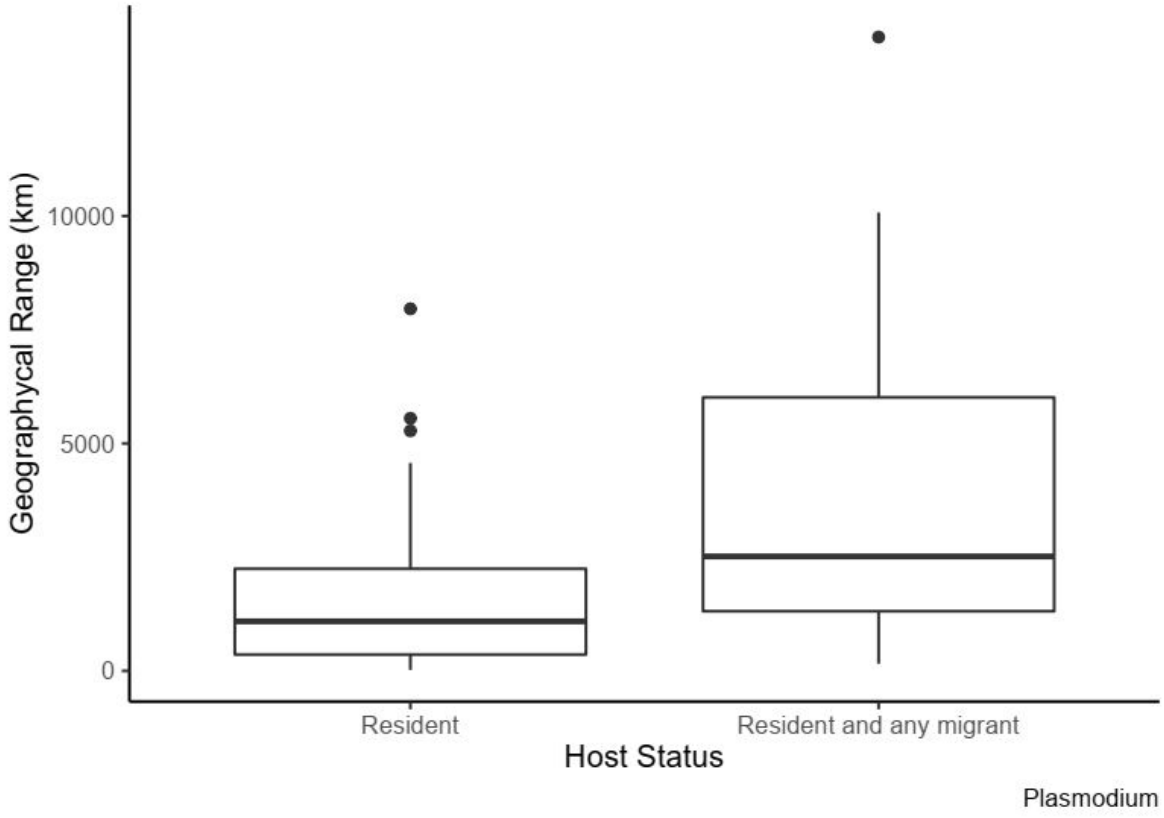


Figure S4: Median geographical range in kilometers in which *Plasmodium* lineages are detected according to the type of birds they are found plotted from our raw dataset.

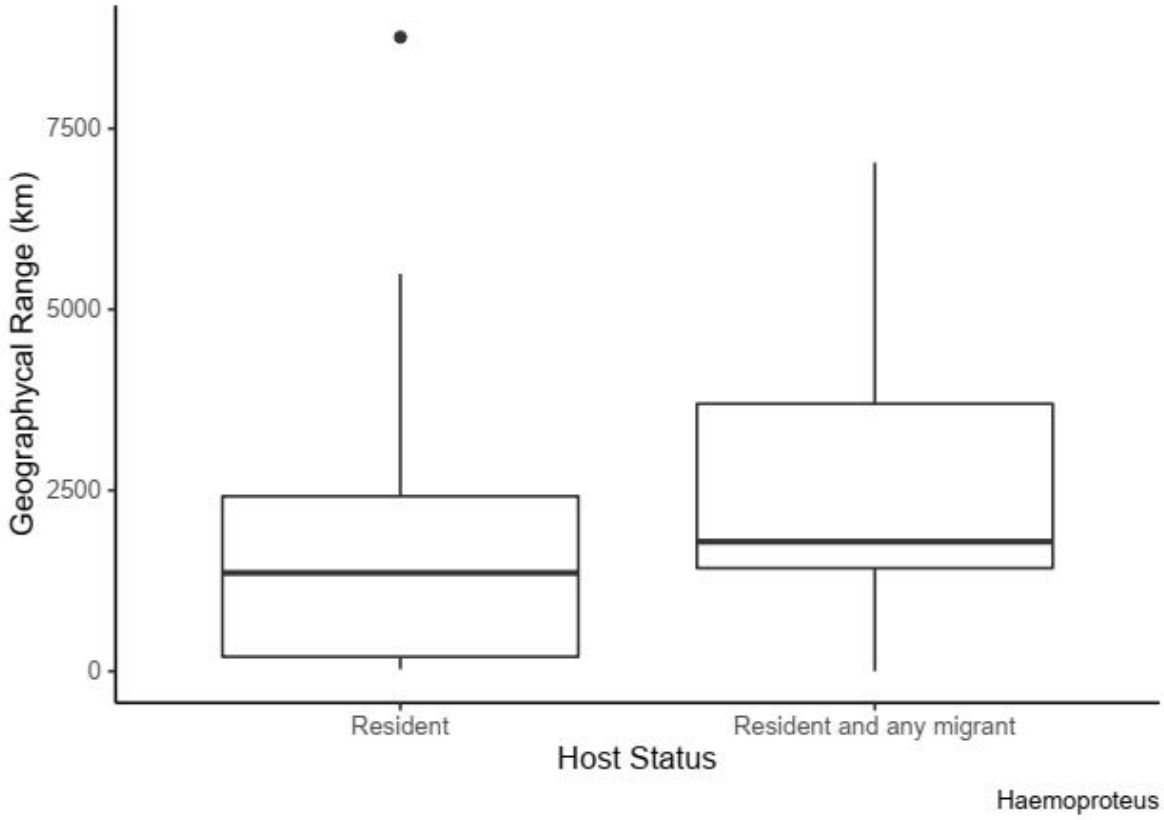
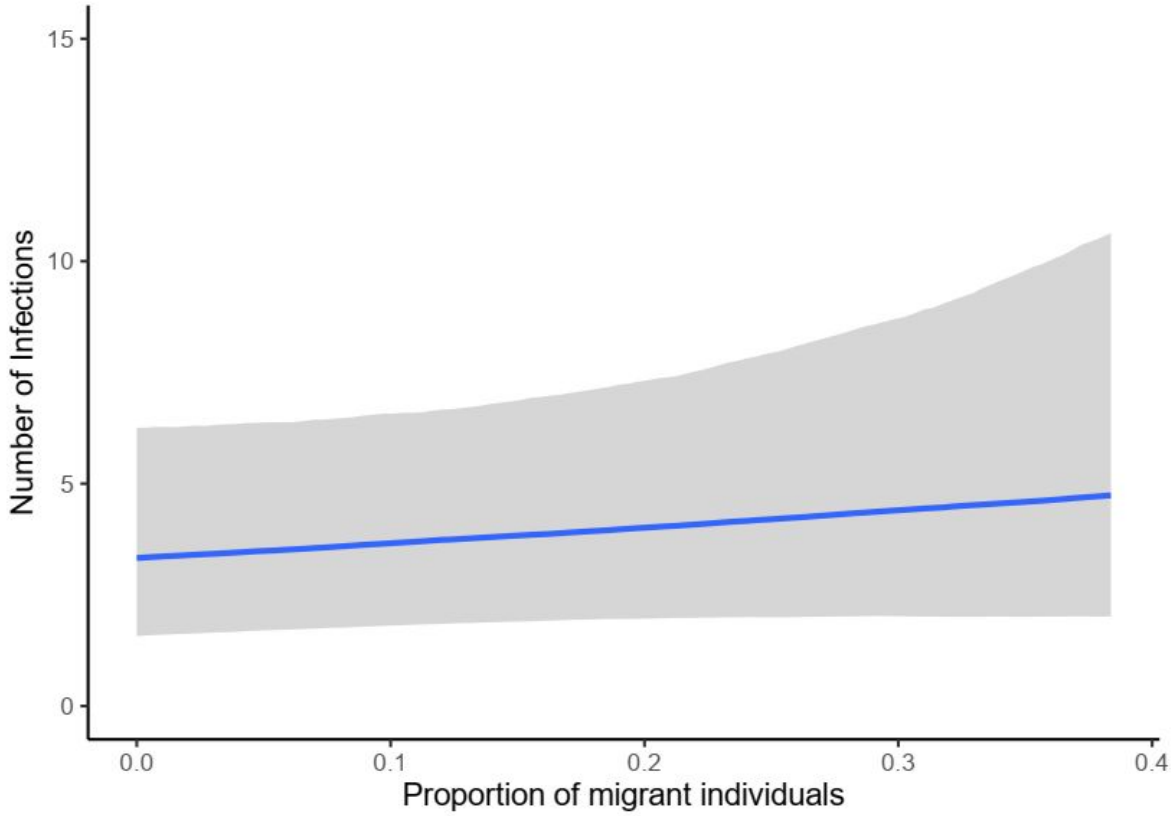


Figure S5: Median geographical range in kilometers in which *Haemoproteus* lineages are detected according to the type of birds they are found plotted from our raw dataset.



Supplementary Figure 6: Predicted model relationship (±95% confidence intervals) between local number of infections for haemosporidian and proportion of migrant in an area.

Supplementary Table 5: Parameter estimates, standard errors, confidence intervals for the Bayesian model testing the variation of local number of birds infected by haemosporidian as a function of the proportion of migratory all individual birds sampled per locality and parasite richness. Residual Moran value = -0.005.

	Estimate	**Std. error**	**Conf. Inter (95%)**	
Intercept	0.38	0.40	-0.44	1.13
Proportion of migrant individuals	0.91	1.05	-1.09	3.03
Parasite richness	0.02	0.01	0.00	0.03

Supplementary Table 6: Parameter estimates, standard errors, and confidence intervals for the Bayesian model testing the variation of local parasite richness by *Plasmodium* as a function of the proportion of migratory individuals out of all individual birds sampled per locality, prevalence and host richness. Residual Moran value = 0.016.

	Estimate	**Std. error**	**Conf. Inter (95%)**	
Intercept	0.77	0.21	0.34	1.18
Proportion of migrant individuals	-0.03	0.02	-0.07	0.01
Proportion of migrant species	0.03	0.02	-0.02	0.08
Prevalence	0.05	0.01	0.04	0.07
Host Richness	0.01	0.00	0.01	0.02

Supplementary Table 7: Parameter estimates, standard errors, and confidence intervals for the Bayesian model testing the variation of local parasite richness by *Haemoproteus* as a function of the proportion of migratory individuals out of all individual birds sampled per locality, prevalence and host richness. Residual Moran value = -0.04.

	Estimate	**Std. error**	**Conf. Inter (95%)**	
Intercept	-0.20	0.30	-0.82	0.39
Proportion of migrant individuals	0.01	0.03	-0.04	0.07
Proportion of migrant species	-0.02	0.03	-0.08	0.04
Prevalence	0.15	0.02	0.10	0.19
Host Richness	0.01	0.00	0.01	0.02

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Table S2. List of bird species in the full dataset, with number of individua

Bird species	Status	n_bird_individuals
Accipiter_striatus	R	1
Accipiter_superciliosus	R	2
Adelomyia_melanogenys	R	5
Agelaioides_badius	R	15
Agelasticus_cyanopus	R	1
Aglaiocercus_kingi	R	2
Amaurospiza_moesta	R	1
Amazilia_fimbriata	R	7
Amazilia_versicolor	R	4
Amazona_mercenaria	R	1
Amazonetta_brasiliensis	R	2
Amblycercus_holosericeus	R	3
Ammodramus_humeralis	R	89
Ampelion_rubrocristatus	R	3
Ampelion_rufaxilla	R	2
Anabacerthia_amaurotis	R	1
Anabacerthia_striaticollis	R	9
Anabazenops_fuscus	R	8
Anhima_cornuta	R	1
Anhinga_anhinga	R	1
Anisognathus_lacrymosus	R	6
Anisognathus_somptuosus	R	10
Anthus_hellmayri	R	1
Antilophia_galeata	R	13
Anurolimnas_viridis	R	1
Aramides_cajanea	R	2
Aratinga_aurea	R	4
Aratinga_cactorum	R	5
Aratinga_jandaya	R	2
Aratinga_leucophthalma	R	5
Aratinga_pertinax	R	1
Ardea_cocoi	R	1
Arremon_aurantiirostris	R	10
Arremon_brunneinucha	R	13
Arremon_flavirostris	R	4
Arremon_taciturnus	R	12
Arremon_torquatus	R	5
Arundinicola_leucocephala	R	2
Asthenes_baeri	R	13
Athene_cunicularia	R	2
Atlapetes_rufinucha	R	4
Attila_cinnamomeus	R	2
Attila_phoenicurus	M	4
Attila_spadiceus	R	16
Aulacorhynchus_prasinus	R	8
Automolus_infuscatus	R	29

Status
R = resident
PM = partial migrant
M = migrant

Automolus_leucophthalmus	R	7
Automolus_ochrolaemus	R	14
Automolus_rubiginosus	R	1
Automolus_rufipileatus	R	5
Avocettula_recurvirostris	R	1
Baryphthengus_martii	R	1
Basileuterus_coronatus	R	16
Basileuterus_culicivorus	R	36
Basileuterus_flaveolus	R	112
Basileuterus_hypoleucus	R	24
Basileuterus_leucoblepharus	R	35
Basileuterus_leucomelas	R	1
Basileuterus_leucophrys	R	1
Basileuterus_luteoviridis	R	6
Basileuterus_tristriatus	R	13
Boissonneaua_matthewsii	R	1
Brachygalba_lugubris	R	4
Brotogeris_chiriri	R	6
Bucco_capensis	R	5
Bucco_tamatia	R	4
Busarellus_nigricollis	R	1
Buteo_magnirostris	R	2
Butorides_striata	R	2
Cacicus_cela	R	1
Cacicus_solitarius	R	6
Cacicus_uropygialis	R	6
Calliphlox_amethystina	R	1
Campephilus_melanoleucos	R	1
Campephilus_rubricollis	R	7
Camptostoma_obsoletum	R	80
Campylopterus_largipennis	R	2
Campylorhamphus_falcularius	R	3
Campylorhamphus_procurvoides	R	3
Campylorhamphus_pusillus	R	5
Campylorhamphus_trochilirostris	R	7
Campylorhynchus_turdinus	R	4
Cantorchilus_leucotis	R	1
Cantorchilus_longirostris	R	34
Caprimulgus_maculicaudus	R	3
Caprimulgus_parvulus	R	3
Caprimulgus_sericocaudatus	R	1
Capsiempis_flaveola	R	5
Caracara_plancus	R	4
Carduelis_magellanica	R	1
Carduelis_olivacea	R	2
Caryothraustes_canadensis	R	1
Casiornis_fuscus	PM	29
Casiornis_rufus	PM	13
Casmerodius_albus	R	1
Catamblyrhynchus_diadema	R	4

Catamenia_homochroa	R	1
Catharus_fuscater	R	2
Catharus_fuscescens	M	3
Celeus_elegans	R	6
Celeus_flavescens	R	1
Celeus_grammicus	R	1
Celeus_undatus	R	3
Cephalopterus_ornatus	R	2
Cercomacra_cinerascens	R	5
Cercomacra_melanaria	R	5
Cercomacra_nigrescens	R	9
Cercomacra_serva	R	2
Certhiaxis_cinnamomeus	R	2
Chamaeza_campanisona	R	2
Charitospiza_eucosma	R	4
Chiroxiphia_caudata	R	18
Chiroxiphia_pareola	R	15
Chlorestes_notata	R	1
Chloroceryle_aenea	R	23
Chloroceryle_amazona	R	2
Chloroceryle_americana	R	5
Chloroceryle_inda	R	5
Chlorochrysa_calliparaea	R	1
Chlorophanes_spiza	R	23
Chlorophonia_cyanea	R	4
Chlorornis_riefferii	R	7
Chlorospingus_ophthalmicus	R	3
Chlorospingus_parvirostris	R	1
Chlorostilbon_mellisugus	R	1
Chordeiles_pusillus	R	1
Chrysuronia_oenone	R	5
Cinclus_leucocephalus	R	2
Cinnycerthia_peruana	R	6
Claravis_pretiosa	R	6
Cnemoscopus_rubrirostris	R	2
Cnemotriccus_fuscatus	R	106
Cnipodectes_subbrunneus	R	4
Coccycua_cinerea	R	2
Coccycua_minuta	R	2
Coccyzus_melacoryphus	M	25
Cochlearius_cochlearius	R	1
Coeligena_coeligena	R	15
Coeligena_torquata	R	6
Coeligena_violifer	R	1
Coereba_flaveola	R	218
Colaptes_campestris	R	5
Colaptes_melanochloros	R	7
Colaptes_rivolii	R	1
Colaptes_rubiginosus	R	2
Colibri_serrirostris	R	3

Colibri_thalassinus	R	1
Columbina_minuta	R	419
Columbina_passerina	R	54
Columbina_picui	R	56
Columbina_squammata	R	26
Columbina_talpacoti	R	57
Conirostrum_sitticolor	R	1
Conirostrum_speciosum	R	8
Conopias_cinchoneti	R	4
Conopophaga_aurita	R	17
Conopophaga_castaneiceps	R	5
Conopophaga_lineata	R	48
Conopophaga_melanops	R	15
Conopophaga_roberti	R	2
Contopus_cinereus	R	2
Contopus_cooperi	M	1
Contopus_fumigatus	R	2
Coryphistera_alaudina	R	17
Coryphospingus_cucullatus	R	10
Coryphospingus_pileatus	R	63
Corythopis_delalandi	R	3
Corythopis_torquatus	R	11
Cranioleuca_obsoleta	R	1
Cranioleuca_pyrrhophia	R	1
Cranioleuca_semicinerea	R	5
Cranioleuca_vulpina	R	8
Creurgops_verticalis	R	7
Crotophaga_ani	R	21
Crypturellus_obsoletus	R	1
Crypturellus_parvirostris	R	2
Crypturellus_soui	R	1
Crypturellus_undulatus	R	1
Crypturellus_variegatus	R	1
Culicivora_caudacuta	R	2
Cyanerpes_caeruleus	R	9
Cyanerpes_cyaneus	R	2
Cyanocompsa_brissonii	R	8
Cyanocompsa_cyanoides	R	13
Cyanocorax_cyanomelas	R	5
Cyanocorax_cyanopogon	R	13
Cyanocorax_yncas	R	4
Cyanoloxia_brissonii	R	2
Cyclarhis_gujanensis	R	86
Cymbilaimus_lineatus	R	4
Cyphorhinus_arada	R	5
Cyphorhinus_thoracicus	R	4
Cypsnagra_hirundinacea	R	26
Dacnis_cayana	R	33
Dacnis_lineata	R	10
Deconychura_longicauda	R	20

Deconychura_stictolaema	R	23
Dendrexetastes_rufigula	R	1
Dendrocincla_fuliginosa	R	50
Dendrocincla_merula	R	81
Dendrocincla_turdina	R	30
Dendrocincla_tyrannina	R	2
Dendrocolaptes_certhia	R	15
Dendrocolaptes_picumnus	R	8
Dendrocolaptes_platyrostris	R	19
Dendrocygna_autumnalis	R	2
Dendroplex_kienerii	R	1
Dendroplex_picus	R	7
Dichrozona_cincta	R	11
Diglossa_albilatera	R	1
Diglossa_caerulescens	R	3
Diglossa_cyanea	R	3
Diglossa_lafresnayii	R	3
Dixiphia_pipra	R	2
Donacobius_atricapilla	R	6
Donacospiza_albifrons	R	1
Doryfera_johannae	R	3
Doryfera_ludovicae	R	1
Drymophila_caudata	R	4
Drymophila_ferruginea	R	3
Drymophila_ochropyga	R	1
Drymophila_squamata	R	20
Drymornis_bridgesii	R	6
Dryocopus_lineatus	R	6
Dubusia_taeniata	R	2
Dysithamnus_mentalis	R	30
Dysithamnus_plumbeus	R	11
Egretta_caerulea	R	1
Egretta_thula	R	2
Elaenia_albiceps	R	15
Elaenia_chilensis	M	262
Elaenia_chiriquensis	PM	271
Elaenia_cristata	R	338
Elaenia_flavogaster	R	40
Elaenia_mesoleuca	R	18
Elaenia_obscura	R	7
Elaenia_pallatangae	R	1
Elaenia_parvirostris	PM	40
Elaenia_ruficeps	R	1
Elaenia_spectabilis	PM	22
Emberizoides_herbicola	R	14
Empidonomus	R	1
Empidonomus_aurantioatrocristatus	R	5
Empidonomus_varius	PM	20
Entomodestes_leucotis	R	4
Epinecrophylla_haematonota	R	53

Epinecrophylla_leucophthalma	R	22
Epinecrophylla_ornata	R	3
Eubucco_versicolor	R	4
Eucometis_penicillata	R	2
Eupetomena_macroura	R	5
Euphonia_chalybea	R	1
Euphonia_chlorotica	R	12
Euphonia_laniirostris	R	1
Euphonia_mesochrysa	R	4
Euphonia_minuta	R	1
Euphonia_pectoralis	R	1
Euphonia_plumbea	R	3
Euphonia_violacea	R	3
Euphonia_xanthogaster	R	6
Euscarthmus_meloryphus	R	12
Euscarthmus_rufomarginatus	R	1
Eutoxeres_condamini	R	5
Falco_femoralis	R	6
Florisuga_fusca	PM	1
Florisuga_mellivora	R	1
Fluvicola_nengeta	R	4
Formicarius_analis	R	5
Formicarius_colma	R	44
Formicarius_rufipectus	R	3
Formicivora_grisea	R	19
Formicivora_melanogaster	R	51
Formicivora_rufa	R	4
Formicivora_serrana	R	2
Forpus_xanthopterygius	R	4
Frederickena_viridis	R	1
Furnarius_figulus	R	1
Furnarius_leucopus	R	22
Furnarius_rufus	R	20
Galbula_albirostris	R	5
Galbula_cyanescens	R	3
Galbula_cyanicollis	R	16
Galbula_ruficauda	R	17
Gallus_gallus	R	30
Geothlypis_aequinoctialis	R	5
Geothlypis_velata	R	1
Geotrygon_frenata	R	1
Geotrygon_montana	R	35
Geotrygon_violacea	R	1
Glaucidium_brasilianum	R	14
Glaucis_hirsutus	R	15
Glyphorynchus_spirurus	R	141
Gnorimopsar_chopi	R	5
Grallaria_blakei	R	4
Grallaria_carrikeri	R	3
Grallaria_guatimalensis	R	1

Grallaria_hypoleuca	R	1
Grallaria_squamigera	R	1
Grallaricula_ferrugineipectus	R	2
Grallaricula_flavirostris	R	4
Grallaricula_peruviana	R	3
Granatellus_pelzelni	R	3
Gubernatrix_cristata	R	3
Gymnopithys_leucaspis	R	7
Gymnopithys_rufigula	R	10
Gymnopithys_salvini	R	47
Habia_rubica	R	14
Haplophaedia_aureliae	R	8
Haplospiza_rustica	R	2
Haplospiza_unicolor	R	21
Harpagus_bidentatus	R	1
Heliactin_bilophus	R	1
Heliangelus_amethysticollis	R	6
Heliobletus_contaminatus	R	6
Heliodoxa_leadbeateri	R	4
Heliodoxa_rubinoides	R	11
Heliomaster_longirostris	R	1
Hemispingus_atropileus	R	1
Hemispingus_frontalis	R	7
Hemispingus_melanotis	R	2
Hemispingus_superciliaris	R	2
Hemispingus_xanthophthalmus	R	3
Hemithraupis_flavicollis	R	1
Hemithraupis_guira	R	11
Hemithriccus_margaritaceiventer	R	7
Hemitriccus_diops	R	19
Hemitriccus_flammulatus	R	2
Hemitriccus_granadensis	R	2
Hemitriccus_inornatus	R	1
Hemitriccus_kaempferi	R	1
Hemitriccus_margaritaceiventer	R	115
Hemitriccus_minor	R	8
Hemitriccus_obsoletus	R	8
Hemitriccus_striaticollis	R	7
Hemitriccus_zosterops	R	1
Henicorhina_leucophrys	R	17
Henicorhina_leucoptera	R	9
Herpsilochmus_atricapillus	R	4
Herpsilochmus_pectoralis	R	34
Herpsilochmus_sellowi	R	43
Heterocercus_linteatus	R	14
Hydropsalis_albicollis	R	2
Hydropsalis_maculicaudus	R	1
Hydropsalis_parvulus	PM	9
Hydropsalis_torquata	R	40
Hylexetastes_brigidai	R	3

Hylexetastes_perrotii	R	2
Hylexetastes_uniformis	R	1
Hylocharis_chrysura	R	4
Hylocharis_cyanus	R	8
Hylocryptus_rectirostris	R	2
Hyloctistes_subulatus	R	8
Hylophilus_amaurocephalus	R	54
Hylophilus_brunneiceps	R	1
Hylophilus_ochraceiceps	R	20
Hylophilus_pectoralis	R	1
Hylophilus_poicilotis	R	4
Hylophilus_semicinereus	R	1
Hylophylax_naevius	R	21
Hylophylax_punctulatus	R	8
Hypocnemis_cantator	R	8
Hypocnemis_flavescens	R	7
Hypocnemis_hypoxantha	R	2
Hypocnemis_ochrogyna	R	3
Hypocnemis_peruviana	R	5
Hypocnemis_striata	R	32
Hypocnemoides_maculicauda	R	16
Ibycter_americanus	R	1
Icterus_cayanensis	R	6
Icterus_jamacaii	R	3
Ictinia_plumbea	PM	2
Ilicura_militaris	R	11
Inezia_inornata	PM	2
Iridosornis_analis	R	9
Iridosornis_rufivertex	R	8
Jabiru_mycteria	R	1
Jacamerops_aureus	R	6
Jacana_jacana	R	2
Klais_guimeti	R	1
Knipolegus_cyanirostris	R	26
Knipolegus_franciscanus	R	1
Knipolegus_nigerrimus	R	2
Knipolegus_poecilocercus	R	6
Lafresnaya_lafresnayi	R	2
Lanio_cucullatus	R	42
Lanio_fulvus	R	1
Lanio_penicillatus	R	2
Lanio_pileatus	R	190
Lanio_versicolor	R	1
Laniocera_hypopyrra	R	6
Laterallus_viridis	R	1
Lathrotriccus_euleri	PM	50
Lepdocolaptes_angustirrostris	R	1
Lepdocolaptes_wagleri	R	2
Lepidocolapes_wagleri	R	1
Lepidocolaptes_affinis	R	6

Lepidocolaptes_albolineatus	R	2
Lepidocolaptes_angustirostris	R	95
Lepidocolaptes_falcinellus	R	2
Lepidocolaptes_squamatus	R	8
Lepidocolaptes_wagleri	R	2
Lepidothrix_coronata	R	91
Lepidothrix_iris	R	1
Lepidothrix_isidorei	R	2
Lepidothrix_nattereri	R	71
Lepidothrix_serena	R	9
Lepidothrix_vilasboasi	R	3
Leptasthenura_platensis	R	5
Leptopogon_amaurocephalus	R	50
Leptopogon_rufipectus	R	2
Leptopogon_superciliaris	R	8
Leptopogon_taczanowskii	R	7
Leptotila_rufaxilla	R	19
Leptotila_verreauxi	R	45
Leucochloris_albicollis	R	1
Leucopternis_albicollis	R	1
Leucopternis_kuhli	R	1
Leucopternis_melanops	R	1
Lipaugus_vociferans	R	9
Lochmias_nematura	R	1
Lophotriccus_galeatus	R	4
Lophotriccus_pileatus	R	7
Machaeropterus_pyrocephalus	R	13
Machaeropterus_regulus	R	13
Mackenziaena_severa	R	1
Malacoptila_fulvogularis	R	3
Malacoptila_fusca	R	2
Malacoptila_rufa	R	20
Malacoptila_striata	R	9
Manacus_manacus	R	35
Margarornis_squamiger	R	5
Mecocerculus_stictopterus	R	1
Megaceryle_torquata	R	3
Megarynchus_pitangua	R	4
Megascops_choliba	R	2
Megascops_ingens	R	4
Megascops_watsonii	R	3
Megastictus_margaritatus	R	10
Melanerpes_cactorum	R	1
Melanerpes_cruentatus	R	1
Melanopareia_torquata	R	4
Mesembrinibis_cayennensis	R	2
Metallura_tyrianthina	R	2
Micrastur_gilvicollis	R	3
Micrastur_mintoni	R	5
Micrastur_ruficollis	R	5

Micrastur_semitorquatus	R	1
Microbates_collaris	R	4
Microcerculus_marginatus	R	22
Micromonacha_lanceolata	R	3
Microrhopias_quixensis	R	5
Mimus_gilvus	R	10
Mimus_saturninus	R	18
Mimus_triurus	M	1
Mionectes_macconnelli	R	32
Mionectes_oleagineus	R	30
Mionectes_olivaceus	R	14
Mionectes_rufiventris	R	9
Mionectes_striaticollis	R	24
Mitrephanes_olivaceus	R	3
Molothrus_bonariensis	R	15
Molothrus_bosiriensis	R	2
Molothrus_rufoaxillaris	R	11
Momotus_momota	R	14
Monasa_morphoeus	R	9
Monasa_nigrifrons	R	5
Myadestes_ralloides	R	11
Mycteria_americana	R	1
Myiarchus_cephalotes	R	3
Myiarchus_ferox	R	22
Myiarchus_swainsoni	PM	112
Myiarchus_tuberculifer	R	5
Myiarchus_tyrannulus	R	103
Myiobius_atricaudus	R	1
Myiobius_barbatus	R	25
Myiobius_villosus	R	11
Myioborus_melanocephalus	R	1
Myioborus_miniatus	R	3
Myiodynastes_maculatus	PM	71
Myiopagis_caniceps	R	5
Myiopagis_gaimardii	R	2
Myiopagis_viridicata	PM	58
Myiophobus_fasciatus	PM	28
Myiophobus_flavicans	R	2
Myiopsitta_monachus	R	4
Myiornis_albiventris	R	1
Myiornis_ecaudatus	R	1
Myiotheretes_fumigatus	R	4
Myiothlypis_flaveola	R	2
Myiozetetes_cayanensis	R	3
Myiozetetes_similis	R	7
Myrmeciza_atrothorax	R	1
Myrmeciza_ferruginea	R	1
Myrmeciza_fortis	R	12
Myrmeciza_hemimelaena	R	16
Myrmeciza_loricata	R	5

Myrmeciza_ruficauda	R	2
Myrmoborus_leucophrys	R	3
Myrmoborus_myotherinus	R	58
Myrmorchilus_strigilatus	R	3
Myrmornis_torquata	R	9
Myrmotherula_axillaris	R	73
Myrmotherula_gularis	R	2
Myrmotherula_guttata	R	6
Myrmotherula_gutturalis	R	2
Myrmotherula_hauxwelli	R	40
Myrmotherula_iheringi	R	1
Myrmotherula_longicauda	R	2
Myrmotherula_longipennis	R	49
Myrmotherula_menetriesii	R	12
Myrmotherula_multostriata	R	2
Myrmotherula_schisticolor	R	10
Myrmotherula_unicolor	R	1
Myrmotherula_urosticta	R	3
Nandayus_nenday	R	3
Nemosia_pileata	R	7
Neopelma_pallescens	R	56
Neothraupis_fasciata	R	127
Nonnula_rubecula	R	3
Notharchus_tectus	R	4
Nothocercus_nigrocapillus	R	1
Nyctibius_aethereus	R	2
Nyctibius_bracteatus	R	1
Nyctidromus_albicollis	R	11
Nyctiprogne_leucopyga	R	2
Nystalus_chacuru	R	19
Nystalus_maculatus	R	55
Ochthoeca_cinnamomeiventris	R	1
Ochthoeca_pulchella	R	6
Ochthoeca_rufipectoralis	R	4
Ocreatus_underwoodii	R	3
Odontophorus_speciosus	R	1
Onychorhynchus_coronatus	R	17
Opisthoprora_euryptera	R	1
Ornithion_inerme	R	1
Oryzoborus_angolensis	R	17
Pachyramphus_castaneus	R	1
Pachyramphus_marginatus	R	7
Pachyramphus_minor	R	3
Pachyramphus_polychopterus	PM	49
Pachyramphus_rufus	R	4
Pachyramphus_validus	PM	3
Pachyramphus_versicolor	R	2
Pachyramphus_viridis	R	2
Paroaria_capitata	R	76
Paroaria_coronata	R	18

Paroaria_dominicana	R	15
Parula_pitiayumi	R	1
Passer_domesticus	R	1
Patagioenas_fasciata	PM	1
Patagioenas_maculosa	R	1
Patagioenas_plumbea	R	7
Patagioenas_subvinacea	R	2
Patagioesis_cayennensis	R	1
Penelope_superciliaris	R	2
Percnostola_rufifrons	R	8
Periporphyrus_erythromelas	R	1
Phacellodomus_ruber	R	4
Phacellodomus_rufifrons	R	66
Phaeomyias_murina	PM	38
Phaeomyias_murina	R	47
Phaeothlypis_fulvicauda	R	8
Phaethornis_bourcieri	R	5
Phaethornis_eurynome	R	3
Phaethornis_guy	R	8
Phaethornis_malaris	R	4
Phaethornis_ruber	R	7
Phaethornis_subochraceus	R	2
Phaethornis_superciliosus	R	14
Phaethornis_syrmatophorus	R	8
Phalacrocorax_brasilianus	R	2
Pharomachrus_auriceps	R	1
Pheucticus_aureoventris	M	1
Pheugopedius_genibarbis	R	8
Philohydor_lictor	R	1
Philydor_atricapillus	R	12
Philydor_erythrocercum	R	16
Philydor_lichtensteini	R	1
Philydor_pyrrhodes	R	6
Philydor_ruficaudatum	R	3
Philydor_rufum	R	4
Phimosus_infuscatus	R	2
Phlegopsis_erythroptera	R	10
Phlegopsis_nigromaculata	R	46
Phoenicircus_carnifex	R	7
Phyllomyias_cinereiceps	R	1
Phyllomyias_fasciatus	R	4
Phylloscartes_difficilis	R	1
Phylloscartes_ophthalmicus	R	1
Phylloscartes_poecilotis	R	5
Phylloscartes_ventralis	R	7
Phylloscartes_virescens	R	3
Piaya_cayana	R	22
Picoides_fumigatus	R	1
Piculus_flavigula	R	3
Picumnus_albosquamatus	R	5

Picumnus_cirratus	R	5
Picumnus_fulvescens	R	11
Picumnus_lafresnayi	R	1
Picumnus_limae	R	1
Picumnus_nebulosus	R	3
Picumnus_pygmaeus	R	10
Picumnus_steindachneri	R	1
Picumnus_temminckii	R	2
Pionites_leucogaster	R	1
Pionus_menstruus	R	1
Pipile_cujubi	R	1
Pipra_chloromeros	R	9
Pipra_erythrocephala	R	18
Pipra_fasciicauda	R	27
Pipra_pipra	R	45
Pipra_rubrocapilla	R	83
Pipreola_arcuata	R	2
Pipreola_chlorolepidota	R	1
Pipreola_riefferii	R	17
Piprites_chloris	R	8
Piranga_flava	R	6
Pitangus_lictor	R	5
Pitangus_sulphuratus	PM	89
Pithys_albifrons	R	26
Platalea_ajaja	PM	1
Platyrinchus_mystaceus	R	33
Platyrinchus_platyrhynchos	R	16
Platyrinchus_saturatus	R	10
Poecilotriccus_capitalis	R	1
Poecilotriccus_fumifrons	R	3
Poecilotriccus_latirostris	R	6
Poecilotriccus_sylvia	R	1
Polioptila_dumicola	R	4
Polioptila_guianensis	R	1
Polioptila_plumbea	R	56
Polystictus_superciliaris	R	2
Polytmus_theresiae	R	3
Poospiza_cabanisi	R	6
Poospiza_lateralis	R	5
Poospiza_melanoleuca	R	3
Poospiza_nigrorufa	R	1
Poospiza_thoracica	R	1
Premnoplex_brunnescens	R	8
Premnornis_guttuligera	R	16
Procacicus_solitarius	R	3
Procnias_nudicollis	R	1
Progne_tapera	PM	1
Psarocolius_angustifrons	R	3
Psarocolius_bifasciatus	R	3
Psarocolius_decumanus	R	3

Pseudocolaptes_boissonneautii	R	1
Pseudoseisura_cristata	R	1
Pseudoseisura_lophotes	R	9
Pseudotriccus_pelzelni	R	3
Pseudotriccus_ruficeps	R	6
Psophia_crepitans	R	3
Psophia_viridis	R	2
Pteroglossus_aracari	R	3
Pteroglossus_azara	R	5
Pteroglossus_bitorquatus	R	1
Pteroglossus_viridis	R	4
Pulsatrix_perspicillata	R	1
Pygiptila_stellaris	R	2
Pygochelidon_cyanoleuca	PM	2
Pyriglena_leuconota	R	11
Pyriglena_leucoptera	R	42
Pyrocephalus_rubinus	M	38
Pyroderus_scutatus	R	5
Pyrrhocoma_ruficeps	R	1
Pyrrhomyias_cinnamomeus	R	9
Pyrrhura_lepida	R	4
Ramphastos_ambiguus	R	1
Ramphastos_dicolorus	R	1
Ramphastos_tucanus	R	6
Ramphastos_vitellinus	R	7
Ramphocaenus_melanurus	R	3
Ramphocelus_bresilius	R	1
Ramphocelus_carbo	R	40
Ramphodon_naevius	R	1
Ramphotrigon_ruficauda	R	12
Rhegmatorhina_berlepschi	R	12
Rhegmatorhina_gymnops	R	4
Rhegmatorhina_hoffmannsi	R	11
Rhegmatorhina_melanosticta	R	36
Rhopornis_ardesiacus	R	9
Rhynchocyclus_olivaceus	R	5
Rhytipterna_immunda	R	1
Rhytipterna_simplex	R	17
Rupicola_peruvianus	R	3
Rupornis_magnirostris	R	3
Sakesphorus_cristatus	R	29
Saltator_atricollis	R	6
Saltator_aurantiirostris	R	10
Saltator_coerulescens	R	16
Saltator_grossus	R	5
Saltator_maxillosus	R	4
Saltator_maximus	R	10
Saltator_similis	R	35
Sayornis_nigricans	R	2
Schiffornis_turdina	R	54

Schiffornis_virescens	R	6
Schistes_geoffroyi	R	1
Schistochlamys_melanopis	R	1
Schistochlamys_ruficapillus	R	35
Schistocichla_humaythae	R	1
Schistocichla_leucostigma	R	11
Schoeniophylax_phryganophilus	R	3
Sclateria_naevia	R	3
Sclerurus_albigularis	R	1
Sclerurus_caudacutus	R	10
Sclerurus_mexicanus	R	9
Sclerurus_rufigularis	R	21
Sclerurus_scansor	R	4
Scytalopus_atratus	R	1
Scytalopus_femoralis	R	2
Selenidera_gouldii	R	2
Selenidera_maculirostris	R	1
Selenidera_piperivora	R	2
Selenidera_reinwardtii	R	3
Sericossypha_albocristata	R	6
Serpophaga_munda	PM	4
Serpophaga_subcristata	R	10
Sicalis_citrina	R	1
sicalis_flaveola	R	3
Sicalis_flaveola	R	28
Sicalis_luteola	PM	6
Sirystes_sibilator	R	1
sittasomus_griseicapillus	R	2
Sittasomus_griseicapillus	R	80
Sporophila_albogularis	R	6
Sporophila_americana	R	2
Sporophila_caerulescens	PM	9
Sporophila_collaris	R	2
Sporophila_leucoptera	R	4
Sporophila_minuta	R	1
Sporophila_nigricollis	R	8
Sporophila_palustris	M	1
Sporophila_plumbea	R	35
Stelgidopteryx_ruficollis	PM	4
Stephanophorus_diadematus	R	6
Stephanoxis_lalandi	R	2
Stigmatura_napensis	R	3
Streptoprocne_rutila	R	1
Strix_huhula	R	1
Strix_virgata	R	1
Sublegatus_modestus	PM	18
Suiriri_islerorum	R	16
Suiriri_suiriri	R	51
Synallaxis_albescens	R	32
Synallaxis_albilora	R	3

Synallaxis_azarae	R	2
Synallaxis_cinerea	R	1
Synallaxis_frontalis	R	55
Synallaxis_gujanensis	R	3
Synallaxis_hypospodia	R	4
Synallaxis_ruficapilla	R	7
Synallaxis_rutilans	R	26
Synallaxis_scutata	R	22
Synallaxis_spixi	R	4
Synallaxis_unirufa	R	4
Syndactyla_rufosuperciliata	R	15
Syndactyla_subalaris	R	6
Syrigma_sibilatrix	R	1
Tachornis_squamata	R	1
Tachyphonus_coronatus	R	17
Tachyphonus_cristatus	R	5
Tachyphonus_luctuosus	R	3
Tachyphonus_phoenicius	R	4
Tachyphonus_rufiventer	R	5
Tachyphonus_rufus	R	211
Tachyphonus_surinamus	R	6
Taeniotriccus_andrei	R	3
Tangara_argyrofenges	R	3
Tangara_cayana	R	148
Tangara_chilensis	R	12
Tangara_cyanicollis	R	5
Tangara_cyanoptera	R	2
Tangara_gyrola	R	3
Tangara_labradorides	R	3
Tangara_mexicana	R	1
Tangara_nigrocincta	R	4
Tangara_nigroviridis	R	12
Tangara_palmarum	R	9
Tangara_parzudakii	R	5
Tangara_ruficervix	R	2
Tangara_sayaca	R	83
Tangara_schrankii	R	2
Tangara_vassorii	R	2
Tangara_viridicollis	R	3
Tangara_xanthocephala	R	5
Tangara_xanthogastra	R	1
Tapera_naevia	R	2
Taphrospilus_hypostictus	R	2
Taraba_major	R	39
Terenotriccus_erythrurus	R	13
Tersina_viridis	R	3
Thalurania_furcata	R	28
Thalurania_glaucopis	R	3
Thamnomanes_ardesiacus	R	15
Thamnomanes_caesius	R	57

Thamnomanes_saturninus	R	30
Thamnophilus_aethiops	R	48
Thamnophilus_amazonicus	R	2
Thamnophilus_ambiguus	R	72
Thamnophilus_caerulescens	R	22
Thamnophilus_capistratus	R	6
Thamnophilus_capstratus	R	1
Thamnophilus_doliatus	R	16
Thamnophilus_doliatus_capistratus	R	21
Thamnophilus_murinus	R	14
Thamnophilus_nigrocinereus	R	11
Thamnophilus_palliatus	R	1
Thamnophilus_pelzelni	R	76
Thamnophilus_schistaceus	R	12
Thamnophilus_stictocephalus	R	9
Thamnophilus_torquatus	R	5
Thamnophilus_unicolor	R	6
Theristicus_caudatus	R	1
Thlypopsis_sordida	R	9
Thraupis_bonariensis	R	4
Thraupis_cyanocephala	R	3
Thraupis_episcopus	R	3
Thraupis_palmarum	R	3
Thraupis_sayaca	R	28
Threnetes_leucurus	R	2
Thripadectes_holostictus	R	4
Thryothorus_coraya	R	5
Thryothorus_euophrys	R	4
Thryothorus_genibarbis	R	8
Thryothorus_leucotis	R	12
Thryothorus_longirostris	R	5
Tiaris_fuliginosus	R	6
Tigrisoma_lineatum	R	2
Tityra_semifasciata	R	4
Todirostrum_cinereum	R	9
tolmomyias_flaviventris	R	1
Tolmomyias_flaviventris	R	94
Tolmomyias_sulphurescens	R	29
Topaza_pella	R	3
Trichothraupis_melanops	R	27
Troglodytes_aedon	R	47
Troglodytes_musculus	R	93
Trogon_collaris	R	3
Trogon_curucui	R	18
Trogon_melanurus	R	2
Trogon_personatus	R	4
Trogon_rufus	R	6
Trogon_surrucura	R	2
Trogon_viridis	R	4
Turdus_albicollis	R	82

Turdus_amaurochalinus	PM	299
Turdus_flavipes	M	20
Turdus_fulviventris	R	1
Turdus_fumigatus	R	11
Turdus_hauxwelli	R	1
Turdus_ignobilis	R	2
Turdus_leucomelas	R	261
Turdus_leucops	R	6
Turdus_nigriceps	R	10
Turdus_rufiventris	R	50
Turdus_serranus	R	10
Turdus_subalaris	PM	7
Tyranneutes_stolzmanni	R	6
Tyrannidae	R	2
Tyrannus_melancholicus	PM	29
Tyrannus_savana	PM	8
Tyto_alba	R	2
Veliniornis_passerinus	R	2
Veniliornis_affinis	R	5
Veniliornis_mixtus	R	19
Veniliornis_nigriceps	R	2
Veniliornis_passerinus	R	36
Veniliornis_spilogaster	R	1
Venilliornis_mixtus	R	1
Vireo_gilvus	M	1
Vireo_olivaceus	M	44
Vireolanius_leucotis	R	3
Volatinia_jacarina	R	218
Willisornis_poecilinotus	R	128
Xenopipo_atronitens	R	7
Xenopipo_unicolor	R	20
Xenops_minutus	R	41
Xenops_rutilans	R	8
Xenopsaris_albinucha	R	4
Xiphocolaptes_albicollis	R	3
Xipholena_lamellipennis	R	1
Xiphorhynchus_elegans	R	47
Xiphorhynchus_fuscus	R	34
Xiphorhynchus_guttatus	R	24
Xiphorhynchus_obsoletus	R	8
Xiphorhynchus_ocellatus	R	18
Xiphorhynchus_pardalotus	R	37
Xiphorhynchus_picus	R	1
Xiphorhynchus_spixii	R	7
Xiphorhynchus_triangularis	R	14
Xolmis_irupero	R	3
Xyphocolaptes_falcirostris	R	1
Zenaida_auriculata	R	13
Zimmerius_viridiflavus	R	1
Zonotrichia_capensis	R	129

als sampled, and their migratory statu

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

Daniela de Angeli Dutra, Antoine Filion, Alan Fecchio, Érika Martins Braga, Robert Poulin

Spacial Correlation and Phylogenetic Signal

```
library(gdata)
library(gstat)
library(sp)
library(dplyr)

Dados <- read_excel("dados.xlsx")
Dados <- filter(PD7, Parasiterichness !="NA")
class(Dados)
Dados$Parasiterichness <- as.numeric(Dados$Parasiterichness)

data <- as.matrix(dist(cbind(data$Longitude, data$Latitude)))
data1 <- 1/data
diag(data1) <- 0
data1 <-ifelse(data1=="Inf",0,data1 )

data1[1:5, 1:5]

library(ape)
Moran.I(Dados$Parasiterichness, data1, na.rm = TRUE)

### repeat procedure for parasite prevalence###

library(devtools)
library(treeman)
library(ape)
library(picante)
library(adephylo)
library(ade4)
library(phylobase)
```

```
library(geiger)
library(dplyr)

allTrees <- readTree("AllBirdsHackett1.tre")
random_trees <-sample(allTrees@treelst, size = 100)
random_trees1 <- as(random_trees, 'TreeMen')
random_trees2 <- as(random_trees1, 'multiPhylo')

str(random_trees2)
tree <- consensus(random_trees2)
str(tree)
tree <- as.phylo(tree)

library(phytools)

tree2 <- phylog.extract(tree, node, distance = TRUE)

library(readxl)
data1 <- read_excel("dados.xlsx")
x <- as.vector(data1$Species)
x1 <- as.vector((data1$Infection))
data2 = data1 %>%
  dplyr::group_by(`Species`) %>%
  dplyr::summarise(n_sites = n_distinct(Locality),
                   n_bird_individuals = n(),
                   n_infections = sum(Infection)) %>%
  dplyr::arrange(-n_bird_individuals)

fullbirds <- as.data.frame(tree$tip.label)
mybirds <- as.data.frame(data2$Species)
class(fullbirds)
class(mybirds)
fullbirds <- as.data.frame(fullbirds)
```

```
mybirds <- as.data.frame(mybirds)

length(which(tree$tip.label%in%as.character(mybirds[,1])))
todrop<-tree$tip.label[which(tree$tip.label%in%as.character(mybirds[,1])==FALSE)]
mybirds_tree<-drop.tip(tree,todrop)

keep.tip(tree,as.character(mybirds[,1]))

drop2 <- as.data.frame(mybirds_tree$tip.label)
drop2 <- left_join()
names(drop2) <- c('SpeciesTotal')

data2 <- as.data.frame(data2)
data2$n_infections <- as.numeric(data2$n_infections)
data2$n_bird_individuals <- as.numeric(data2$n_bird_individuals)
data2 <- data2 %>%
  mutate(prevalence = n_infections/n_bird_individuals)

drop3 <- drop2$SpeciesTotal
drop3 <- as.data.frame(drop3)

data3 <- select_if(data2$Species, vars(drop2$SpeciesTotal), .predicate = TRUE, nm=NULL)
data4 <- as.tbl(data2)
data3 <- filter_if(data4, data4$Species == c("Todirostrum_margaritaceiventer", "Elaenia_sp.",
"Setopagis_parvulus", "Lepidocolaptes_wagleri", "Rupornis_magnirostris", "Sporophila_sp.",
"Fringilla_brissonii", "Leptotila_sp.", "Myiothlypis_flaveolus", "Picus_passerinus", "Pseudopipra_pipra",
"Basileuterus_leucomelas", "Columbina_sp.", "Empidonomus", "Euphonia_sp.", "Hylophilus_sp.",
"Lanius_lictor", "Lepidocolaptes_angustirrostris", "Myiobius_sp.", "Picumnus_sp.", "Rallus_viridis",
"Stenopsis_maculicaudus", "Synallaxis_cinereus", "Synallaxis_sp.", "Thamnophilus_capstratus",
"tolmomyias_flaviventris", "Tolmomyias_flaviventris", "Venilliornis_mixtus", "Xiphorhynchus_picus",
"Xyphocolaptes_falcirostris"), .preserve = FALSE)

myvars <- names(data2$Species) %in% c("Todirostrum_margaritaceiventer", "Elaenia_sp.",
"Setopagis_parvulus", "Lepidocolaptes_wagleri", "Rupornis_magnirostris", "Sporophila_sp.",
"Fringilla_brissonii", "Leptotila_sp.", "Myiothlypis_flaveolus", "Picus_passerinus", "Pseudopipra_pipra",
"Basileuterus_leucomelas", "Columbina_sp.", "Empidonomus", "Euphonia_sp.", "Hylophilus_sp.",
"Lanius_lictor", "Lepidocolaptes_angustirrostris", "Myiobius_sp.", "Picumnus_sp.", "Rallus_viridis",
"Stenopsis_maculicaudus", "Synallaxis_cinereus", "Synallaxis_sp.", "Thamnophilus_capstratus",
```

```
"tolmomyias_flaviventris", "Tolmomyias_flaviventris", "Venilliornis_mixtus", "Xiphorhynchus_picus",
"Xyphocolaptes_falcirostris")

newdata <- data2[!mybirds2]


todrop1<-data2$Species[which(data2$Species%in%as.character(drop2[,1])==FALSE)]

print(todrop1)

data3 <- filter_all(data2$Species == todrop1)


tree2 <- select(tree$tip.label, mybirds)


mybirds_tree$tip.label


data3 <- left_join(drop2, data2, by = c("SpeciesTotal" = "Species") )


phylosig(mybirds_tree, data3$prevalence , method="lambda", test=FALSE, nsim=1000, se=NULL,
start=NULL,

      control=list())


### repeat the procedure for parasite richness###
```

Geographical Range Calculation:

```
library(brms)

library(ggplot2)

library(readxl)

library(GeoRange)

library(fossil)

library(data.table)

library(tidyverse)

library(readODS)


data1 <- read_excel("Lineages1.xlsx")

data2 <- read_excel("Lineages2.xlsx", sheet = "Sheet2")

class(data2)

data2 <- as.data.frame(data2)
```

```
data2 <- data2[ , c("site", "Latitude", "Longitude")]
data2 <- distinct(data2)

dados <- left_join(data1, data2, by = c("site" = "site"))
dados <- as.data.frame(dados)

data <- create.matrix(dados, tax.name ="Lineage_Name", locality ="site", abund = FALSE)
data3 <- t(data)
data3 <- as.data.frame(data3)
setDT(data3, keep.rownames = "site")
data4 <- left_join(data3, data2, by = c("site" = "site"))
setcolorder(data4, c("Longitude", "Latitude"))
data4$site <- NULL
data4[data1 == 0] <- NA

data4$Longitude=as.numeric(paste(data4$Longitude))
data4$Latitude=as.numeric(paste(data4$Latitude))
data4 <- data4 %>% drop_na(Longitude)
data4<- as.data.frame(data4)
class(data4)

Range <- GeoRange_MultiTaxa(OccMatrix=data4,TaxaStart=3)
Range1 <- filter(Range, NLocs > 1)

write.csv(Range1, "Range.csv")
```

Bayesian Model 1

```
dados1 <- read_ods("LineagesGeoRange.ods")
dados1$MST=as.numeric(paste(dados1$MST))
dados1 <- filter(dados1, NLoc > 1)

variaveis1 <- bf(MST~Host_Status + n_bird_individuals + richness, family = Gamma(link = log)) #check
```

```
prior1 <- get_prior(variaveis1, data = dados1)
prior1

dados1$Host_Status=as.factor(paste(dados1$Host_Status))
dados1$Host_Status<- relevel(dados1$Host_Status, ref="R")

levels(dados1$Host_Status)

model2 <- brm(
  MST~Host_Status + n_bird_individuals + riqueza, data = dados1,
  family = Gamma(link = "log"), chains = 4,
  iter = 4000,
  prior = c(
    prior(student_t(3, 7.3, 2.5), "Intercept"),
    prior(gamma(0.01, 0.01),"shape")
  ))

summary(model2)
plot(model2, N = 4, ask =FALSE)

a <- theme(panel.grid.major = element_blank(), panel.grid.minor = element_blank(),
          panel.background = element_blank(), axis.line = element_line(colour = "black"))

plot <- plot(conditional_effects(model2), points = FALSE, theme = a)

plot2 <- plot$Host_Status + labs(x = "Host Status", y = "Geographical Range (km)") #caption =
"Plasmodium")
+ geom_boxplot(aes(color = Host_Status))
plot2
```

Bayesian Model 2:

```
library(tidyverse)
library(ggplot2)
library(brms)
```

```
library(readxl)
library(ggpubr)

dados1 <- read_excel("dados.xlsx", sheet = "Objetivo2b>=10",
                     col_types = c("text", "text", "numeric",
                                   "numeric", "numeric", "numeric",
                                   "numeric", "numeric", "numeric",
                                   "numeric", "text", "numeric", "numeric",
                                   "numeric", "numeric", "numeric",
                                   "numeric", "numeric", "numeric", "numeric",
                                   "numeric"))
dados1 <- filter(dados1, Parasiterichness != "NA")

hist(dados2$Pos, breaks = 100)
hist(dados1$Parasiterichness)
hist(dados1$RiquezadeHospedeiros)
hist(dados1$migrantindividuals)
hist(dados1$Temp)
hist(dados1$Prec)
hist(dados1$n_migrants)

dados1$Species = gsub(' ', '_', dados1$Species)
dados1$Species=as.factor(paste(dados1$Species))
haemo_species <- dados1$Species

myphy <- readRDS("C:/Users/danid/Documents/Lab Poulin/PhD/PhD/Dados/PhD/myphy.rds")

library(ape)

matches2 <-match(haemo_species, myphy$tip.label)
matches2 <-na.omit(matches2)
haemo_tree <-drop.tip(myphy, myphy$tip.label[-matches2])
```

```
sptest=as.factor(haemo_tree$tip.label)
sp=as.data.frame(sptest)

dados2=dados1 %>%
  filter(Species %in% sp$sptest)

inv.phylo <- MCMCglmm::inverseA(haemo_tree, nodes = "TIPS", scale = TRUE)
A <- solve(inv.phylo$Ainv)
rownames(A) <- rownames(inv.phylo$Ainv)

dados2$phylo <- dados2$Species

teste <- brm(Pos~Totalsample + Parasiterichness + (1|Bioma) + (1|Locality) + (1|phylo),
             data = dados1,
             family = negbinomial(),
             chain = 4, iter = 4000, cov_ranef = list(phylo = A))
summary(teste)

teste2 <- brm(Pos~Totalsample +  Prec + (1|Bioma) + (1|Locality) + (1|phylo),
              data = dados1,
              family = negbinomial(),
              chain = 4, iter = 4000, cov_ranef = list(phylo = A))
summary(teste2)

teste3 <- brm(Pos~Totalsample +  Temp + (1|Bioma) + (1|Locality) + (1|phylo),
              data = dados1,
              family = negbinomial(),
              chain = 4, iter = 4000, cov_ranef = list(phylo = A))

summary(teste3)

teste4 <- brm(Pos~Totalsample +  n_migrants + (1|Bioma) + (1|Locality) + (1|phylo),
              data = dados1,
```

```
        family = negbinomial(),
        chain = 4, iter = 4000, cov_ranef = list(phylo = A))

summary(teste4)

variaveis <- bf(Pos~Totalsample+migrantindividuals + Parasiterichness +
            (1|Bioma) + (1|Locality) + (1|phylo), family = negbinomial())

prior <- get_prior(variaveis, data = dados2)
prior

model <- brm(Pos~Totalsample+ migrantindividuals + Parasiterichness + (1|Bioma) + (1|Locality) +
(1|phylo),
        data = dados2,
        family = negbinomial(),
        chain = 4, iter = 4000,
        cov_ranef = list(phylo = A),
        prior = c(
          prior(student_t(3, 1.1, 2.5), "Intercept"),
          prior(student_t(3, 0, 2.5), "sd" ),
          prior(gamma(0.01, 0.01), "shape")
        )
)

summary(model)
plot(model, N = 4, ask = FALSE)

plot1 <- plot(conditional_effects(model), points = FALSE, theme = a)
a <- theme(panel.grid.major = element_blank(), panel.grid.minor = element_blank(),
      panel.background = element_blank(), axis.line = element_line(colour = "black"))

plot2 <- plot1$migrantindividuals + labs(x = "Proportion of migrant individuals", y = "Number of Infections")
+ coord_cartesian(ylim = c(0, 15)) #caption = "Plasmodium")
+ geom_boxplot(aes(color = migrantindividuals))
```

```
plot2

res1 <- residuals(model)
res1 <- as.data.frame(res1)
dados2$residuals <- res1$Estimate
dados2$residuals <- as.numeric(dados2$residuals)

dados2a <- as.matrix(dist(cbind(dados2$Longitude, dados2$Latitude)))
dados2b <- 1/dados2a
diag(dados2b) <- 0
dados2b <-ifelse(dados2b=="Inf",0,dados2b )

dados2b[1:5, 1:5]

Moran.I(dados2$residuals, dados2b, na.rm = TRUE)
```

Bayesian Model 3

```
library(tidyverse)
library(ggplot2)
library(brms)
library(readxl)
library(ggpubr)

dados1 <- read_excel("PD7.xlsx", sheet = "Objetivo 2.txt",
                     col_types = c("text", "numeric", "numeric",
                                   "numeric", "numeric", "numeric",
                                   "numeric", "numeric", "numeric",
                                   "numeric", "numeric", "text", "numeric",
                                   "numeric", "numeric", "numeric",
                                   "numeric", "numeric", "numeric", "numeric",
                                   "numeric",
                                   "numeric"))
dados1 <- filter(dados1, Parasiterichness != "NA")
```

```
hist(dados1$Parasiterichness)
hist(dados1$Prevalence)
hist(dados1$Hostrichness)
hist(dados1$migrantspecies)
hist(dados1$Temp)
hist(dados1$Prec)
hist(dados1$n_migrants)

teste <- brm(Parasiterichness~TotaldeAves + Prevalencia + (1|Bioma) + (1|Locality),
             data = dados1,
             family = negbinomial(),
             chain = 4, iter = 4000)
summary(teste)

teste2 <- brm(Parasiterichness~TotaldeAves + log1p(Temp) + (1|Bioma) + (1|Locality),
             data = dados1,
             family = negbinomial(),
             chain = 4, iter = 4000)
summary(teste2)

teste3 <- brm(Parasiterichness~TotaldeAves + Prec + (1|Bioma) + (1|Locality),
             data = dados1,
             family = negbinomial(),
             chain = 4, iter = 4000)

summary(teste3)

teste4 <- brm(Parasiterichness~TotaldeAves + log1p(n_migrants) + (1|Bioma) + (1|Locality),
             data = dados1,
             family = negbinomial(),
             chain = 4, iter = 4000)
```

```
summary(teste4)

teste5 <- brm(Parasiterichness~TotaldeAves + RiquezadeHospedeiros + (1|Bioma) + (1|Locality),
              data = dados1,
              family = negbinomial(),
              chain = 4, iter = 4000)

summary(teste5)

variaveis <- bf(Parasiterichness~TotaldeAves + migrantspecies + Prevalencia +
                  (1|Bioma) + (1|Locality), family = negbinomial())

prior <- get_prior(variaveis, data = dados1)
prior

model <- brm(Parasiterichness~TotaldeAves + migrantindividuals + migrantspecies + Parasiterichness +
(1|Bioma) + (1|Locality),
             data = dados1,
             family = negbinomial(),
             chain = 4, iter = 4000,
             prior = c(
               prior(student_t(3, 1.1, 2.5), "Intercept"),
               prior(student_t(3, 0, 2.5), "sd" ),
               prior(gamma(0.01, 0.01), "shape")
             )
)

summary(model)
plot(model, N = 4, ask = FALSE)

plot1 <- plot(conditional_effects(model), points = FALSE, theme = a)
a <- theme(panel.grid.major = element_blank(), panel.grid.minor = element_blank(),
           panel.background = element_blank(), axis.line = element_line(colour = "black"))
```

```
plot2 <- plot1$migrantindividuals + labs(x = "Proportion of migrant individuals", y = "Number of Infections")
+ coord_cartesian(ylim = c(0, 15)) #caption = "Plasmodium")

+ geom_boxplot(aes(color = migrantindividuals))

plot2


res1 <- residuals(model)

res1 <- as.data.frame(res1)

dados1$residuals <- res1$Estimate

dados1$residuals <- as.numeric(dados1$residuals)


dados1a <- as.matrix(dist(cbind(dados1$Longitude, dados1$Latitude)))

dados1b <- 1/dados1a

diag(dados1b) <- 0

dados1b <-ifelse(dados1b=="Inf",0,dados1b )


dados1b[1:5, 1:5]


Moran.I(dados1$residuals, dados1b, na.rm = TRUE)
```

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. 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 (i) in both migrants and residents, and (ii) 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 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

24 demonstrate migrants enhance pathogens spread and their presence may influence parasite
25 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). 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 (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, 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.

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 et al., 2019; 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 *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 Bell et al. 2015, Fallon et al. 2003 and Hellgren et al. 2004. 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 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,

140 therefore, we incorporated avian phylogeny in the second Bayesian model. All Bayesian
141 models were checked for chain convergence using "plot" function in R.

142

143 *Bayesian models*

144 To determine whether migratory birds spread parasite lineages along their migratory
145 routes and to evaluate the parasite connectivity among localities due to migratory behavior,
146 we used multi-level modeling (MLM) with the "brms" package (Bürkner 2017) to evaluate
147 the geographical range in which each haemosporidian lineage occurred depending on
148 whether they were found only in resident birds or in both residents and migrants. We used
149 Bayesian modelling as it allows to statistically estimate the geographical range among which
150 lineages are distributed according to their host migratory status. Naturally, for parasites to be
151 dispersed by migrant hosts, they need not only to be moved around by migratory hosts, but
152 also infect the resident community. Hence, we compared the geographic range of parasites
153 found in resident birds only with that of parasites shared by resident and migratory host
154 species. However, for this last group, we discarded all localities where lineages were found
155 infecting only migrant hosts since only when the parasite is also present in the resident
156 community would there be real evidence of parasite dispersal.

157 To understand the variation of geographical range (estimated by minimum spanning
158 tree distance - i.e., shortest total distance of all lines connecting each locality where a lineage
159 was found, see supplementary material) among haemosporidian lineages, we built a model
160 including the migratory status of hosts used by a lineage. We ran a model comparing lineages
161 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 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 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,

185 we calculated the proportion of migrant individuals in an area based on the data on captured
186 birds in our dataset, and calculated local parasite richness across all birds in an area
187 independently of their migratory category.

188 We initially evaluated if host richness (i.e., number of bird species sampled per
189 locality), local parasite richness, proportion of migratory species, number of migrant
190 individuals, temperature and precipitation had significant effects on prevalence. Following
191 these analyses, only parasite richness was retained as fixed factors since we did not detect
192 any influence of the other factors on parasite infections. The negative binomial distribution
193 was applied in this model to account for the overdispersion of prevalence data, thus avoiding
194 production of biased estimates. We used 4 chains with MCMC 4000 total iterations per chain
195 (2000 for warmup interactions, 2000 for sampling). Further, we considered biome and
196 locality ID as random variables. Also, we created a matrix with phylogenetic distances
197 between species and added as random variable in the model to account for possible
198 phylogenetic influence on parasite infections. The model results were plotted using the
199 "conditional_effects" function to visualize the predictions based on the independent variable.
200 Moran's I value was checked for model residuals. Again, we ran three models: one for all
201 two parasite genera combined, one for *Plasmodium* lineages only, and one for *Haemoproteus*
202 lineages only; in these last two models we fitted the data to a zero inflated negative binomial
203 distribution.

204 Another Bayesian model was performed to estimate whether localities with more
205 migratory birds have greater richness of haemosporidian lineages. We considered parasite
206 richness as our dependent variable and proportion of migratory individuals per locality (N=63
207 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 4 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.

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 remaining mostly belonging to the orders Columbiformes, Piciformes and Apodiformes. Haemosporidian lineages occurred in anywhere from one to 38 localities, with many of them

231 (15%) occurring in multiple biomes. Only 175 out of 675 lineages were observed in two or
232 more localities and were used to estimate lineage spread in our analyses, besides, 426 linages
233 were singletons. All models presented well converged chains.

234 Our first Bayesian model analyses revealed that lineages shared by migrants and
235 residents showed the broadest geographical range (Figure 2, Table 1). Lineages shared by
236 resident and any type of migrant species presented a geographical range almost 50% greater
237 than that of lineages occurring only in resident species. More specifically, we observed
238 distinct patterns of distribution for *Plasmodium* and *Haemoproteus* lineages. For
239 *Plasmodium* linages shared by residents and migrants were also more spatially widespread,
240 whereas for *Haemoproteus* no difference in geographical range was observed between
241 lineages found in residents only and those shared by residents and migrants (Figure S1,
242 Figure S2, Table S2 and Table S3). It is important to notice that similar patterns regarding
243 parasite geographical range was also observed when plotting data from our raw dataset
244 (Figure S3-5).

245 Our next Bayesian model analysed the relationship between local number of infected
246 birds and the proportion of migratory bird individuals in the local avian community. We
247 observed no correlation between the relative occurrence of migrants and number of infected
248 hosts (Figure S6, Table S4). However, when we repeated the analysis separately for only
249 *Plasmodium* or *Haemoproteus* lineages, we observed negative and positive relationships
250 between the number of infections per locality and local proportion of migrants in an area,
251 respectively (Figure 3, Table 2 and 3). Parasite richness had a significant positive association
252 with the local number of infected birds, whether when considering all haemosporidian
253 lineages (Table S4), 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, Figure 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 (Table S6 and S7). 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 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 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

277 the ecology and evolution of haemosporidian dispersal in South America leading to an
278 increase in parasite spread and influencing parasite prevalence and composition. In addition,
279 we also demonstrate that generalist parasites may be more successful in colonizing new
280 regions since parasites that infected both residents and migrant hosts had broader geographic
281 distributions.

282 Dispersal of haemoporidians might be an important step toward parasite
283 diversification for local community composition since parasites, after establishing in new
284 regions, can evolve into new and distinct parasite lineages (Ellis et al. 2019, Fecchio et al.
285 2019a). Indeed, Ellis et al. (2019) found that South America presents high rates of parasite
286 diversification, with the greatest proportion of sympatric nodes for *Plasmodium* spp. and one
287 of the greatest *Haemoproteus* diversification rates. Hence, considering the potential
288 contribution of migrant birds toward parasite dispersal, these hosts might play a fundamental
289 role in parasite evolution and diversification in South America. Indeed, many species migrate
290 in between the breeding season and relapses (increases in parasite intensity circulating in the
291 host) mainly occur after this period (Valkiūnas 2005), thus facilitating parasite dispersal to
292 new regions. However, we did not observe a clear relation between the presence of migrant
293 birds and local haemosporidian prevalence since our data suggest that *Plasmodium* and
294 *Haemoproteus* parasites respond differently to the presence of migrant hosts. The fact that
295 most of our lineages were observed only in resident birds could explain the lack of a
296 relationship between avian migrants and general haemosporidian prevalence, since the
297 greatest haemosporidian diversity occurs in resident avian species. However, Hellgren et al.
298 (2007) also suggest that new haemosporidian introductions into resident bird faunas are not
299 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. 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 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

346 in Tropical Andes birds. Further, Fecchio et al. (2019a) also suggested that historical
347 processes, such as host speciation, are also key drivers of haemosporidian diversity in South
348 America. However, present-day environmental factors, mainly precipitation patterns, may be
349 important for host range expansion across regions in haemosporidian parasites, as these
350 vector-transmitted parasites exhibit greater host specificity in localities with pronounced
351 seasonality and wetter dry seasons (Fecchio et al. 2019b). Thus, it seems other processes
352 (apart from parasite dispersal through migrants) might also be important in determining
353 parasite richness and prevalence in South America.

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

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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: 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 4: Predicted model relationship (±95% confidence intervals) between local haemosporidian richness and proportion of migrants in an area.

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