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Can migratory birds spread avian haemosporidian parasites?

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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. Here, we hypothesize and aim to evaluate if (1) migratory birds spread parasite lineages along their routes, and (2) localities crossed by more migratory birds have greater prevalence and richness of haemosporidians. For the first hypothesis, we tested whether parasite lineages found (i) only in migratory birds, (ii) in both migrants and residents, and (iii) only in residents, differ in their frequencies of occurrence among localities. For the second hypothesis, we tested for a relationship among localities between the overall local haemosporidian parasite richness and prevalence, and the proportion of migratory bird individuals present in a locality. We combined a dataset on 13200 bird samples with additional data from the MalAvi database (total: ~2800 sequenced parasites comprising 675 distinct lineages, from 506 host species and 156 localities) from South America, and used Bayesian multi-level and mixed models to test our hypotheses. We demonstrate that parasites shared between resident and migratory species are the most spatially widespread, highlighting the potential of migrants to carry and transmit haemosporidians. Further, the presence of migrants in a locality was negatively related to local parasite richness, but not associated with local prevalence. Here, we confirm that migrants can contribute to parasite dispersal and visiting migrants are present in regions with lower Plasmodium prevalence. Also, we observed their presence might raise Haemoproteus community prevalence. Indeed, migrants may decrease the richness of avian haemosporidians, probably due to local constraints on transmission. Therefore, we demonstrate migrants enhance pathogens spread and their presence may influence parasite community transmission.

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constraints on transmission. Therefore, we demonstrate migrants enhance pathogens spread and their presence may influence parasite community transmission.

1.Introduction

Migration has an important impact on the transmission of disease across the world as migrant species disperse pathogens and parasites between localities, while also being exposed to more infectious agents (Bartel et al. 2011, Bauer and Hoye 2014, Teitelbaum et al. 2018). In this way, migrant species might play an important role in the evolution and distribution of parasites and promote the spread of pathogens to new areas and new hosts species. At the same time, human-introduced pathogens and host species can decrease the fitness and survival of resident and native host species, compromising the population abundance of local species and reducing community richness (Callaway and Ridenour 2004, Prenter et al. 2004). Conversely, the spread of pathogens might increase host richness by reducing local competition pressures and, consequently, preventing competitive exclusion. Hence, pathogen spread might act as an environmental filter to new species colonization. Recent studies have demonstrated that migratory birds harbor a greater diversity of parasites than resident species (Koprivnikar and Leung 2015, Gutiérrez et al. 2019). In addition, several studies have documented the influence of migratory birds on the spread of important pathogens (Morshed et al. 2005, Hellgren et al. 2007, Ricklefs et al. 2017) with some of these able to infect humans (Morshed et al. 2005, Poupon et al. 2006, Lindeborg et al. 2012). Thus, the migratory behavior of birds may directly influence host local richness and population size, as well as the local richness of parasite species.

Avian malaria parasites and related haemosporidians could be used as geographical markers for migratory birds (Marzal 2012). Previous research has demonstrated differences in the timing of the main occurrence of haemosporidian infection in migrating birds. These studies have suggested that differences in haemosporidian lineages harbored could indicate

whether birds had become infected in different areas (Marzal 2012). Since most haemosporidians cause life-long infections (Valkiūnas 2005), parasites may travel across long distances with their bird host during migration, allowing them to infect new vectors and new avian hosts in novel environments. Indeed, migratory species are known for their potential to connect distant habitats and transfer large amounts of biomass, nutrients and other organisms between ecosystems (Bauer and Hoye 2014). Furthermore, O'Connor et al. 2020 have demonstrated that migratory birds do not possess higher immune gene richness in wetter areas, which jointly with temperature is one of the main climatic factors that influence haemosporidian prevalence (Illera et al. 2017). Therefore, migratory birds may be more susceptible to pathogens in those regions. For this reason, it might also be expected that migratory birds harbor a more diverse range of parasites and might be more susceptible to parasite infections.

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

Furthermore, the great avian richness (~3500 species) and abundance in South America (Remsen et al. in press) could also enhance the probability of parasite host-shifting between

72 migratory and resident birds, given the likely presence of susceptible birds in any particular
73 area. Besides that, the great richness and abundance of vectors (Consoli and Oliveira 1994,
74 Santiago-Alarcon et al. 2012a) could also increase the chances of host-shifting between
75 migratory and resident birds as it increases the chances of compatible vectors being present
76 in any given locality. These features make the South American avian haemosporidians a great
77 model system to investigate the putative transmission of pathogens via host migration in
78 nature.

79 In this context, the main goal of this study is to evaluate the influence of migratory
80 birds on the spread of haemosporidian parasites in South America. Specifically, we evaluated
81 the hypothesis that (1) migratory birds spread parasite lineages along their migratory routes,
82 and (2) localities crossed by more migratory routes have greater prevalence and richness of
83 haemosporidian lineages. For the first hypothesis, we tested whether parasite lineages found
84 (i) in both migrants and residents and (ii) only in residents, differ in their geographical range.
85 Due to the fact migrants can carry parasites from many sites and potentially infect resident
86 birds, we predicted that parasite lineages using migratory birds should occur across a greater
87 spatial range than those using only resident birds. Moreover, migration behavior increases
88 the exposure of birds to more parasite lineages and hence their contact with different parasites
89 as migrants are present in regions that harbor different parasite communities. Therefore, we
90 expect higher haemosporidian richness and prevalence in regions with more migratory birds.
91 For the second hypothesis, we tested for a relationship among localities between the overall
92 local haemosporidian parasite richness and prevalence, and the proportion of migratory birds
93 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 916 species from 63 different localities sampled from 2005 to 2018 in South America, with a subset of those samples previously used in Fecchio, Bell, et al., 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 one of these three genera: *Plasmodium*, *Haemoproteus* and *Leucocytozoon*). Each locality was assigned to a biome based on the classification of Turchetto-Zolet et al. 2013. The parasite prevalence per bird species and locality was estimated using PCR diagnostic protocols described by Hellgren et al. 2004, Fallon et al. 2003, and Bell et al. 2015. The parasite lineages were sequenced by the PCR protocol described by Hellgren et al. 2004 and identified by comparing the sequences with the ones deposited in MalAvi and GenBank (https://www.ncbi.nlm.nih.gov/genbank/). This protocol produces a *cyt b* fragment of 478 bp. The birds present in each locality were

117 classified into three ecological classes: (1) resident; (2) partial migrant and (3) full migrant,
118 according to the Brazilian Committee of Ornithology Records - CRBO 2014, Somenzari et
119 al. 2018 and BirdLife International (https://www.birdlife.org/).

120

121 **2.2 Statistical Analyses**

122 All analyses were conducted in R version 4.02 (R Core Team, 2019). Aiming to
123 evaluate the potential impact of locality, avian phylogenetic relationships and climate in our
124 models, we calculated spatial autocorrelation, phylogenetic signal and extracted climate data
125 from Worlclim (see supplementary material). The spatial autocorrelation analyses revealed
126 there was no substantial effect of space on parasite richness (Moran Index = -0.0007),
127 however, for prevalence, we observed a Moran Index of 0.15 which differed from the null
128 expectation. For this reason, biome and locality ID were used as nested random effects in our
129 second Bayesian and mixed models to control for idiosyncratic characteristics of localities.
130 Likewise, considerable phylogenetic signals were observed among birds for prevalence
131 (Pagel's lambda = 0.49) and parasite richness (0.17) and, therefore, we incorporated avian
132 phylogeny in the second Bayesian model.

133

134 *Bayesian models*

135 In order to determine whether migratory birds spread parasite lineages along their
136 migratory routes and to evaluate the parasite connectivity among localities due to migratory
137 behavior, we used multi-level modeling (MLM) with the "brms" package (Bürkner 2017) to
138 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 decided to use Bayesian modelling as it allows to statistically estimate the geographical range among which lineages are distributed according to their host 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 accounted only for the localities where lineages were infecting both resident and migrant hosts as only when the parasite is also present in the resident community is there 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 decided to build a single model including the migratory status of hosts used by a lineage (categorical variable with four levels: resident, partial migratory and resident, full migratory and resident, and both partial/full migratory and resident; reference category = resident) while also controlling for sample size (i.e. number of birds positive for that lineage) and number of host species used by a lineage. We also performed a second model comparing lineages present in resident birds only and lineages present in residents plus any migratory category. Geographical range was the response variable and migratory status of hosts used by a lineage was the independent variable. We chose our priors using the "get_prior" function. As our response variable had a continuous but skewed distribution, we applied the Gamma distribution family, using 4 chains with MCMC 4000 total iterations per chain (2000 for warmup, 2000 for sampling). The model results were plotted using the "conditional_effects" function to visualize the

predicted geographical range as a function of the host migratory status. We ran three models per analyses: one for all three parasite genera combined, one for *Plasmodium* lineages only, and one for *Haemoproteus* lineages only.

Next, we analysed the prevalence of infection in each bird species among localities, to test whether haemosporidian prevalence is generally higher in localities with more migratory birds. For this, we considered the local number of infected individuals out of the total sample per locality as our dependent variable, and local proportion of migratory bird 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. We initially evaluated if host richness (i.e., number of bird species sampled per locality, log-transformed scaled value), local parasite richness (log-transformed scaled value), proportion of migratory species (log-transformed scaled value), number of migrant individuals (log-transformed scaled value), temperature (log-transformed scaled value) and precipitation had significant effects on bird prevalence. Following these analyses, only the proportion of migratory bird individuals and parasite richness were retained as fixed factors. In addition, we used only our original dataset and excluded the data from the MalAvi database, since the latter presents only positive and sequenced samples. Thus, our analyses were based in 142 bird species distributed among 63 localities. Also, in this model, we grouped the dataset per bird species and localities and we filtered our data in order to include only species with 10 or more bird individuals analysed. The negative binomial distribution was applied in this model to account for the overdispersion of prevalence data, thus avoiding production of biased estimates. We used 4 chains with MCMC 4000 total iterations per chain (2000 for warmup interactions, 2000 for sampling). Further, we considered biome and locality ID as nested random variables

and also used the function "cov_ranef" to account for phylogenetic influence. The model results were plotted using the "conditional_effects" function to visualize the predictions based on the independent variable. Again, we ran three models: one for all three parasite genera combined, one for *Plasmodium* lineages only, and one for *Haemoproteus* lineages only; in these last two models we fitted the data to a zero inflated negative binomial distribution.

Mixed model

A mixed model was performed to estimate whether localities with more migratory birds have greater prevalence and richness of haemosporidian lineages. We considered parasite richness as our dependent variable and proportion of migratory individuals per locality (N=63 localities) as our and independent variable. Here, we also used only our original dataset, not data from the MalAvi database, because our dataset provides more information regarding the localities, such as prevalence data and host richness. We firstly tested our variables for normal distribution and created models including variables that presented an effect on our dependent variable, and then selected the best model among them using the Akaike information criterion (AIC). We used generalized linear mixed model applying the "glmer" function from the "lme4" package (Bates et al. 2015) with a Poisson distribution. We considered local host richness (log-transformed scaled value), prevalence across all birds sampled (log-transformed scaled value), proportion of migratory species (log-transformed scaled value), number of migrant individuals (log-transformed scaled value), temperature (log-transformed scaled value) and precipitation as fixed variables. Biome and locality ID were set as random intercept. We ran three models: one for all three parasite

208 genera combined, one for *Plasmodium* lineages only, and one for *Haemoproteus* lineages
209 only.

210

211 **3. Results**

212 Out of the 914 bird species considered in the analyses, 862 were classed as residents,
213 and 32 as partial, 12 as full migrants. Most species (86%) were passerines, with the rest
214 mostly belonging to the orders Columbiformes, Piciformes and Apodiformes.
215 Haemosporidian lineages occurred in anywhere from one to 38 localities, with many of them
216 (15%) occurring in multiple biomes. Only 175 lineages were observed in two or more
217 localities and were used to estimate lineage spread in our analyses, besides, 426 linages were
218 singletons.

219 Our first Bayesian model analyses revealed the lineages shared by resident and full
220 migratory species only are the most widespread spatially, as they occupy a broader
221 geographical range. Further, we observed that the lineages shared among residents and other
222 type of migrants (partial migrant and partial plus full migrant) are as widely distributed as
223 the lineages present in only resident hosts (Figure 2, Table 1). However, when analysing
224 both parasite genera separately no difference was observed in the geographical range of
225 lineages with different types of bird hosts (Figure S1, Figure S2, Table S2 and Table S3).
226 Nevertheless, when repeating these analyses grouping lineages as those found only in
227 residents, versus those found in residents as well as any type of migrants, we observed
228 lineages shared by migrants and residents showed the broadest geographical range (Figure 3,
229 Table 2). More specifically, we observed distinct patterns of distribution for *Plasmodium* and
230 *Haemoproteus* lineages. For *Haemoproteus*, no difference in geographical range was

231 observed between lineages found in residents only and those shared by residents and
232 migrants, while for *Plasmodium* linages shared by residents and migrants were more spatially
233 widespread (Figure S3, Figure S4, Table S4 and Table S5).

234 Our next Bayesian model analysed the relationship between local number of infected
235 birds and proportion of migratory bird individuals in the local avian community. We
236 observed no correlation between the relative occurrence of migrants and number of infected
237 hosts (Figure S5, Table S6). However, when we repeated the analysis separately for only
238 *Plasmodium* or *Haemoproteus* lineages, we observed negative and positive relationships
239 between local percent of migrants and number of positive birds per locality, respectively
240 (Figure 4 and 5, Table 3 and 4). Parasite richness had a significant positive effect on local
241 number of infected birds, whether when considering all haemosporidian lineages (Table S6),
242 or only *Haemoproteus* lineages (Table 4).

243 Our mixed model examining the influence of migrants on parasite richness revealed
244 no effect of the proportion of migrants in the local community considering both
245 haemosporidian genera together (Figure 6, Table 5). The Akaike information criterion
246 revealed that the best model set considered only local host richness, prevalence across all
247 birds sampled, proportion of migratory species, number of migrant individuals and
248 temperature as fixed factors (Table S7). However, we observed a negative relation between
249 the proportion of migratory species and parasite richness. Further, we also observed no effect
250 of the proportion of migratory bird individuals on local parasite richness for *Plasmodium* and
251 *Haemoproteus* infections when the two genera were treated separately (Figure S6 and S7,
252 Table S8 and S9). Further, the proportion of migratory species was also negatively correlated
253 to *Haemoproteus* lineage richness, with the total number of migrants showing the opposite

pattern. Moreover, we observed positive effects on parasite richness of two other predictors in all models: local host richness and overall local prevalence.

4. Discussion

Animal migrations can play important roles in both the geographical dispersal of disease agents, and in the local epidemiology of diseases for both resident and migratory species (Bradley and Altizer 2005, Bauer and Hoye 2014, Teitelbaum et al. 2018). Here, we demonstrated that migratory birds may disperse parasite lineages through their migratory routes, such that lineages infecting both migrants and residents are more widespread. Despite migration leading to lineages dispersing across South America, we did not observe higher prevalence of infection in localities with higher proportions of migratory birds. Nevertheless, we observed different patterns for *Plasmodium* and *Haemoproteus* parasites, such that *Plasmodium* prevalence negatively correlated with an increasing proportion of migrants, whereas *Haemoproteus* prevalence was higher in the presence of migrants. Moreover, haemosporidian richness decreased as the proportion of migratory species rose across localities. However, parasite richness also seems to be positively related to local host richness and prevalence. Thus, migrant birds could potentially influence the ecology and evolution of haemosporidian dispersal in South America leading to an increase in parasite spread and influencing parasite prevalence, composition and richness.

Further, parasites infecting only resident and partial migrant or full and partial migrant birds occurred across a similar geographical range as those infecting only resident avian hosts. We believe insufficient sampling of certain migrant avian species in many areas

276 could have led to the limited geographical range in which lineages infecting only resident
277 and partial and full and partial migrant birds were found. In addition, we also demonstrate
278 that generalist parasites may be more successful in colonizing new regions since parasites
279 that infected both residents and migrant hosts had broader geographic distributions.

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

299 Therefore, it seems environmental and host features could be more important in determining
300 local parasite richness than dispersal patterns.

301 It is worth mentioning that distinct parasite taxa can respond differently to the
302 presence of migrant hosts. As we reported in this study, despite the fact no relation was
303 observed for general haemosporidian prevalence, *Plasmodium* and *Haemoproteus* showed
304 contrasting responses to an increase in the local proportion of migrant individuals. Whereas
305 *Plasmodium* prevalence was negatively correlated with an increase of migrants in the local
306 bird community, we observed a rise in *Haemoproteus* infections. Such behavior illustrates
307 that different pathogens do not respond identically to host migratory behavior. Indeed,
308 previous research has documented different effects of host migration on parasite-host
309 dynamics (Hellgren et al. 2007, Koprivnikar and Leung 2015, Teitelbaum et al. 2018). This
310 distinct pattern for haemosporidians can occur due to the fact haemosporidians are vector-
311 borne parasites whose vectors differ between parasite genera. Thus, the broad host
312 preferences of *Haemoproteus* vectors (Santiago-Alarcon et al. 2012b) could explain the
313 increase in parasite prevalence observed for this genus as the chance of parasite transmission
314 between hosts should increase for parasites vectored by highly generalist hosts. On the other
315 hand, migrant birds might choose localities with lower prevalence of *Plasmodium* parasites,
316 which explains the pattern found in this study.

317 We also demonstrated that where the proportion of migrant species in a community
318 is higher, local haemosporidian richness is lower. In fact, migration often allows species to
319 escape environments that present higher risks of infection, a mechanism that could decrease
320 infection levels and favor the evolution of less-virulent pathogens (Altizer et al. 2011, Poulin
321 et al. 2012, Satterfield et al. 2015). This could lead to reduced haemosporidian richness in

localities with higher proportions of migrant species since long-distance migratory behavior can remove infected individuals from bird communities, as diseased animals are less likely to successfully migrate because of the physiological requirements of migration and the energetic costs of disease (Bradley and Altizer 2005, Altizer et al. 2011). However, Hahn et al. (2018) experimentally verified that low intensity haemosporidian infections do not affect the capacity of birds to migrate, thus, most infected birds could still migrate and potentially spread their parasites into new areas. Meanwhile, the fact that migration filters out highly and moderately infected birds, which are the most likely to infect new vectors (Pigeault et al. 2015), allows community prevalence and parasite richness to remain low. At the same time, it is also possible migrant birds select localities with lower parasite richness. Certainly, further research will be required to confirm the importance of migratory behavior in modulating haemosporidian community richness.

Previous studies have tried to explain parasite species assembly patterns globally and also specifically in South America (Clark et al. 2014, Fecchio et al. 2019a). These authors have reported that South America presents the greatest diversity of *Plamodium* and *Haemoproteus* parasites on the globe; indeed, Fecchio et al. (2019a) have proposed parasite dispersal as one of the main processes driving parasite diversity in this region. In contrast, we detected a negative effect on parasite richness in regions with greater proportions of migrant species, while host richness and prevalence seem to be the main factors that positively drive parasite diversity. Also, we did not observe a clear relationship between migratory behavior and prevalence. Recently, Barrow et al. (2019) suggested that susceptibility to haemosporidian infection is partially driven by conserved, latent aspects of anti-parasite defense, and that prevalence of infection is strongly linked to avian phylogeny

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

353 In summary, we demonstrated that South American migrant birds play a moderate
354 role in parasite dispersal and, consequently, in their evolution and diversity. Further, as
355 observed by Ricklefs et al. (2017), most haemosporidian lineages are not shared between
356 resident and migrant species, indeed, most of our parasite lineages were observed only in
357 resident birds, demonstrating that resident host species harbor the greatest parasite richness
358 in our study system. We also demonstrated that, despite the fact 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 appear to select bird communities with lower parasite prevalence and
363 richness in our study system, as their presence seems to be related to lower community-wide
364 haemosporidian richness and *Plasmodium* prevalence. By comparing the distribution of
365 different pathogen lineages, our analyses demonstrate that migrant hosts can carry
366 haemosporidians and possibly other pathogens throughout their migration routes, thereby
367 contributing to the spread of disease on a continental scale.

368

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468

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

471 Figure 2: Mean (±confidence intervals) geographical range in kilometers in which
472 haemosporidian lineages are detected according to the type of birds in which they are found.

M = full migratory, PM = partial migratory, R = resident, R_M = resident and full migratory, R_PM = resident and partial migratory and R_PM_M = resident, partial migratory and full migratory. Number of lineages in each of the four categories are shown on the graph.

Figure 3: Mean (±confidence intervals) geographical range in kilometers in which haemosporidian lineages are detected according to the type of birds in which they are found. Number of lineages in each of the two categories are shown on the graph.

Figure 4: Predicted model relationship (±95% confidence intervals) between local number of infections of *Plasmodium* parasites and proportion of migratory host individuals per locality. We observed negative effect of the proportion of migratory individuals on number of infected birds.

Figure 5: Predicted model relationship (±95% confidence intervals) between local number of infections of *Haemoproteus* parasites and proportion of migratory host individuals per locality. We observed positive effect of the proportion of migratory individuals on number of infected birds.

Figure 6: Parameter estimates relating to their influence on parasite richness. No correlation was found between the proportion of migratory individuals and haemosporidian richness.

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

	Estimate	Std. error	Conf. Inter (95%)	
Intercept	7.20	0.12	6.87	7.33
Resident and full migrant	0.54	0.29	0.00	1.13
Resident and partial migrant	0.29	0.24	-0.17	0.79
Resident, partial and full migrant	0.53	0.41	-0.21	1.41
Number of bird individuals	0.00	0.01	-0.02	0.03
Number of host species per lineage	0.05	0.03	-0.01	0.11

494

495 Table 2: Parameter estimates, standard errors, and confidence intervals for the Bayesian
496 model testing the differences in the geographical range of haemosporidian lineages among
497 those that occur in migratory and/or resident avian host species. (Residents only = reference
498 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

499

500 Table 3: Parameter estimates, standard errors, and confidence intervals for the Bayesian
501 model testing the variation of local number of birds infected by *Plasmodium* as a function of
502 the proportion of migratory individuals out of all individual birds sampled per locality and
503 parasite richness.

	Estimate	Std. error	Conf. Inter (95%)	
Intercept	-0.47	0.77	-2.07	0.87
Proportion of migrant individuals	-2.78	1.40	-5.58	0.07
Parasite Richness	0.02	0.01	-0.01	0.04

Table 4: Parameter estimates, standard errors, and confidence intervals for the Bayesian model testing the variation of local number of birds infected by *Haemoproteus* as a function of the proportion of migratory individuals out of all individual birds sampled per locality and parasite richness.

	Estimate	Std. error	Conf. Inter (95%)	
Intercept	-2.37	0.84	-4.07	-0.76
Proportion of migrant individuals	6.78	2.30	2.40	11.37
Parasite Richness	0.04	0.02	0.01	0.07

Table 5: Parameter estimates, standard errors, z and p values for the mixed model testing the variation of local haemosporidian richness as a function of the proportion of migratory individuals out of all individual birds sampled per locality, as well as other predictors.

	Estimate	Std. error	Z	P
Intercept	-6.16	1.71	-3.60	<0.001
Proportion of migrant individuals	0.57	1.07	0.53	0.59
Host richness	0.92	0.12	7.87	<0.001

Prevalence	0.70	0.10	6.97	<0.001
Proportion of migrant species	-0.26	0.13	-2.03	0.04
Number of migrants	0.11	0.10	1.04	0.30
Temperature	0.62	0.32	1.95	0.05

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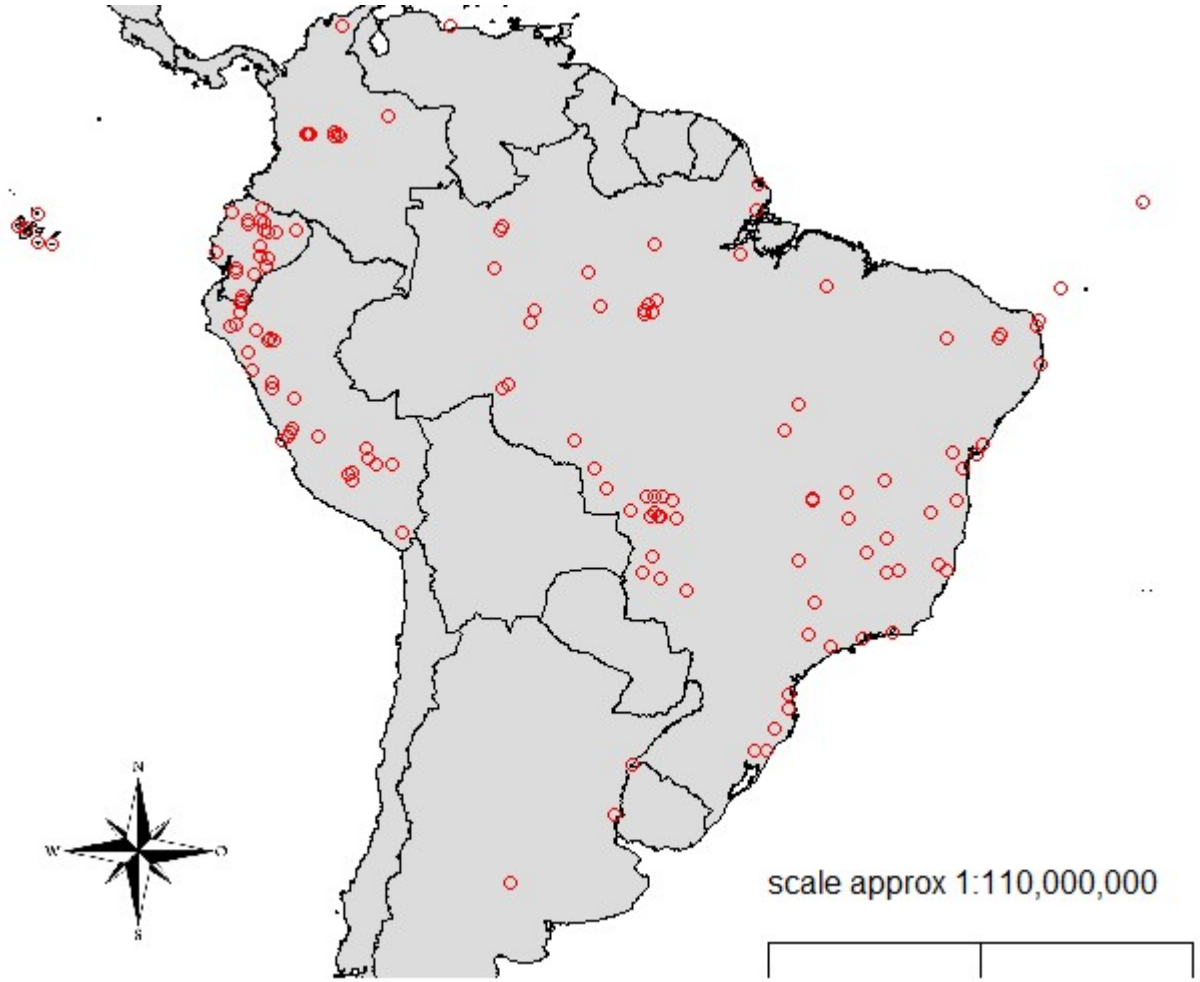
515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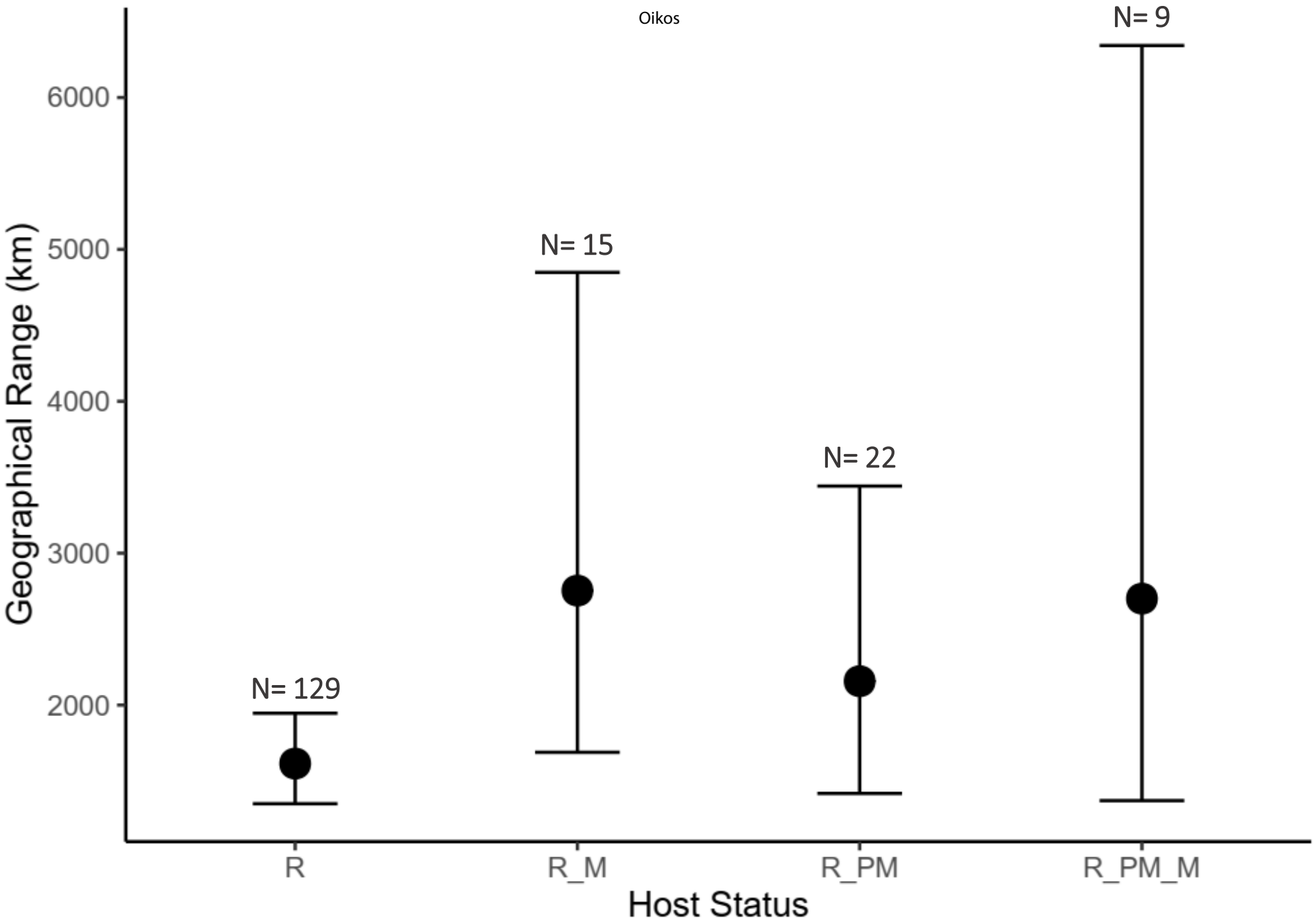
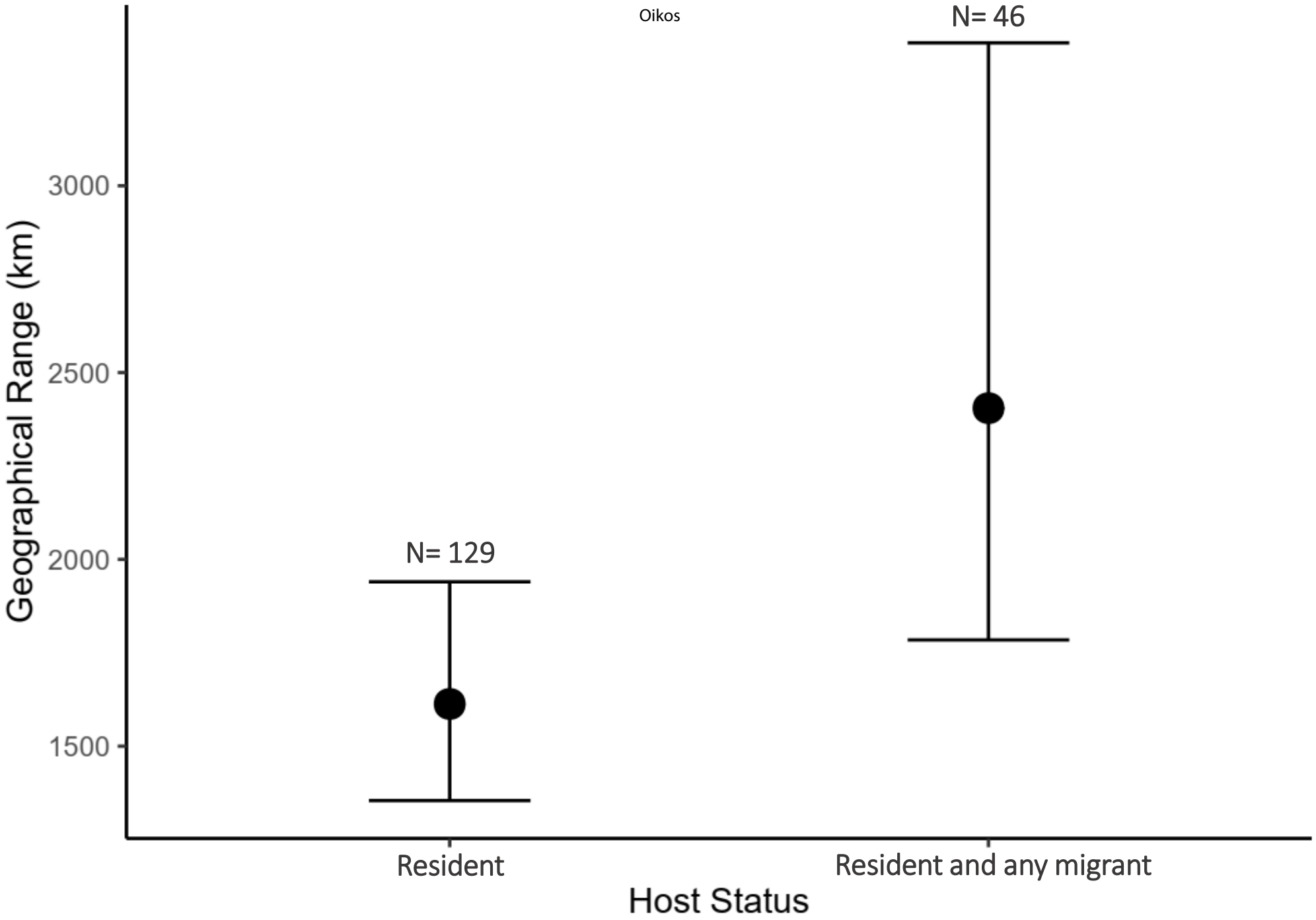
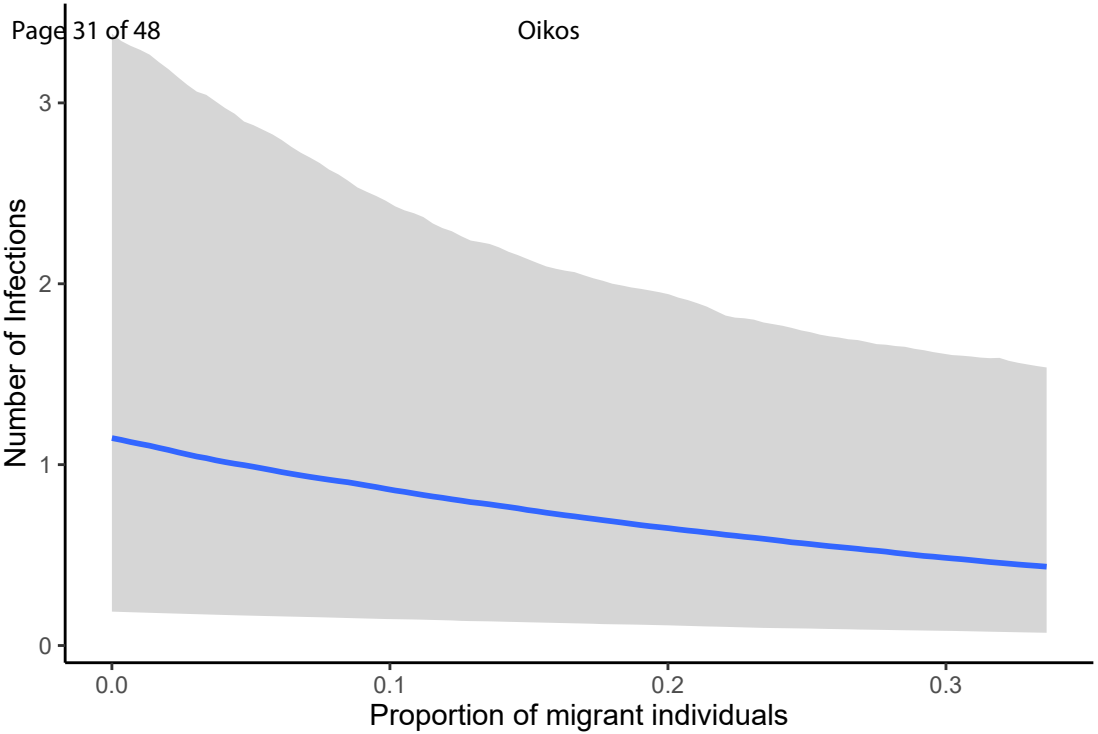
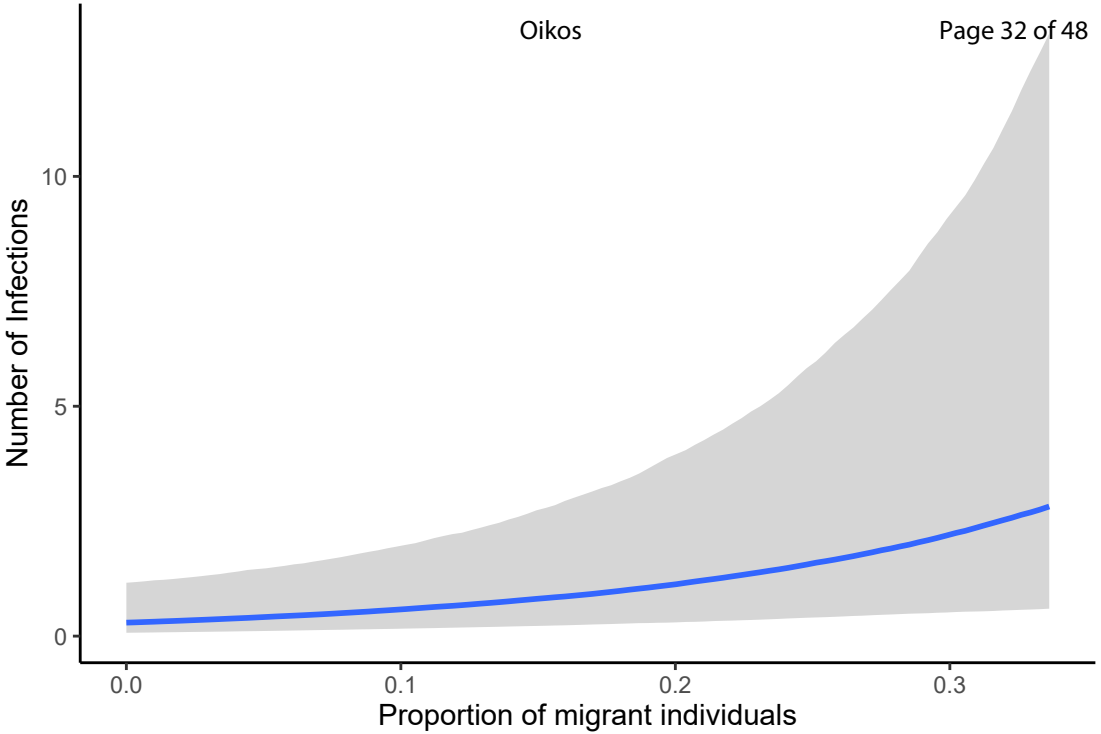

N= 9
6000
5000
N= 15
Geographical Range (km)
4000
N= 22
3000
N= 129
2000
R
R_M
R_PM
R_PM_M
Host Status

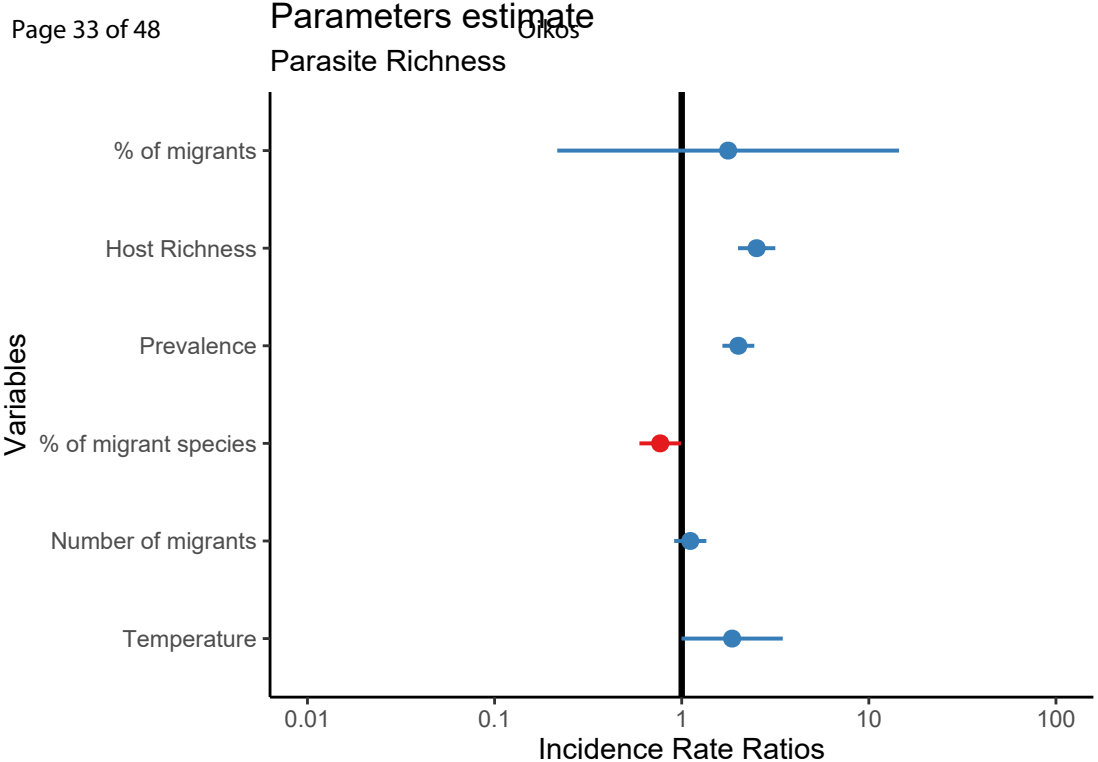

N= 46
3000
2500
2000
1500
Geographical Range (km)
N= 129
Resident
Resident and any migrant
Host Status


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

Plasmodium



Haemoproteus


Parameters estimate
Parasite Richness
% of migrants
Host Richness
Prevalence
% of migrant species
Number of migrants
Temperature
Variables
0.01
0.1
1
10
100
Incidence Rate Ratios

Can migratory birds spread avian haemosporidian parasites?

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	914					

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).

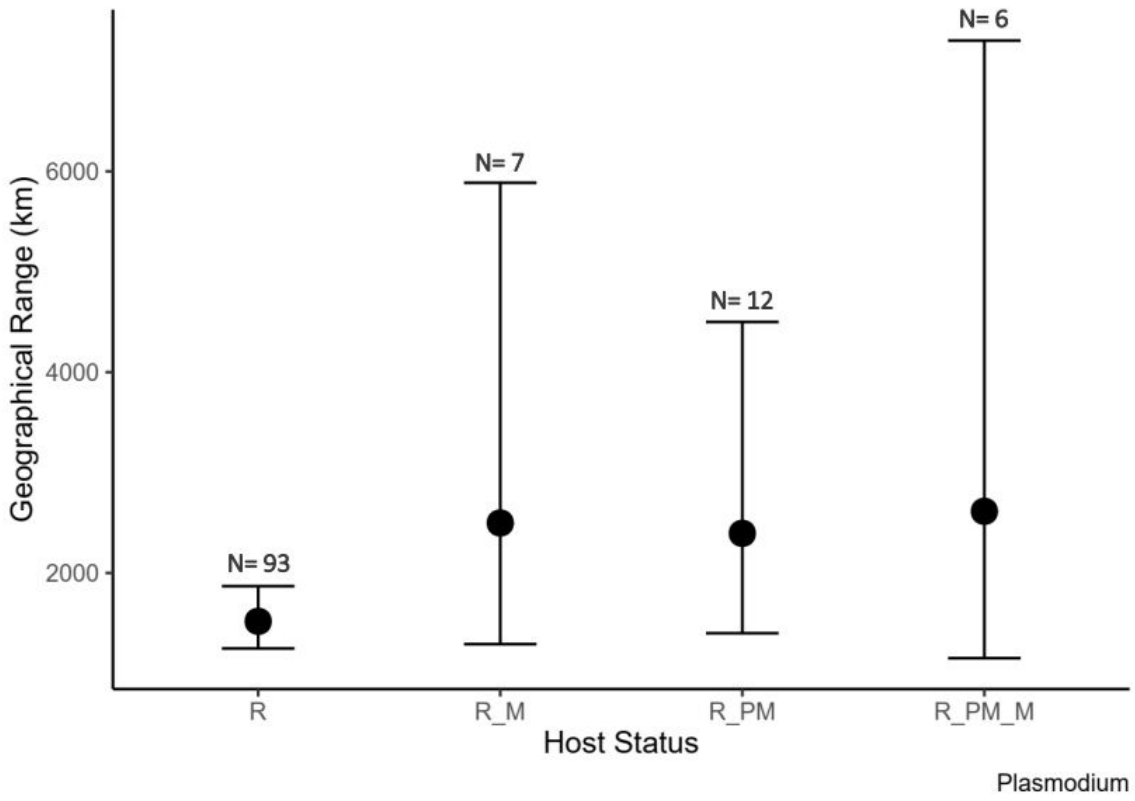
Climate variables

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.

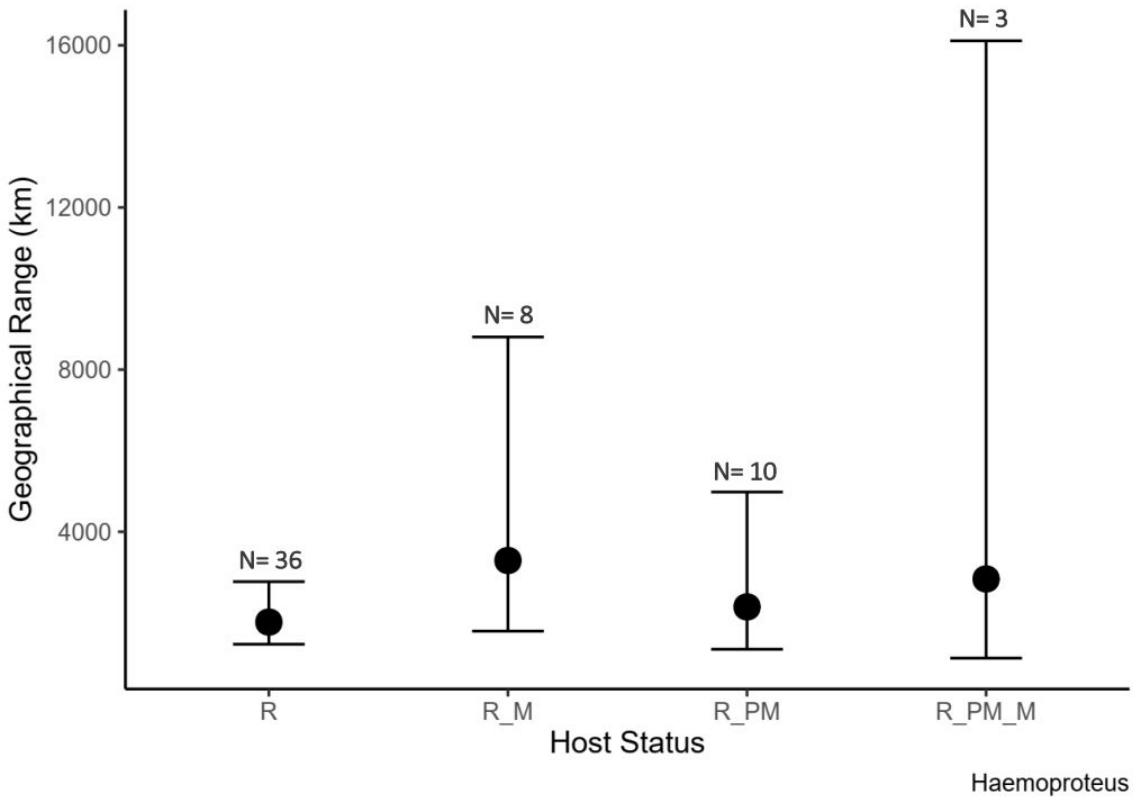
Supplementary Results



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. R = resident, R_M = resident and full migratory, R_PM = resident and partial migratory and R_PM_M = resident, partial migratory and full migratory. Number of lineages in each of the four categories are shown on the graph.

Supplementary Table 2: 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	6.96	0.14	6.69	7.23
Resident and full migrant	0.52	0.40	-0.20	1.39
Resident and partial migrant	0.47	0.32	-0.13	1.13
Resident, partial and full migrant	0.57	0.49	-0.32	1.60
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

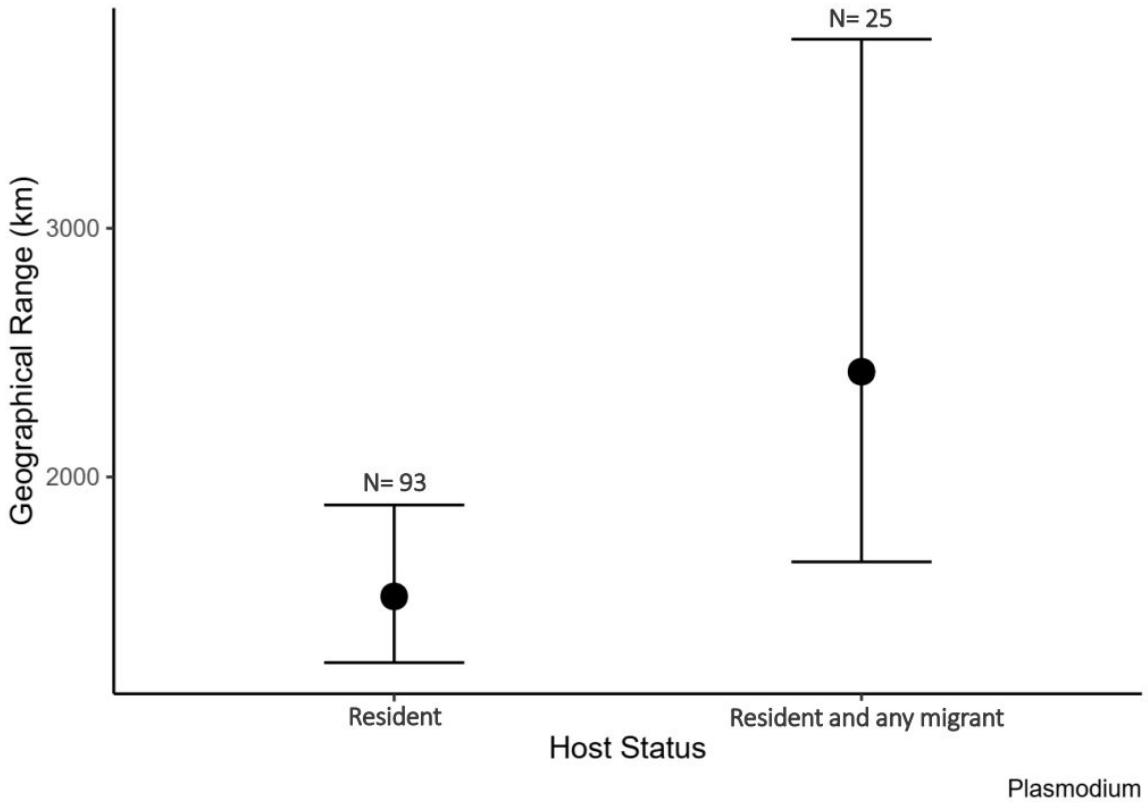


Supplementary Figure 2: Mean (±confidence intervals) geographical range in kilometers in which *Haemoproteus* lineages are detected according to the type of birds in which they are found. R = resident, R_M = resident and full migratory, R_PM = resident and partial

migratory and R_PM_M = resident, partial migratory and full migratory. Number of lineages in each of the four categories are shown on the graph.

Supplementary Table 3: 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	0.23	6.91	7.80
Resident and full migrant	0.64	0.50	-0.27	1.70
Resident and partial migrant	0.21	0.45	-0.65	1.13
Resident, partial and full migrant	0.57	0.79	-0.81	2.24
Number of bird individuals	0.01	0.02	-0.02	0.06
Number of host species per lineage	0.01	0.04	-0.07	0.10



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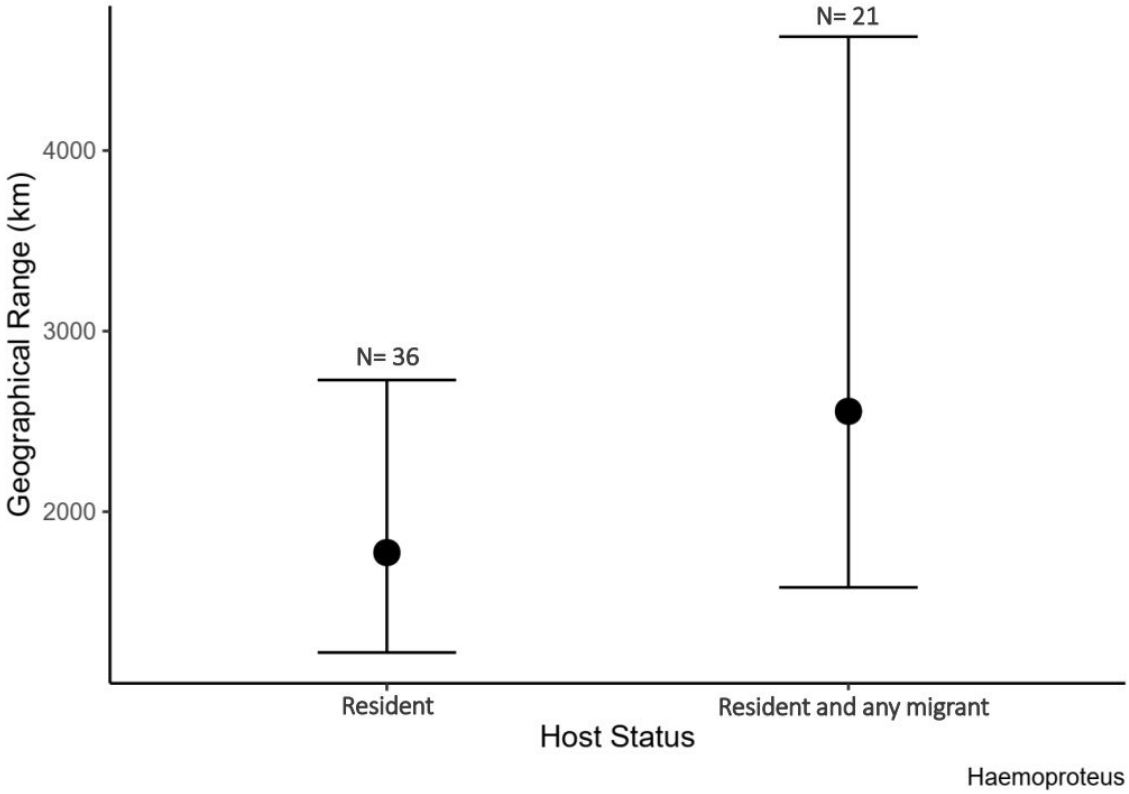
Supplementary Table 4: Parameter estimates, standard errors, and confidence intervals for the Bayesian model testing the differences in the geographical range of *Plasmodium* lineages among those that occur in migratory and/or resident avian host species. (Residents only = reference category)

	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



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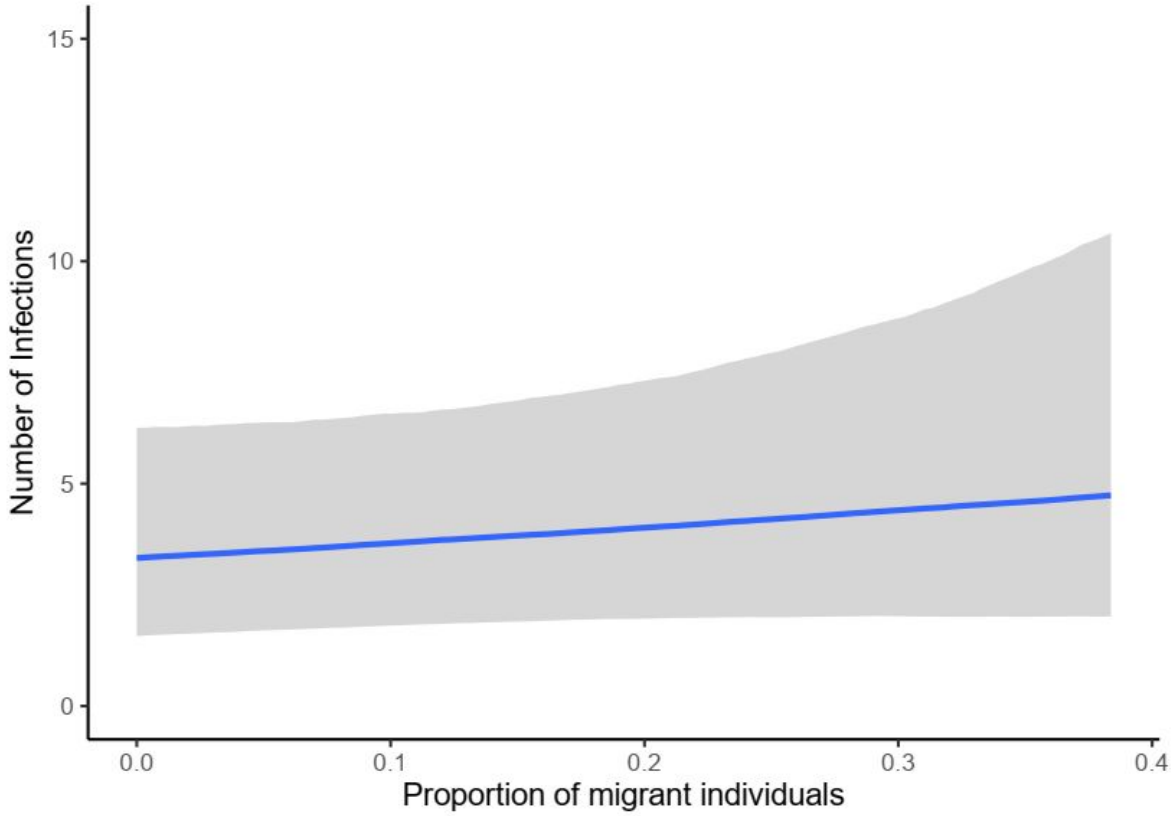
Supplementary Table 5: Parameter estimates, standard errors, and confidence intervals for the Bayesian model testing the differences in the geographical range of *Haemoproteus* lineages among those that occur in migratory and/or resident avian host species. (Residents only = reference category)

	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



Supplementary Figure 5: : Predicted model relationship (±95% confidence intervals) between local number of bird individuals positive for haemosporidian and proportion of migratory host individuals per locality. We observed a no effect of the proportion of migratory individuals on number of infected birds.

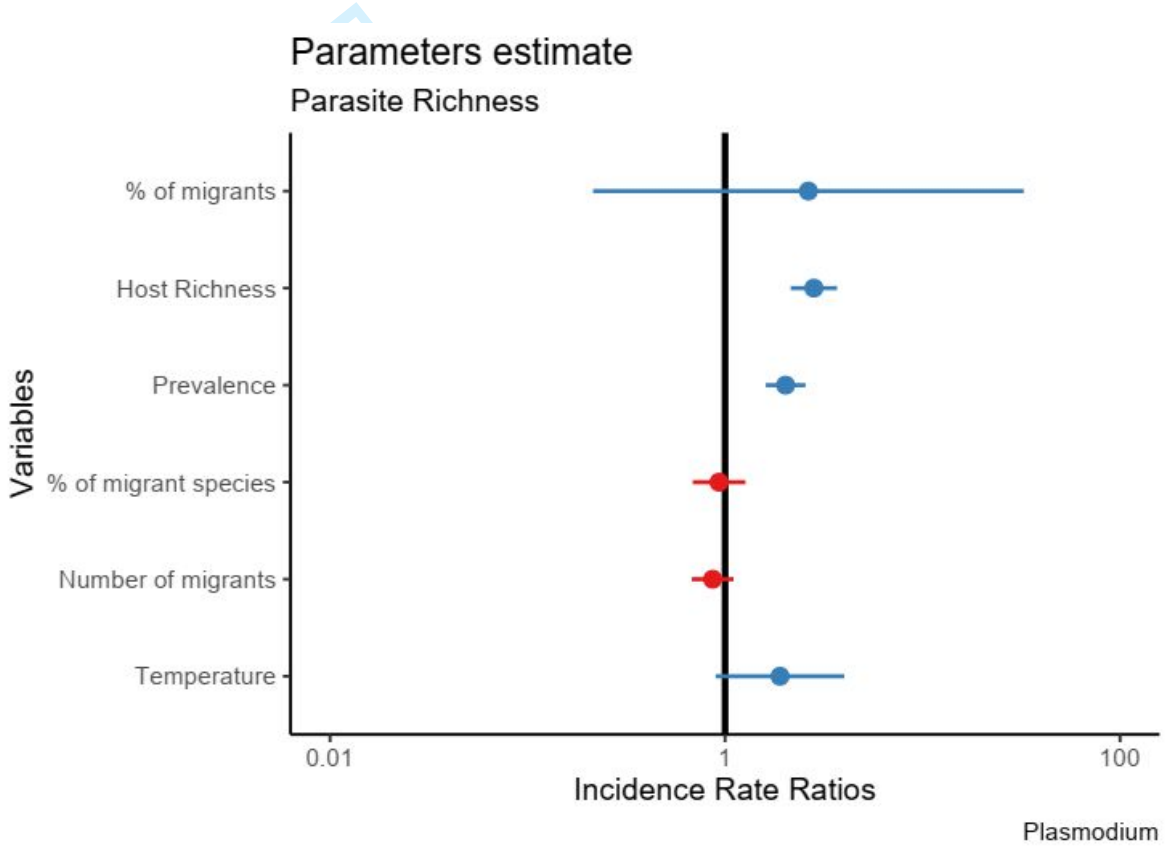
Supplementary Table 6: Parameter estimates, standard errors, confidence intervals for the Bayesian model testing the variation of local number of birds infected by haemosporidian as a function of the proportion of migratory all individual birds sampled per locality and parasite richness.

	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 7: AIC values for mixed models. Below all models tested are shown with all fixed effects and AIC test value.

	Variables	**AIC value**	**⊿AIC**
Model1	No fixed variables	470.20	79.32
Model2	Host Richness	437.94	47.06
Model3	Prevalence	449.75	58.87
Model4	Host Richness + Prevalence	399.67	8.79
Model5	Proportion of Migrants	470.85	79.97
Model6	Host Richness + Prevalence + Proportion of Migrants	397.50	6.62
Model7	Number of Migrants	458.68	67.8
Model8	Host Richness + Prevalence + Proportion of Migrants + Number of Migrants	399.08	8.2
Model9	Temperature	460.94	70.06

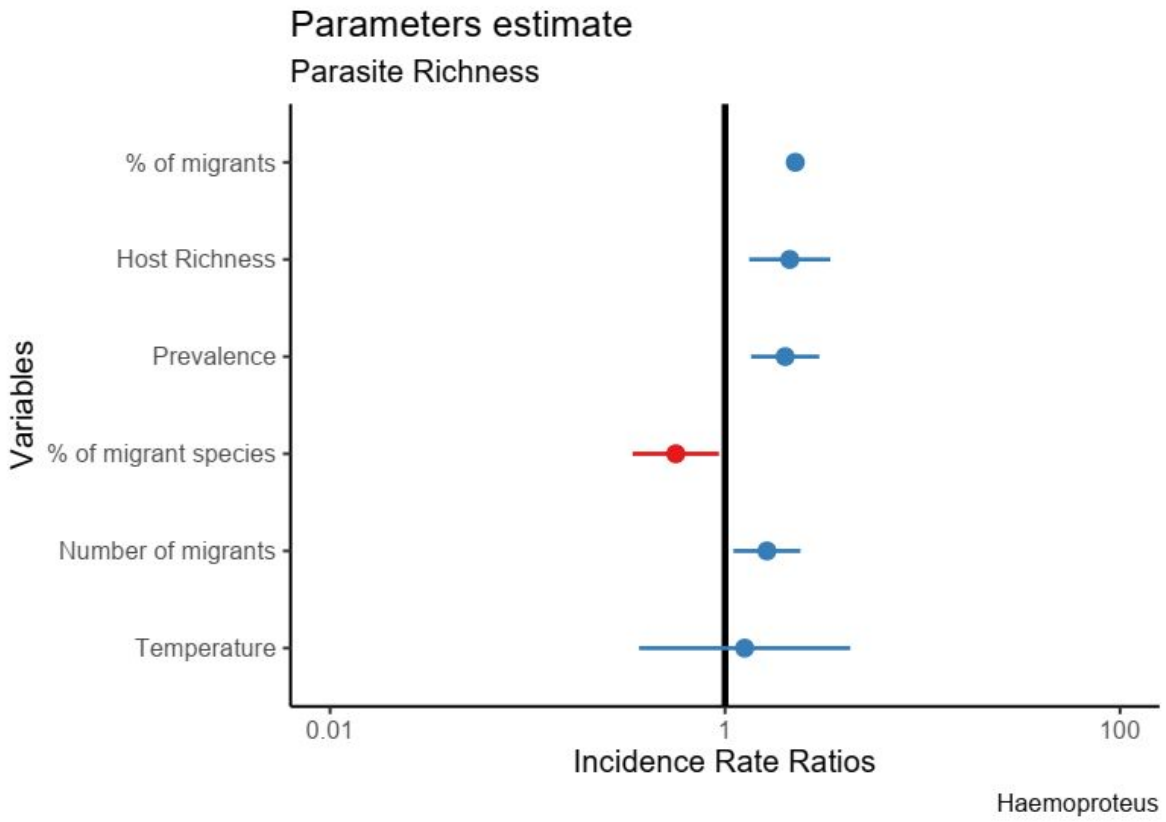
Model10	Host Richness + Prevalence + Proportion of Migrants + Number of Migrants + Temperature	390.88	0
Model11	Precipitation	460.43	69.55



Supplementary Figure 6: : Parameter estimates relating to their influence on *Plasmodium* richness. No correlation was found between the proportion of migratory individuals and *Plasmodium* richness.

Supplementary Table 8: Parameter estimates, standard errors, z and p values for the mixed model testing the variation of local *Plasmodium* richness as a function of the proportion of migratory individuals out of all individual birds sampled per locality, as well as other potential predictors.

	Estimate	**Std. error**	**Z**	**P**
Intercept	-6.92	2.06	-3.35	<0.001
Proportion of migrant individuals	0.97	1.28	0.76	0.45
Host richness	1.04	0.14	7.51	<0.001
Prevalence	0.71	0.12	5.97	<0.001
Proportion of migrant species	-0.07	0.16	-0.44	0.66
Number of migrants	-0.14	0.12	-1.16	0.24
Temperature	0.64	0.38	1.67	0.09



Supplementary Figure 7: : Parameter estimates relating to their influence on *Haemoproteus* richness. No correlation was found between the proportion of migratory individuals and *Haemoproteus* richness.

Supplementary Table 9: Parameter estimates, standard errors, z and p values for the mixed model testing the variation of local *Haemoproteus* richness as a function of the proportion of migratory individuals out of all individual birds sampled per locality, as well as other potential predictors.

	Estimate	**Std. error**	**Z**	**P**
Intercept	-5.09	3.34	-1.52	0.13
Proportion of migrant individuals	0.82	2.07	0.40	0.69

Host richness	0.75	0.24	3.13	0.002
Prevalence	0.70	0.20	3.45	<0.001
Proportion of migrant species	-0.57	0.26	-2.24	0.02
Number of migrants	0.49	0.20	2.45	0.01
Temperature	0.23	0.63	0.36	0.72

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