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Can migratory birds spread avian haemosporidian parasites?

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Abstract:	<p>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 likely dispersed through migration. South America provides an ideal opportunity to investigate the role of migration and parasite dispersal as it holds the greatest richness of birds (~3500 species). We hypothesize that (1) migratory birds spread parasite lineages along their routes, and (2) localities crossed by more migratory routes 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 passing through a locality. We combined a dataset on 13200 bird samples with data from the MalAvi database (~2800 sequenced parasites comprising 668 distinct lineages, from 506 host species and 156 localities), and used Bayesian multi-level and mixed models to test our hypotheses. Our results demonstrate that parasites shared between resident and full or partial migratory species are the most widespread, however, parasites shared among all three bird categories presented the lowest dispersal. Further, the proportion of migrant species in a locality was negatively related to local parasite richness, but not associated with local prevalence. We confirm that migrants can contribute to parasite dispersal, however, bird migration and visiting migrants do not raise local prevalence and decrease richness of avian haemosporidians, probably due to local constraints on transmission such as environmental filtering or incompatibility between haemosporidian lineages and their vector host.</p>

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 Høye 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 host species. At the same time, human-introduced pathogens and host species can decrease the fitness and survival of resident and native 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, therefore, 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 with some of these able to infect humans (Alekseev et al. 2001, Morshed et al. 2005, Poupon et al. 2006, Hellgren et al. 2007, Lindeborg et al. 2012, Ricklefs et al. 2017). Thus, the migratory behavior of birds may influence directly host local richness and population size.

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 and nutrients between ecosystems (Bauer and Hoyer 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 factors that influence haemosporidian prevalence (Illera et al. 2017). Thereby, 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. Previous research has documented the prevalence of avian malaria in different regions of Brazil, and markedly different prevalence for *Plasmodium* spp, which is the most prevalent haemosporidian in this region, have been reported between these regions (Braga et al. 2011). *Plasmodium* parasites present higher host-shifting rates than other bird haemosporidians (Hellgren et al. 2007), which could certainly contribute to 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 (Rensen 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. Thus, these features make the South American avian haemosporidians a great model system to investigate the putative transmission of pathogens via host migration in nature.

In this context, the main goal of this study is to evaluate the influence of migratory birds on the spread of haemosporidian parasites in South America. Specifically, we evaluated the hypothesis that (1) migratory birds spread parasite lineages along their migratory routes, and (2) localities crossed by more migratory routes have greater prevalence and richness of haemosporidian lineages. For the first hypothesis, we tested whether parasite lineages found (i) only in migratory birds, (ii) in both migrants and residents, and (iii) only in residents, differ in their frequency of occurrence among localities. Due to the fact migrants can carry parasites from many sites and potentially infect resident birds, we predicted that parasite lineages using migratory birds should occur in a greater percentage of localities than those using only resident birds. Moreover, migration behavior increases the exposure of birds to more parasite lineages and hence their contact with different parasites as migrants pass through 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 passing through 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 Lacorte et al. (2013), Ferreira et al. (2017), Fecchio et al. (2019a), Rodrigues et al. (2020), and supplemented with new, previously unpublished data. In addition to this dataset, we extracted haemosporidian lineages from the MalAvi database (<http://130.235.244.92/Malavi/>, Bensch et al. 2009) including data from the South American region (Figure 1). Combining both datasets, we obtained a total of ~2800 sequenced parasites representing 668 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 identified by the PCR protocol described by Hellgren et al. 2004. 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, according to the Brazilian Committee of Ornithology Records - CRBO 2014, Somenzari et al. 2018 and BirdLife International (<https://www.birdlife.org/>).

2.2 Potential correlates of prevalence and richness

Spatial autocorrelation

All analyses were conducted in R version 3.6 (R Core Team, 2019). We determined whether there was significant spatial autocorrelation among localities for prevalence and parasite richness in our dataset by calculating the Moran Index value. 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 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 one single random 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 both haemosporidian prevalence and parasite richness. Values of λ can range between 0 (no phylogenetic signal) and 1 (strong phylogenetic signal). In order to estimate lambda (λ), we applied the “phylosig” function from the “phytools” package (Revell 2012).

Climate variables

We used mean precipitation seasonality, and annual mean temperature (°C) as predictors in the mixed models. We used R to extract these climate variables from the Worldclim database (<https://worldclim.org/version2>). Using the package “raster”, we extracted the data using the “getData” function, then we selected only the data from the 63 localities included in our original dataset since climate variables were applied only in mixed model and the second Bayesian analyses, for which the MalAvi data were not employed.

2.3 Statistical Analyses

The spatial autocorrelation analyses revealed there was no substantial effect of space on parasite richness, however, for prevalence, we observed a Moran Index effect of 0.15, and for this reason, biome was used as random effects in our mixed and second Bayesian model and to control for idiosyncratic characteristics of localities. Likewise, considerable phylogenetic signals were observed among bird species for prevalence (0.49) and parasite richness (0.17).

Bayesian models

In order to determine whether migratory birds spread parasite lineages along their migratory routes and to evaluate the parasite connectivity among localities due to migratory behavior, we used multi-level modeling (MLM) with the “brms” package (Bürkner 2017) to evaluate the percentage of localities in which haemosporidian lineages occurred depending on whether they were found only in resident birds, only in partial migrant and fully migrant

birds, or in both residents and migrants. We decided to use this approach as it allows us to statistically estimate the percentage of localities among which lineages are distributed according to their host status.

In order to understand the variation of percentage of localities in which each lineage was present, we decided to build a single model including the migratory status of hosts used by a lineage (categorical variable with 6 levels: resident, partial migratory, full migratory, partial migratory and resident, full migratory and resident, and both partial/full migratory and resident; reference category = resident) while also controlling for sample size and number of host species used by a lineage. We chose our priors using the “get_prior” function. As our response variable was proportion data, we applied the Beta distribution family, using 4 chains with 2000 total iterations per chain (1000 for warmup, 1000 for sampling). The model results were plotted using the “conditional_effects” function to visualize the predictions of the host migratory status effects. We ran three models: one for all three parasite genera combined, one for *Plasmodium* lineages only, and one for *Haemoproteus* lineages only.

In the second model, we analysed the prevalence of infection in each bird species among localities. For this, we considered local number of infected individuals out of the total sample of each bird species as our dependent variable, and local percentage of migratory bird individuals (i.e., percentage of migratory individuals, including both partial and full migrants, out of all individual birds sampled in a locality) as our independent variable. Negative binomial distribution was applied in this model as we were working with count data with a left-skewed distribution. We used 4 chains with 2000 total iterations per chain (1000 for warmup interactions, 1000 for sampling). The model results were plotted using the “conditional_effects” function to visualize the predictions of the population-level effects.

Then, we firstly evaluated if host richness (i.e., number of bird species sampled per locality, log-transformed scaled value), parasite richness (log-transformed scaled value), percentage 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 percentage of migratory bird individuals and parasite richness were retained as fixed factors. Further, we considered biome as a random variable and used the function “cov_ranef” to account for phylogenetic influence. 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. In addition, we used only our dataset described above and excluded 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. 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 considered 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 and percentage of migratory individuals per locality (N=63 localities), respectively, as our dependent and independent variable. In this model, we did not use data from the MalAvi database, but only our dataset described above since it provides more information regarding the localities, such as prevalence data and host richness. We firstly

created previous 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 applied the “glmer” function from the “lme4” package (Bates et al. 2015) applying Poisson distribution. For this we considered local host richness (log-transformed scaled value), prevalence across all birds sampled (log-transformed scaled value), percentage 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 was set as random variable. We ran three models: one for all three parasite genera combined, one for *Plasmodium* lineages only, and one for *Haemoproteus* lineages only.

3. Results

Our first Bayesian model analyses revealed the lineages shared by resident and migratory or partial migratory species are the most widespread spatially, as they are found in a higher percentage of localities (Figure 2, Table 1). However, we observed that the lineages shared by all three categories (resident, partial migrant, and full migrant) are the least widespread, followed by those shared only between residents, partial or full migrants. Nevertheless, despite the fact lineages shared by partial or full migratory species and residents are more widely distributed, lineages present in only residents, migratory or partially migratory species presented similar spatial distributions according to our model. When repeating these analyses separately for the two main parasite genera, we observed a similar pattern of distribution among *Plasmodium* and *Haemoproteus* lineages. (Figure S1, Figure S2, Table S1 and Table S2).

For the second model, in which we analysed the relationship between local prevalence per bird species and local percentage of migratory bird individuals, we observed no correlation between the relative occurrence of migrants and prevalence of haemosporidian parasites per species (Figure 3, Table 2). However, when we repeated the analysis separately for only *Plasmodium* or *Haemoproteus* lineages, we observed negative and positive relationships between local percent of migrants and number of positive birds per host species, respectively (Figure S3 and S4, Table S3 and S4). Parasite richness had a significant positive effect on prevalence per bird species, whether when considering all haemosporidian lineages (Table 2), or only *Plasmodium* or *Haemoproteus* lineages (Tables S3 and S4).

Our mixed model examining the influence of migrants on parasite richness revealed no differences depending on whether we considered both haemosporidian genera together or separately. The Akaike information criterion revealed that the best model set considered only local host richness, prevalence across all birds sampled, percentage of migratory species, number of migrant individual and temperature as fixed factors (Table S5). Our first mixed model revealed that there is no effect of the percentage of migratory bird individuals per locality on local parasite richness (Figure 4, Table 3). However, we observed a negative relation between the proportion of migratory species and parasite richness. Further, we also observed no effect of the percentage of migratory bird individuals on local parasite richness for *Plasmodium* and *Haemoproteus* infections when the two genera were treated separately (Figure S5 and S6, Table S6 and S7). Moreover, we observed positive effects on parasite richness of other two predictors: 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 Hoyer 2014, Teitelbaum et al. 2018). Here, we demonstrated that some migratory birds may disperse parasite lineages through their migratory routes, such that lineages infecting both migrants and residents are spread to more localities. 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 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 haemosporidian prevalence, composition, and richness.

Further, despite the fact that lineages shared by resident and full or partial migratory species presented the highest frequency of occurrence among localities, parasites infecting only full or partial migrant birds were present in a similar proportion of localities as those infecting only resident avian hosts. We believe insufficient sampling of certain migrant avian species in many areas could have led to the low percentage of localities in which lineages infecting only partial and full migrant birds were found, since lineages infecting only migrant hosts may be specialist parasites. Besides, no single migrant species passes through all

localities, reducing their likelihood of sampling parasite lineages from all areas. Still, we observed that lineages present in all bird categories showed the most restricted distribution across our localities. However, it is important to note that only a small number (seven) of lineages was shared by all host categories, and this limited number prevents a full assessment of the effect of host migration in parasite dispersal.

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

as host richness and overall local prevalence also influence parasite prevalence. Therefore, it seems environmental and host features could be more important in determining local parasite richness than dispersal patterns.

It is worth mentioning that distinct parasite taxa can respond differently to the presence of migrant hosts. As we reported in this study, despite the fact no relation was observed for general haemosporidian prevalence, *Plasmodium* and *Haemoproteus* presented contrasting responses to an increase in the local proportion of migrant individuals. Whereas *Plasmodium* prevalence was negatively affected by an increase of migrants in the local bird community, we observed a rise in *Haemoproteus* infections. Such behavior illustrates that different pathogens do not respond identically to host migratory behavior. 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 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.

We also demonstrated that where the percentage of migrant species in a community is high, local haemosporidian richness is low, indicating the presence of migrant species can decrease parasite richness in bird communities. 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, Poulin 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. Certainly, further research will be required to confirm the importance of migration behavior in mitigating haemosporidian community richness.

Previous studies have tried to explain parasite species assembly patterns globally and 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 that drive parasite diversity in this region. In contrast, we detected a negative effect on parasite richness in regions with greater proportions of migrant species, while host richness and prevalence seem to be the main factors that positively drive parasite diversity. Also, we did not observe a clear relationship between migratory behavior and prevalence. Recently, Barrow et al. (2019) suggested that susceptibility to haemosporidian infection is partially driven by conserved, latent aspects of anti-parasite defense, and that prevalence of infection is strongly linked to avian phylogeny in Tropical Andes birds. Further, Fecchio et al. (2019a) also suggest that historical processes, such as host speciation, are also key drivers

of haemosporidian diversity in South America. However, present-day environmental factors, mainly precipitation patterns, may be important for host range expansion across regions in haemosporidian parasites, as these vector-transmitted parasites exhibit greater host specificity in localities with pronounced seasonality and wetter dry seasons (Fecchio et al. 2019b). Thus, it seems other processes (apart from parasite dispersal through migrants) might be more important in determining parasite richness and prevalence in South America.

In summary, we demonstrated that South American migrant birds play a moderate role in parasite dispersal and, consequently, in their evolution and diversity. Further, as observed by Ricklefs et al. (2017), most haemosporidian lineages are not shared between resident and migrant species, indeed, most of our parasite lineages were observed only in resident birds, demonstrating that resident host species harbor the greatest parasite richness in our study system. We also demonstrated that, despite the fact migrants might carry haemosporidians to new localities, migration by itself may not affect general parasite prevalence, possibly because parasite spread among local bird communities relies on the capability of haemosporidians to reproduce and develop in their ectothermic vector hosts. In addition, migrants appear to increase the homogeneity of parasites hosted by bird communities in our study system, as their presence seems to be related to lower community-wide haemosporidian richness. By comparing the distribution of different pathogen lineages, our analyses demonstrate that migrant hosts can carry haemosporidians and possibly other pathogens throughout their migration routes, thereby contributing to the spread of disease on a continental scale.

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455 process in South America. - Mol. Ecol. 22: 1193–1213.
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- 457
- 458 Table 1: Parameter estimates, standard errors, and confidence intervals for the Bayesian
459 model testing the differences in the distribution of haemosporidian lineages among those that
460 occur in migratory and/or resident avian host species.

	Estimate	Std. error	Conf. Inter (95%)	
Intercept	-4.71	0.03	-4.76	-4.65
Full migrant	-0.08	0.10	-0.38	0.10
Partial migrant	0.12	0.13	-0.46	0.12
Resident and full migrant	0.31	0.11	0.03	0.52
Resident and partial migrant	0.34	0.08	0.12	0.51
Resident, partial and full migrant	-0.55	0.20	-0.92	-0.04
Number of bird individuals	0.01	0.0	0.01	0.02

Number of host species per lineage	0.06	0.01	0.05	0.07
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Table 2: Parameter estimates, standard errors, and confidence intervals for the Bayesian model testing the variation of local haemosporidian prevalence per species as a function of the percentage of migratory individuals out of all individual birds sampled per locality and parasite richness.

	Estimate	Std. error	Conf. Inter (95%)	
Intercept	0.49	0.36	-0.22	1.25
Percentage of migrant individuals	0.70	0.79	-0.91	2.23
Parasite Richness	0.02	0.01	0.01	0.03

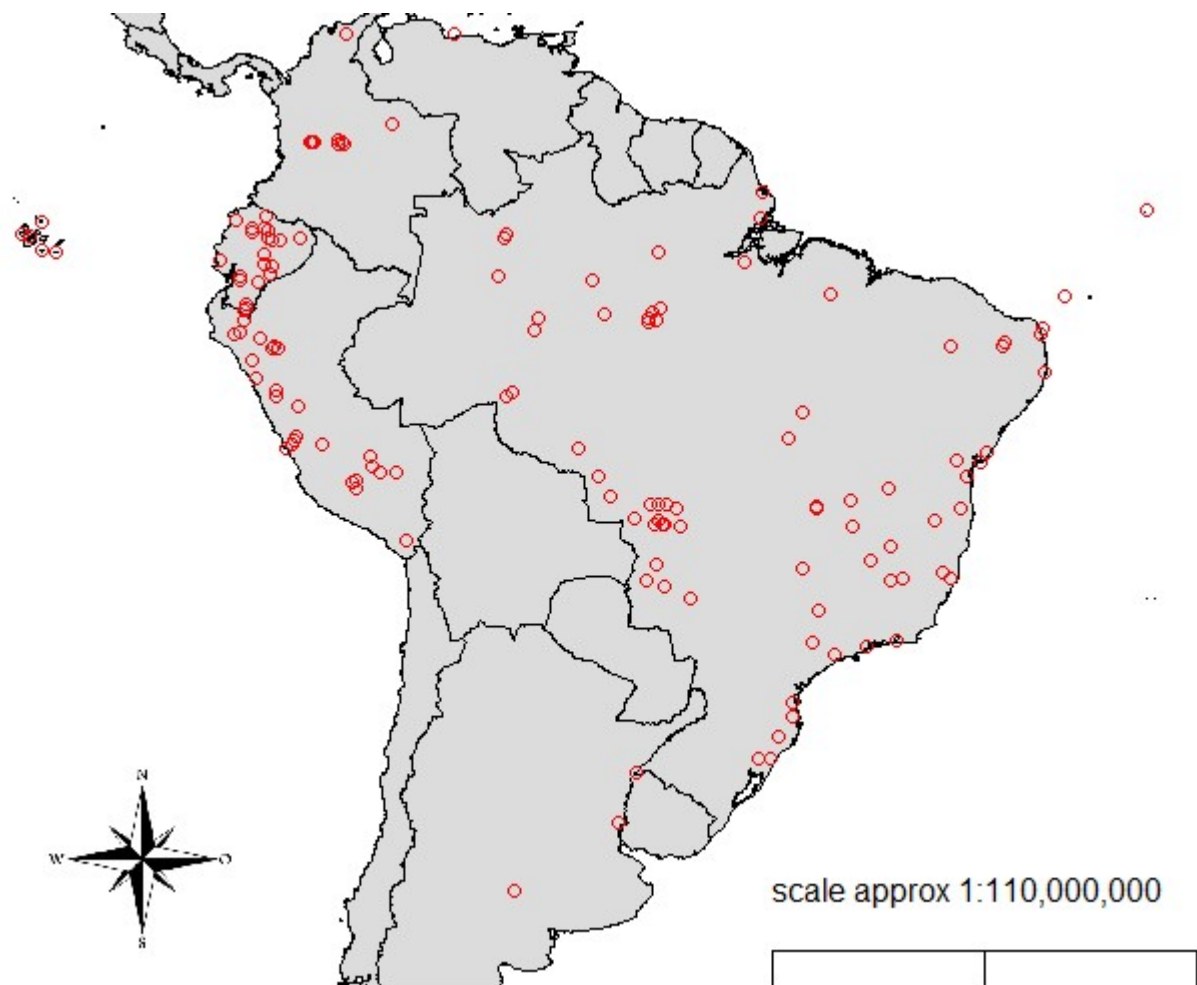
Table 3: Parameter estimates, standard errors, z and p values for the mixed model testing the variation of local haemosporidian richness as a function of the percentage of migratory individuals out of all individual birds sampled per locality, as well as other predictors.

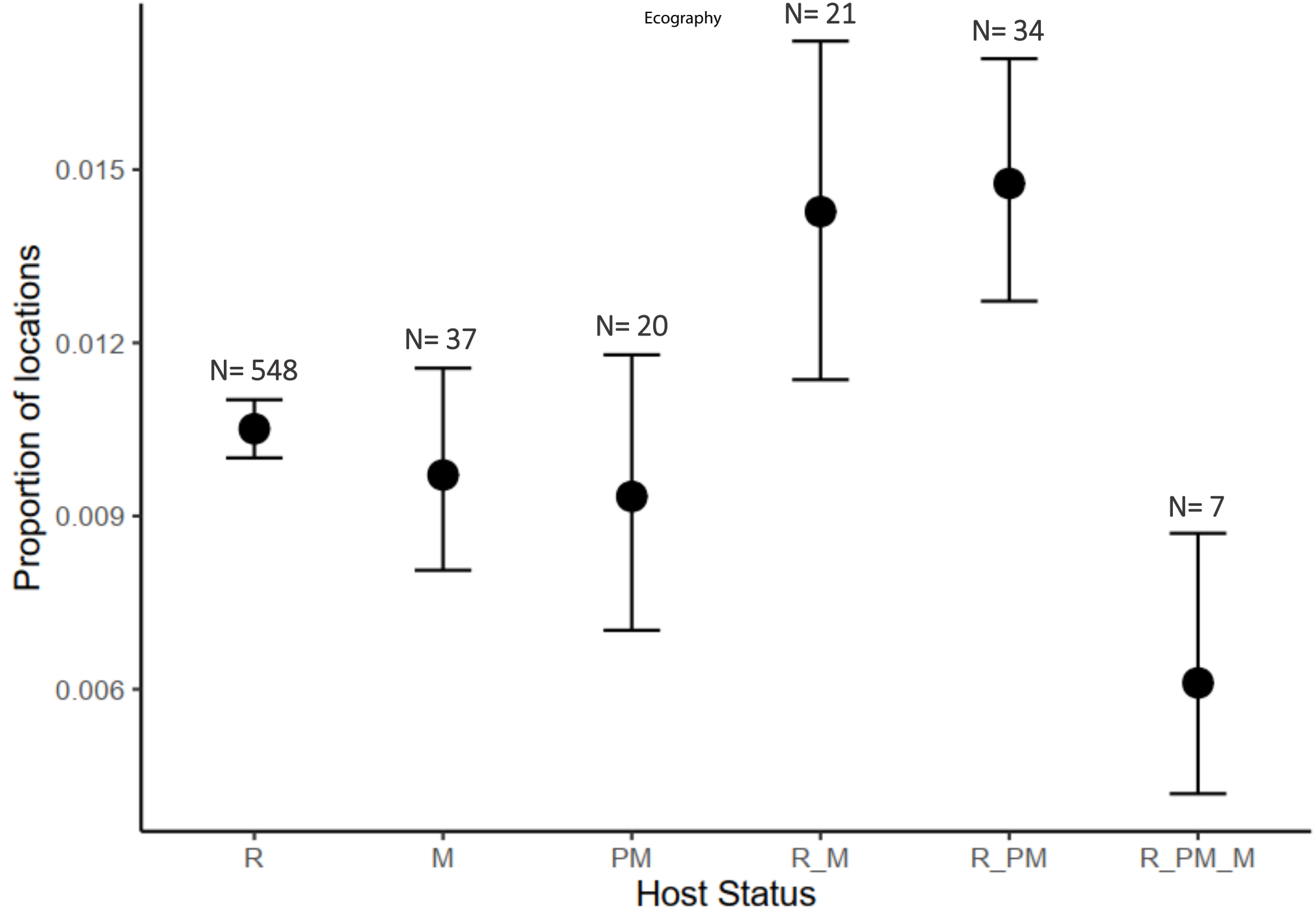
	Estimate	Std. error	Z	P
Intercept	-6.18	1.15	-5.36	<0.001
Percentage of migrant individuals	0.83	0.74	1.11	0.27
Host richness	0.94	0.08	12.10	<0.001
Prevalence	0.69	0.07	9.80	<0.001
Percentage of migrant species	-0.28	0.09	-3.06	0.002
Number of migrants	0.10	0.06	1.52	0.13
Temperature	0.63	0.21	2.93	0.003

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Number of Infections

10

5

0

0.0

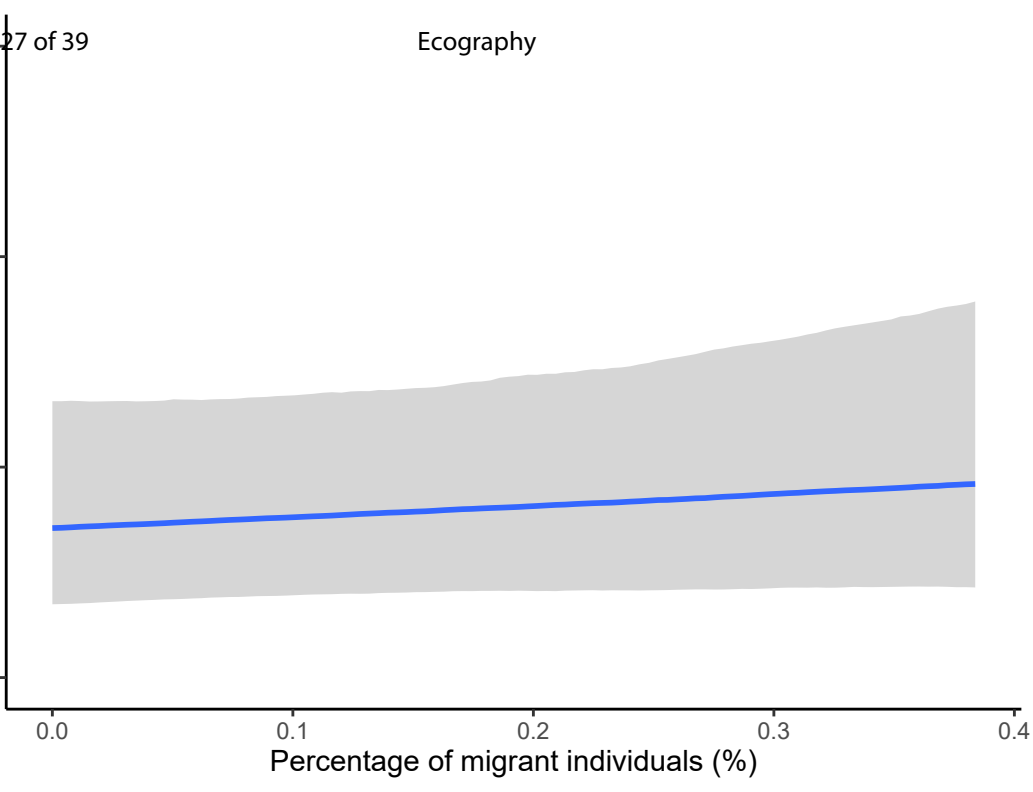
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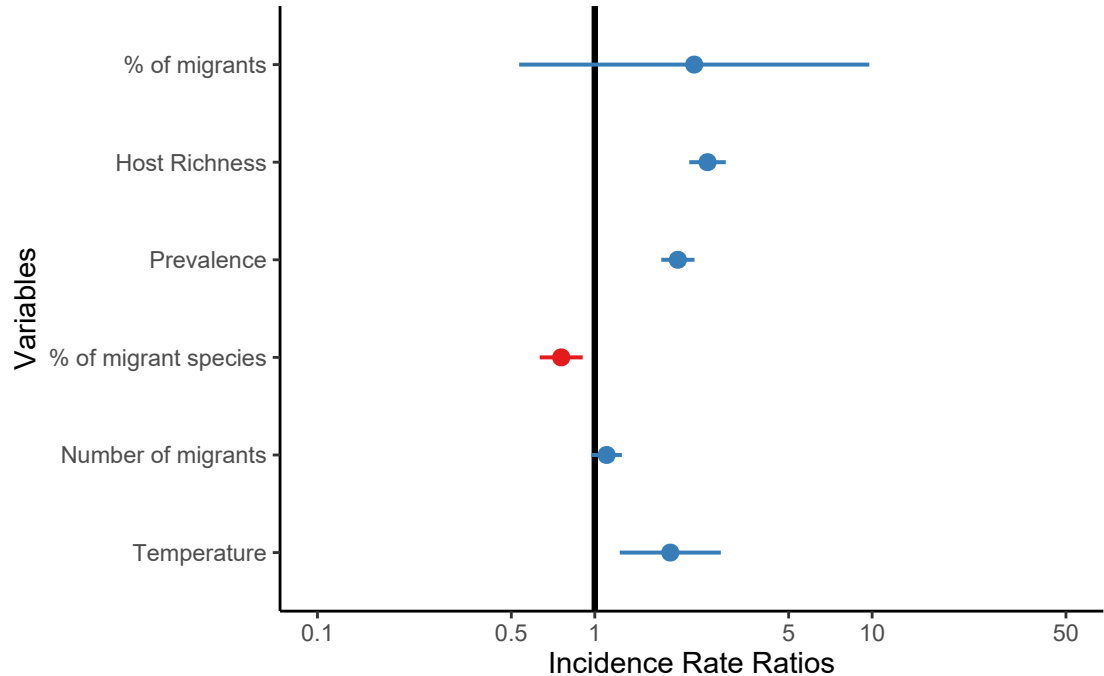
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Percentage of migrant individuals (%)



Parameters estimate

Parasite Richness



SUPPLEMENTARY MATERIAL

Supplementary Figure 1: Mean (\pm confidence intervals) proportions of localities in which *Plasmodium* 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 six categories are shown on the graph.

Supplementary Table 1: Parameter estimates, standard errors, and confidence intervals for the Bayesian model testing the differences in the distribution of *Plasmodium* lineages among those that occur in migratory and/or resident avian host species.

	Estimate	Std. error	Conf. Inter (95%)	
Intercept	-4.76	0.00	-4.83	-4.70
Full migrant	-0.22	0.17	-0.56	0.09
Partial migrant	-0.13	0.18	-0.53	0.19
Resident and full migrant	0.64	0.12	0.38	0.87
Resident and partial migrant	0.29	0.12	0.06	0.51
Resident, partial and full migrant	-1.01	0.48	-1.98	-0.12
Number of bird individuals	-0.01	0.01	-0.03	0.02
Number of host species per lineage	0.12	0.02	0.08	0.16

Supplementary Figure 2: Mean (\pm confidence intervals) proportions of localities in which *Haemoproteus* 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 six 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 distribution of *Haemoproteus* lineages among those that occur in migratory and/or resident avian host species.

	Estimate	Std. error	Conf. Inter (95%)	
	e			
Intercept	-4.73	0.04	-4.81	-4.65
Full migrant	-0.03	0.15	-0.34	0.25
Partial migrant	-0.12	0.18	-0.50	0.20
Resident and full migrant	0.79	0.12	0.54	1.02
Resident and partial migrant	0.22	0.13	0.02	0.52
Resident, partial and full migrant	-1.26	0.42	-2.22	-0.56
Number of bird individuals	0.01	0.00	0.01	0.02
Number of host species per lineage	0.03	0.01	0.01	0.04

Supplementary Figure 3: Correlation between local number of bird individuals positive for *Plasmodium* and percentage of migratory host individuals per locality. We observed a negative effect of the percentage of migratory individuals on parasite prevalence.

Supplementary Table 3: Parameter estimates, standard errors, confidence intervals for the Bayesian model testing the variation of local *Plasmodium* prevalence per species as a

function of the percentage of migratory all individual birds sampled per locality and parasite richness.

	Estimate	Std. error	Conf. Inter (95%)	
Intercept	-0.32	0.65	-1.70	0.90
Percentage of migrant individuals	-3.29	1.22	-5.52	-1.10
Parasite richness	0.01	0.01	0.00	0.03

Supplementary Figure 4: Correlation between local number of bird individuals positive for *Haemoproteus* and percentage of migratory host individuals per locality. We observed a positive effect of the percentage of migratory individuals on parasite prevalence.

Supplementary Table 4: Parameter estimates, standard errors, and confidence intervals for the Bayesian model testing the variation of local *Haemoproteus* prevalence per species as a function of the percentage of migratory all individual birds sampled per locality and parasite richness.

	Estimate	Std. error	Conf. Inter (95%)	
Intercept	-2.34	0.81	-4.05	-0.81
Percentage of migrant individuals	7.00	2.04	2.04	3.29
Parasite richness	0.03	0.01	0.01	0.06

Supplementary table 5: AIC values for mixed model. Below all models tested are shown with all fixed effects and AIC test value.

	Variables	AIC value	Δ AIC
Model1	No fixed variables	714.97	307.79
Model2	Host Richness	521.08	113.9
Model3	Prevalence	602.62	195.44
Model4	Host Richness + Prevalence	422.14	14.96
Model5	Percentage of Migrants	698.13	290.95
Model6	Host Richness + Prevalence + Percentage of Migrants	416.40	9.22
Model7	Number of Migrants	620.46	213.28
Model8	Host Richness + Prevalence + Percentage of Migrants + Number of Migrants	417.34	10.16
Model9	Temperature	671.73	264.55
Model10	Host Richness + Prevalence + Percentage of Migrants + Number of Migrants + Temperature	407.18	0
Model11	Precipitation	666.99	259.81

Supplementary Figure 5: Standardized estimates as a function of *Plasmodium* richness. No correlation was found between the percentage of migratory individuals and *Plasmodium* richness.

Supplementary Table 6: Parameter estimates, standard errors, z and p values for the mixed model testing the variation of local *Plasmodium* richness as a function of the percentage of

migratory individuals out of all individual birds sampled per locality, as well as other potential predictors.

	Estimate	Std. error	Z	P
Intercept	-6.46	1.42	-4.55	<0.001
Percentage of migrant individuals	1.30	0.92	1.45	0.15
Host richness	1.07	0.09	11.67	<0.001
Prevalence	0.71	0.08	8.48	<0.001
Percentage of migrant species	-0.04	0.11	-0.36	0.72
Number of migrants	-0.20	0.09	-2.29	0.02
Temperature	0.54	0.26	2.05	0.04

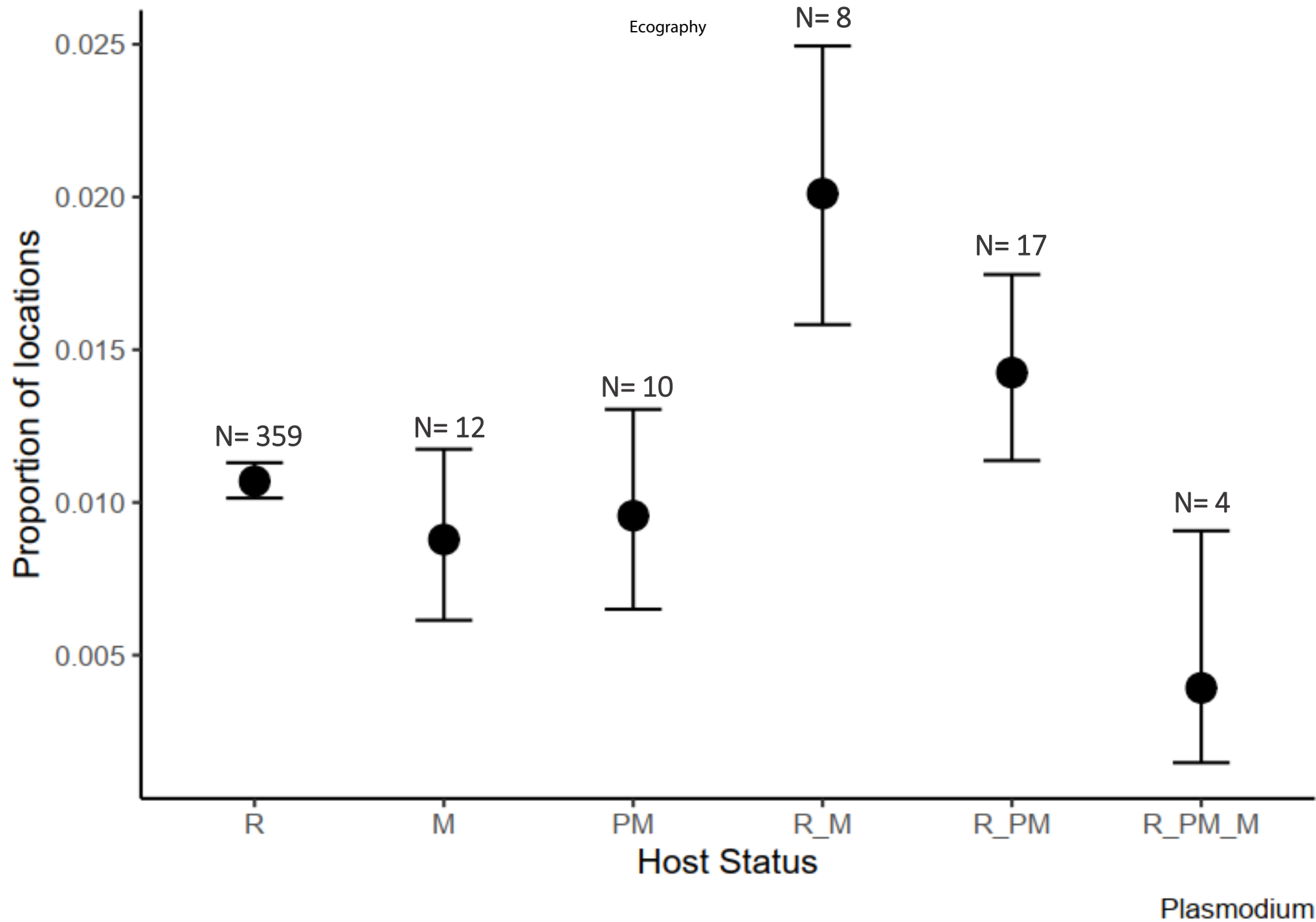
Supplementary Figure 6: Standardized estimates as a function of *Haemoproteus* richness. No correlation was found between the percentage of migratory individuals and *Haemoproteus* richness.

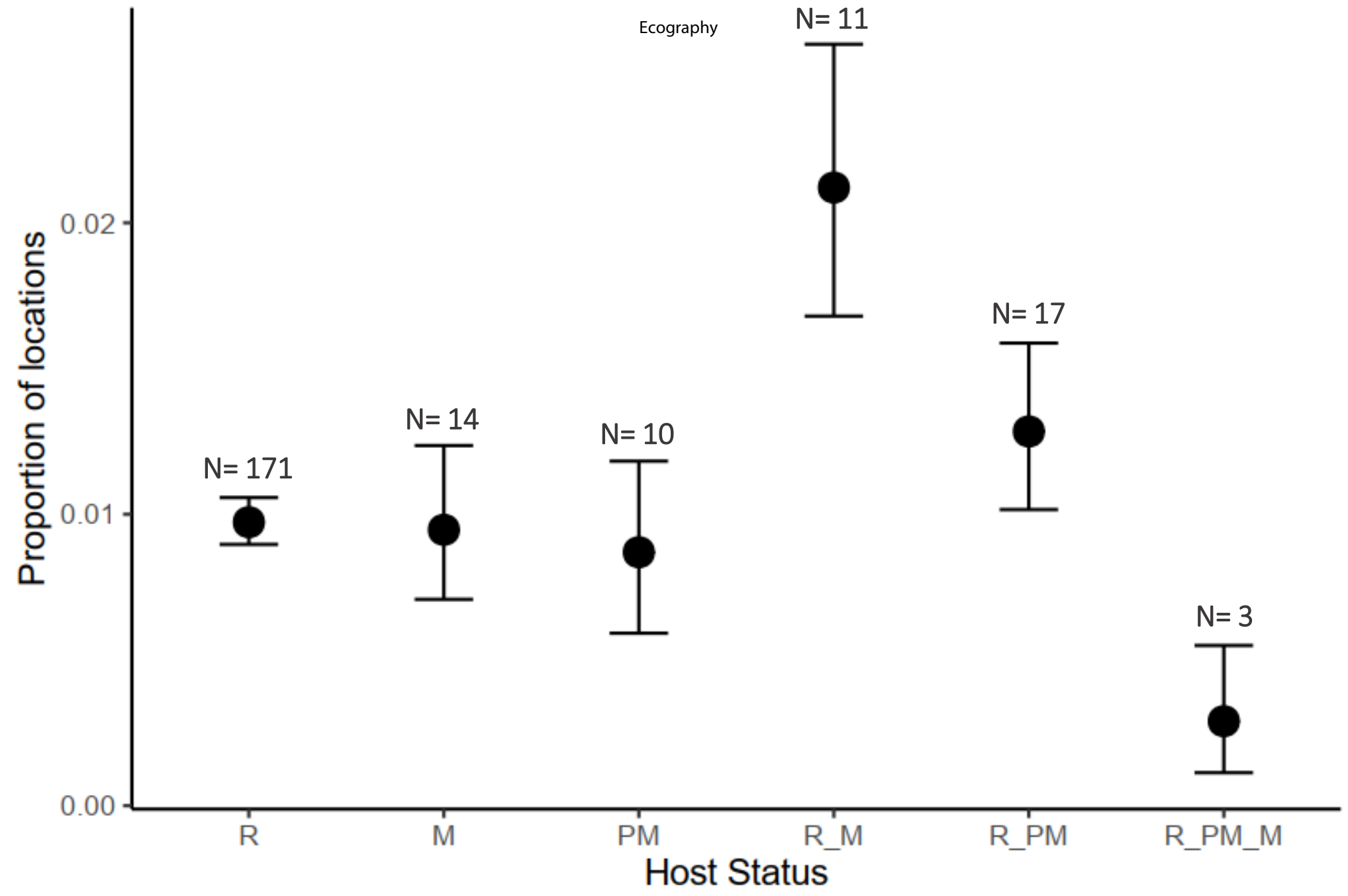
Supplementary Table 7: Parameter estimates, standard errors, z and p values for the mixed model testing the variation of local *Haemoproteus* richness as a function of the percentage of migratory individuals out of all individual birds sampled per locality, as well as other potential predictors.

	Estimate	Std. error	Z	P
Intercept	-6.12	3.44	-1.78	0.08
Percentage of migrant individuals	0.73	1.39	0.53	0.6
Host richness	0.85	0.17	4.89	<0.001

Prevalence	0.51	0.14	3.69	<0.001
Percentage of migrant species	-0.39	0.17	-2.56	0.02
Number of migrants	0.25	0.13	1.88	0.06
Temperature	0.54	0.65	0.83	0.4

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Haemoproteus

Number of Infections

3

2

1

0

0.0

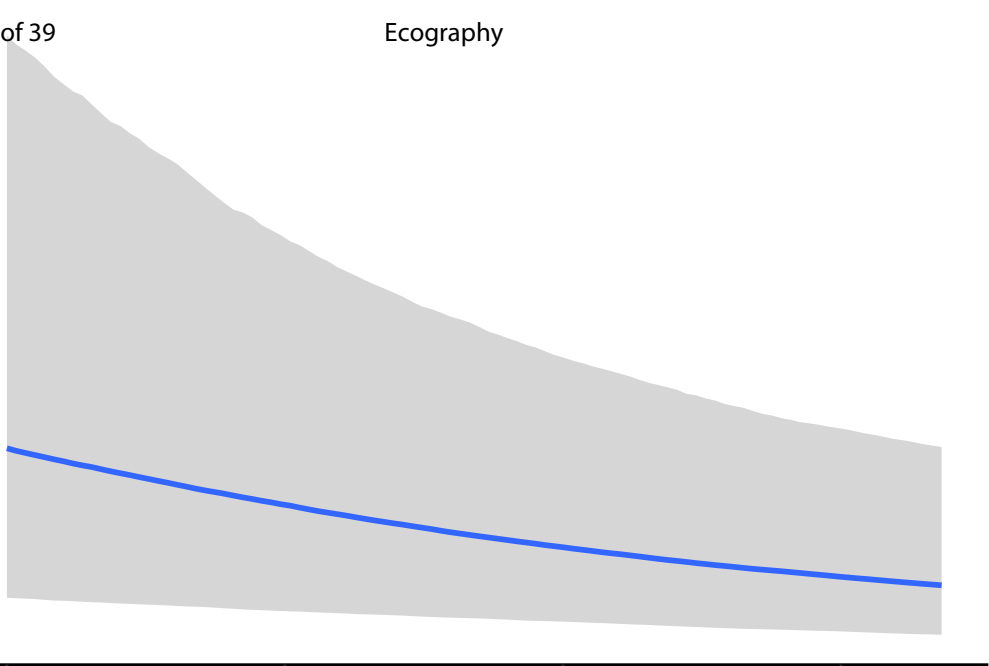
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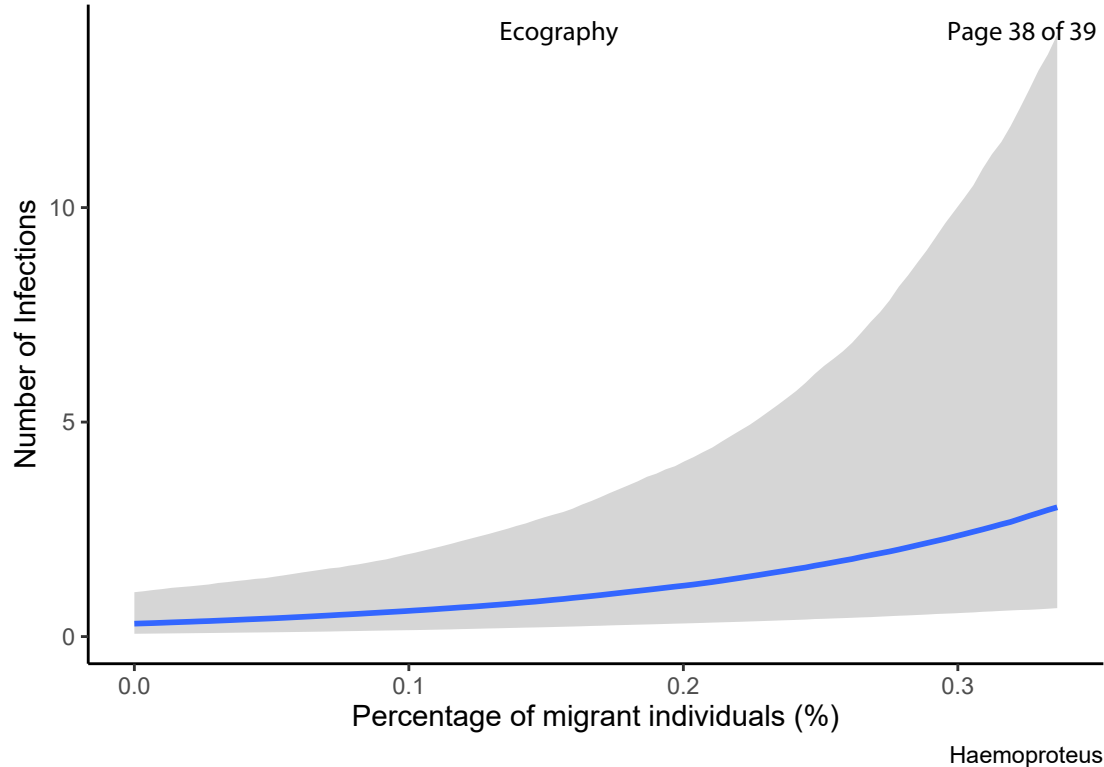
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Percentage of migrant individuals (%)

Plasmodium



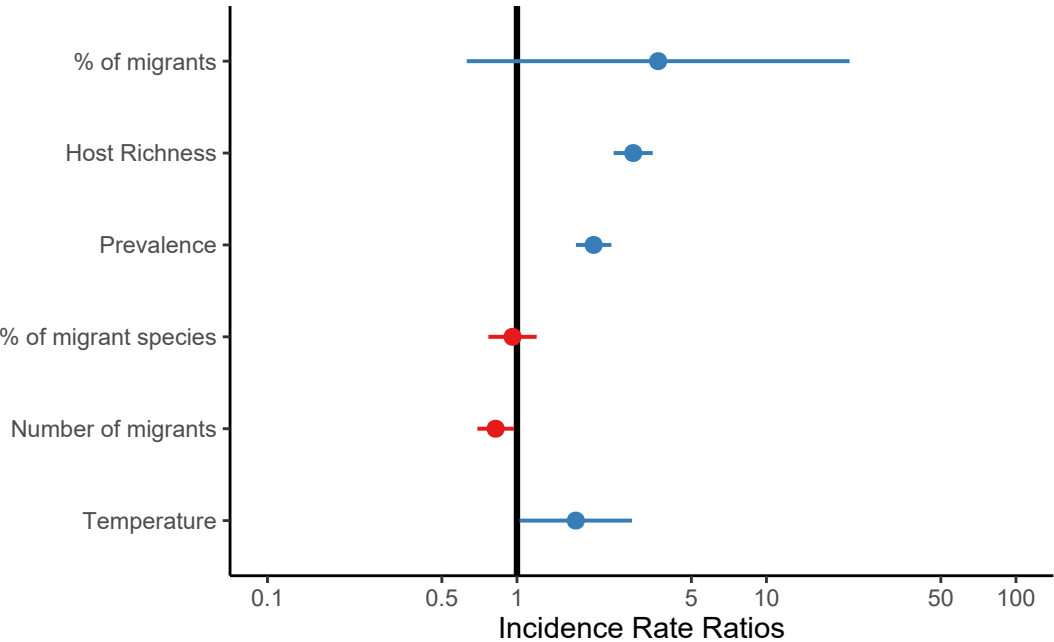


Parameters estimate

Parasite Richness

Ecography

Variables



Plasmodium

Parameters estimate

Parasite Richness

