**Haemosporidian taxonomic composition, network centrality and partner fidelity between resident and migratory avian hosts**

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**Abstract:** Migration can modify interaction dynamics between parasites and their hosts with migrant hosts able to disperse parasites and impact local community transmission. Thus, studying the relationship among migratory hosts and their parasites is fundamental to elucidate how migration shapes interaction among hosts and their pathogens. Avian haemosporidian parasites are some of the most prevalent, diverse, and important wildlife parasites, and are also widely used as models in ecological and evolutionary research. Here, we contrast parasite taxonomic composition, network centrality and partner fidelity among resident and non-resident hosts using avian haemosporidians as study model. In order to evaluate parasite taxonomic composition, we performed permutational multivariate analyses of variance to quantify dissimilarity in parasite composition among host migratory categories. Additionally, we ran multilevel Bayesian models to assess the role of migration in determining centrality and partner fidelity in host-parasite networks of avian hosts and their respective haemosporidian parasites. We observed similar parasite taxonomic composition and partner fidelity among resident and migratory hosts. Conversely, we demonstrate that migratory hosts play a more central role in host-parasite networks than residents. However, when evaluating partially and fully migratory hosts separately, we observed that only partially migratory species presented higher network centrality when compared to resident birds. Therefore, migration does not lead to differences in both parasite taxonomic composition and partner fidelity. However, migratory behavior is positively associated with network centrality, indicating those individuals can play more important roles in shaping host-parasite interactions and influence local transmission.

**Key words:** Haemosporidians, Migratory Behavior, Antagonistic Interactions, Partner Fidelity, Network Centrality

**Introduction**

Migration, i.e. long distance and periodical roundtrip movement of animals between distinct habitats, can alter interaction dynamics among parasites and their hosts by serving as an escape mechanism from some pathogens but also increasing parasite prevalence and richness of certain other pathogens within migrant host species (Altizer et al. 2011; Satterfield et al. 2015; de Angeli Dutra et al. 2021a; Poulin and de Angeli Dutra 2021). Migratory behavior can also modify the availability of hosts for parasites across regions since migrant individuals do not inhabit the same habitat year-round. At the same time, migrants can represent an opportunity for parasites to increase their distribution worldwide, as infected migrant individuals transport their pathogens through their routes and stopovers, therefore, providing new opportunities for host switching into new environments and resident species (de Angeli Dutra et al. 2021b; Poulin and de Angeli Dutra 2021). Indeed, the presence of migratory individuals can also affect local parasite transmission, altering parasite prevalence and richness within resident host community (de Angeli Dutra et al. 2021b; Fecchio et al. 2021). However, despite the fact migration can modulate parasite-host interaction, only a few studies have addressed the implications of host migration for parasite ecology and evolution (Poulin and de Angeli Dutra 2021).

Thus, intrinsic characteristics of host-parasite interactions could be altered by host migratory behavior, including traits such as virulence (i.e. pathogenicity level) or partner fidelity, i.e. the species specificity in pairwise host-parasite associations. Previous research suggests antagonistic interactions display lower partner fidelity than mutualistic ones, indicating host-parasite systems are evolutionarily malleable (Fortuna et al. 2020). Additionally, infecting migratory individuals can pose a challenge to parasites due to the need to adapt to novel resources and conditions, which could lead to looser fidelity among parasites and their migrant hosts. For example, for malaria parasites infecting migratory birds to be transmitted into their hosts’ new habitats, they must to be able to infect and complete their cycle in new vector species under distinct environmental characteristics (Valkiūnas 2005). Hence, the exposure of parasites to abrupt environmental and vector changes may impact the ecological and evolutionary relationship between parasites and their migratory hosts since host migrations represent repeated, predictable, and directional selective pressures (Poulin and de Angeli Dutra 2021). Therefore, it is essential to study how host shifts between migratory and resident hosts occurring in sympatry and under different environmental conditions can alter parasite-host dynamics. This is necessary to elucidate how parasite life-history traits evolve under repeated and predictable changes.

Avian haemosporidian parasites, i.e. malaria and malaria-like vector borne protozoan parasites, are some of the most prevalent, diverse and studied wildlife pathogens. These parasites are an excellent ecological and evolutionary model to study host-parasite relationships due to their high prevalence, diversity, cosmopolitan distribution and variable levels of specificity to their hosts (Valkiūnas 2005). This is particularly relevant for South America, which harbors the highest diversity of birds, vectors and haemosporidian parasites worldwide (Remsen et al.; Santiago-Alarcon et al. 2012; Ellis et al. 2019). This region is also characterized by great vector abundance and considerable haemosporidian prevalence (Braga et al. 2011; Santiago-Alarcon et al. 2012). Furthermore, avian community composition seems to impact parasite composition as well, with avian community turnover driving both haemosporidian and ornithophilic mosquito turnover across the Amazon region (De La Torre et al. 2021). All those features together make South America an ideal region to investigate ecological and evolutionary dynamics of avian haemosporidian interaction.

Therefore, studying the role of host migratory behavior in shaping parasite taxonomic composition (i.e. composition of distinct parasite lineages), network centrality (i.e. property related to the position a species occupies in the network) and partner fidelity is fundamental to understand the impact of migration on life-history traits for parasites. Here, we hypothesize that resident species show higher partner fidelity to their parasites due to the greater stability of environmental conditions and vector species they face. Additionally, since migrants harbor higher richness of haemosporidians (de Angeli Dutra et al. 2021a) and the more unstable environmental conditions and vectors they encounter may favor their infection by generalist parasites, we also expect them to occupy more central positions in host-parasite networks. Moreover, since migrants are exposed to more parasite lineages as they visit regions that harbor different parasite communities, our second hypothesis is that parasite taxonomic composition differs between resident and migratory avian hosts species. In this research, we computed and compared partner fidelity and network centrality levels between haemosporidians and their resident and partially and fully migratory avian hosts using Bayesian multilevel models. Further, using permutational multivariate analyses of variance (PERMANOVA) we evaluated whether resident and migratory hosts harbor similar haemosporidian assemblages.

**Methods**

*Dataset*

All analyses were performed using a dataset comprising ~15200 individual birds representing 974 avian species. Avian communities were sampled in 85 different localities across seven different South American biomes - Amazonia, Atlantic Rain Forest, Cerrado, Temperate Grassland, Caatinga, Pantanal and Andean Forest (Fig. 1). The birds were sampled from 2005 to 2018 with a subset of those samples having previously been used in published research (Lacorte et al. 2013; Ferreira et al. 2017; Fecchio et al. 2019a, 2020; Anjos et al. 2021) and the rest consisting of unpublished data. This large dataset was combined with data available from MalAvi (<http://130.235.244.92/Malavi/>) and represents a total of 2758 sequenced parasites representing 752 distinct lineages, all belonging to one of three genera: *Plasmodium*, *Haemoproteus* and *Leucocytozoon.* Haemosporidian infection was estimated using PCR protocols described previously (Fallon et al., 2003; Hellgren et al., 2004; Bell et al., 2015). All lineages were identified by sequencing a DNA fragments obtained using PCR protocols described by Hellgren et al. 2004 that amplify a cytochrome b fragment of 478 base pairs. Hosts were classified into three migratory categories: (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/>).

*Haemosporidian-Host Partner Fidelity and Network Centrality Analyses*

All analyses were conducted in R version 4.0 (R Core Team, 2019). For haemosporidian-bird partner fidelity and network centrality analyses, we considered only biomes with at least 10 distinct parasite lineages, which involved 249 distinct avian host species and 40 parasite lineages from five biomes – Amazonia, Andean Forest, Cerrado, Caatinga and Atlantic Rain Forest (Supplementary Table 1S). We created incidence matrixes between avian host species and parasite lineages for each biome. Using the “specieslevel” function from the “bipartite” package (Dormann et al. 2008) in R, we computed normalized degree and weighted closeness and betweenness values for hosts infecting birds in each biome. The first value represents the number of distinct realized interactions between hosts and parasites in each biome divided by the total number of distinct potential partners (i.e. parasites) in that same region. Normalized degree values can be employed as a measure of partner fidelity, with hosts presenting higher values being less specific to their partners than hosts with lower values (Fortuna et al. 2020). On the other hand, weighted closeness and betweenness are measures of centrality in a network. Weighted closeness is calculated as the minimum sum of the paths between a species (i.e. hosts) and all their partners (i.e. parasites) in the network, with hosts presenting higher closeness values being more central. In contrast, weighted betweenness represents the degree to which a species stands between another species, i.e. the degree a species connects other species in an ecological network. We then combined all biome values into one single dataset and ran a Bayesian model to compare partner fidelity and network centrality among migratory categories.

In order to run our Bayesian analyses, we employed the function “brm” from the “brms” package (Bürkner 2017). In the first model, we considered normalized degree as the response variable and avian host migratory category (resident; partial migrant and full migrant, reference level = resident) as our population-level effect and used biome as random effect. Likewise, for our second model we employed weighted closeness as the response variable, avian host migratory category (resident; partial migrant and full migrant, reference level = resident) as our population-level effect and again biome as random effect. Then, we ran a third model applying weighted betweenness as our response variable, again host migratory category (resident; partial migrant and full migrant, reference level = resident) as our population-level effect and biome as random effect We downloaded the full avian phylogeny file from the AllBirdsHackett1.tre website (<https://birdtree.org/>), selected only the species used for our analyses and created a matrix with phylogenetic distances between bird species. This matrix was also added to all our model as random effect to account for host phylogenetic influence on partner fidelity. Priors were determined using the “get\_prior” function. We ran the Bayesian models using 4 chains with 4000 total iterations per chain (2000 for warmup, 2000 for sampling) and employed zero-one inflated beta distributions, since normalized degree and weighted closeness and betweenness represent rate data. Further, we combined partial and full migrants into one single category and repeated our Bayesian analyses. Later, we applied the “bip\_ggnet” function from the “ggnet” package ([briatte.github.io/ggnet/](https://briatte.github.io/ggnet/)) to plot a bipartite net representing the relationships among haemosporidian lineages and avian hosts from different migratory categories.

*Haemosporidian Taxonomic Composition Analyses*

For haemosporidian taxonomic composition analyses, we considered only localities with 10 or more individual birds sampled, at least three distinct parasite lineages per biome and at least two distinct host migratory categories, which included 2465 haemosporidian infections from 485 avian species (Supplementary Table S2). We created an incidence matrix between host migratory category and parasite lineages per biome. Later, applying the function “vegdist” (method Bray) from the “vegan” package in R (Dixon 2003), we calculated dissimilarity indices among migratory host categories. We, then, compared dissimilarity in parasite taxonomic composition among migratory categories using an Analyses of Variance with permutation test (PERMANOVA) for homogeneity of multivariate dispersions. For this, we employed the “permutest” function also from the “vegan” package with 999 permutations. Again, we combined partial and full migrants into one migratory category and repeated the analyses above. A non-metric multidimensional scaling plot was used to visualize the dissimilarity in parasite taxonomic composition among avian host migratory categories.

**Results**

Among the 249 avian species included in the Bayesian analyses, 227 bird species were classified as resident whereas 16 and six were considered to be partially and fully migratory species, respectively. In these analyses, we assessed 81 species from Amazonia, 89 from Andean Forest, 73 from Cerrado, 68 from Atlantic Rain Forest and 34 from Caatinga. Our first Bayesian model revealed avian hosts display similar normalized degree (i.e. partner fidelity) among host migratory categories (Table 1) with normalized degree values around 0.10 (Fig. 2). Likewise, no difference was observed for partner fidelity when comparing resident versus non-resident (i.e. partial and full migrant hosts combined, Table 2).

For our next Bayesian models evaluating weighted closeness (i.e. network centrality), we observed that only partially migratory hosts present higher values of network centrality compared to residents (Table 3). On the other hand, when combining fully and partially migratory hosts into a unique category, we observed that non-resident avian hosts present higher network centrality than resident species (Fig. 3, Table 4). Betweenness values were similar among host migratory categories in both models (Supplementary Table 1-2), further only 51 hosts species presented weighted betweenness values higher than 0 being two full migratory, five partial migratory and 44 resident species. In all our Bayesian models phylogeny and biome had significant effects on partner fidelity (Table 1-4, Supplementary Table 3-4). Similarly, our network plot demonstrates most hosts and parasites are found within one main component (i.e. subgroup of vertices within a graph in which there is a path possible between all vertices) and that non-resident hosts are more centrally distributed in our parasite-host network system (Fig. 4). Moreover, we can also observe most parasites can infect multiple hosts while avian hosts seem mainly infected by one or a few distinct haemosporidian lineages.

Out of the 2465 haemosporidian infections included in our composition analyses, most infections (N = 1544) represent *Plasmodium* parasites, followed by *Haemoproteus* parasites with 909, with 590 classified in the subgenus *Parahaemoproteus* and 319 in the subgenus *Haemoproteus*. Only 12 infections of *Leucocytozoon* were included in these analyses. Additionally, most parasites were recovered from Amazonia (N = 638), Cerrado (N = 613) and Atlantic Rain Forest (N = 482). We observed no difference in parasite taxonomic composition among distinct migratory avian host categories when considering both resident versus partial and full migratory hosts separately (Fig. 5, Table 5) or combined (Table 6).

**Discussion**

Avian hosts can disperse haemosporidians across their flyways and are able to modify as well local patterns of infections (de Angeli Dutra et al. 2021b), thus, migrants shall present major roles into host-parasite networks. In this study, we observe that non-resident species possess greater closeness centrality in host-parasites networks, which indicate they rule the overall network connectance (i.e. interaction rate of a network out of the all putative interactions). However, we observe there is no difference between resident and non-resident hosts on betweenness centrality and that most species are not network connectors (betweenness centrality = 0). This result suggests that, despite the fact migrants drive overall network connectance, these hosts do not act as key connectors between species within the network. Additionally, we also observe that resident and non-resident hosts possess similar partner fidelity and parasite taxonomic composition evidencing similar parasites infect resident and non-resident hosts and there is no difference in pairwise parasite specificity among migratory and non-migratory species.

By connecting more species within the network migratory hosts can act as keystone species (i.e. species more important than others for keeping the structure and ecological services and functions within a community) since they interact with more distinct parasites lineages and are more closely associated to further hosts (*sensu* Paine 1969). Therefore, the impact of migrants’ presence in a community could impact local parasite-host dynamics. Indeed, previous research has associated the presence of migratory birds with variation on tick prevalence and haemosporidian prevalence and richness within the local community (de Angeli Dutra et al. 2021b; Fecchio et al. 2021). In contrast, despite the fact that only partial migratory hosts presented higher closeness centrality when evaluated separately, de Angeli Dutra et al. 2021a observed that only full migratory birds possess higher levels of prevalence and richness of haemosporidian parasites. Nevertheless, no difference was observed when evaluating betweenness centrality, suggesting resident and non-resident hosts play similar roles connecting parasites and other hosts. Thus, since migrants are present higher closeness centrality and more interactions within the network, they may shape the host-parasite communities transmission and structure.

Here, we also demonstrate migration do not impact partner fidelity for haemosporidian parasites and their avian hosts, hence, it is possible the predictability of migration patterns allow parasite to co-adapt to these hosts in a similar rate as they do for resident species. Furthermore, the trade-off between adapting to multiple environments and vectors may be compensated by the opportunities to colonize new habitats and host species. Concomitantly, haemosporidian parasites tend to infect wide subset of phylogenetically related hosts (Pinheiro et al. 2016; Huang et al. 2018). Thus, parasite host specificity patterns may remain similar within subsets of hosts which include resident and non-resident hosts leading to resembling parasite fidelity and taxonomic composition among distinct migratory categories. Indeed, we observed host phylogenetic effect in all our Bayesian models, therefore, host phylogeny may be associated to multiple factors shaping host-parasite networks. Furthermore, similarity in environmental conditions seem also to drive network structure for parasite and their hosts as biome category also ruled partner fidelity and centrality in all our models. Likewise, previous research suggest climate variation drivers haemosporidian parasite specificity in South America (Fecchio et al. 2019b). Therefore, host phylogeny and environment seem better predictors of parasite fidelity and taxonomic compositions.

Antagonistic interactions present lower partner fidelity patterns and, therefore, more malleability than mutualistic interactions (Fortuna et al. 2020). Hence, parasites could present looser evolutionary pressures for specialization favoring colonization of new habitats and spillover events. Indeed, in a recent spillover of *Plasmodium juxtanucleare* from domestic hosts (chickens) to wild passerine birds has been reported in Brazil (Ferreira-Junior et al. 2018), demonstrating haemosporidian parasites can adapt to new hosts when placed in alien habitats. Moreover, Krasnov et al. 2012 argued that parasites can infect unrelated hosts when phylogenetically close hosts are exploited by too many pathogens. It shows parasites are malleable enough to exploit hosts that are not usual in a response to adverse resource conditions. This plasticity could lead to looser interaction patterns in avian-haemosporidian networks and similar dynamics for resident and non-resident birds. Nevertheless, host-parasite networks tend to be more compartmentalized in modules (Bascompte 2010; Krasnov et al. 2012), which may reflect an ongoing arms race toward competition of adaptations (Bascompte 2010) and convergence of traits on distinct parasites (Krasnov et al. 2012).

Thus, here we show migratory hosts may be keystone species within host-parasite networks and their presence could putatively rule the avian and haemosporidian interactions by, for example, impact local prevalence and richness of parasites (de Angeli Dutra et al. 2021b). Additionally, most birds are not important connectors in this network with resident and non-resident hosts operating similar parts connecting hosts and parasites. However, it is important to notice that, despite the fact most hosts are not network connectors, most species are found inside a unique component. Moreover, no difference in partner fidelity or parasite taxonomic composition was detected in this study indicating parasite specificity may be associated to other traits of avian and vector hosts apart from migratory behavior. Further, biome and phylogeny seems to play a major role determining network characteristics of hosts in avian-haemosporidian networks, which have already been demonstrated for parasites trophically transmitted (Poulin et al. 2013). Finally, migrants can play fundamental roles in shaping host-parasite interactions and further research should aim to elucidate how migrants structure host-parasite interactions.

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**Availability of data and material**

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

**Authors’ contribution**

Daniela Dutra and Robert Poulin conceived the idea and designed the study. Daniela Dutra performed the data analyses. Daniela Dutra, Érika Braga and Alan Fecchio collected the data. Daniela Dutra wrote the manuscript with input from all other authors. All authors contributed critically to the drafts and gave final approval for publication.

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Fig. 1: Localities where haemosporidians were sampled from birds, comprising a total of 85 localities by combining our dataset and the MalAvi database.

Fig. 2: Mean (±credible intervals) normalized degree of avian hosts in bird-haemosporidian interaction networks according to the migratory category in which they are classified. R = resident, M = full migrant, PM = partial migrant.

Fig. 3: Mean (±credible intervals) weighted closeness of avian hosts in bird-haemosporidian interaction networks according to the migratory category in which they are classified. R = resident, M = full migrant and partial migrant.

Fig. 4: Network representing avian-haemosporidian interactions. Distinct colors represent avian hosts from distinct migratory categories or parasites. Circles represent avian hosts while triangles represent haemosporidian parasites.

Fig. 5: Non-metric multidimensional scaling plot illustrating the dissimilarity in parasite taxonomic composition among avian host migratory categories. R = resident, M = full migrant, PM = partial migrant.

Table 1: Parameter estimates, standard errors, and credible intervals for the Bayesian model testing the differences in partner fidelity to haemosporidian parasites among avian hosts from distinct migratory categories. (Residents only = reference category)

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | **Estimate** | **Std. error** | **Cred. Inter (95%)** | |
| Intercept | -2.27 | 0.16 | -2.59 | -1.94 |
| Full migratory host species | 0.12 | 0.17 | -0.23 | 0.45 |
| Partial migratory host species | 0.06 | 0.11 | -0.15 | 0.27 |
| Biomes | 0.28 | 0.17 | 0.09 | 0.76 |
| Avian host phylogeny | 0.08 | 0.06 | 0.00 | 0.22 |

Table 2: Parameter estimates, standard errors, and credible intervals for the Bayesian model testing the differences in partner fidelity to haemosporidian parasites between resident and non-resident avian hosts. (Residents only = reference category)

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | **Estimate** | **Std. error** | **Cred. Inter (95%)** | |
| Intercept | -2.28 | 0.16 | -2.60 | -1.94 |
| Non-resident host species | 0.08 | 0.09 | -0.11 | 0.26 |
| Biomes | 0.28 | 0.18 | 0.09 | 0.78 |
| Avian host phylogeny | 0.08 | 0.06 | 0.00 | 0.21 |

Table 3: Parameter estimates, standard errors, and credible intervals for the Bayesian model testing the differences in weighted closeness between resident and non-resident avian hosts. (Residents only = reference category)

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | **Estimate** | **Std. error** | **Cred. Inter (95%)** | |
| Intercept | -4.87 | 0.32 | -5.45 | -4.17 |
| Full migratory host species | 0.31 | 0.18 | -0.06 | 0.65 |
| Partial migratory host species | 0.29 | 0.12 | 0.06 | 0.53 |
| Biomes | 0.56 | 0.29 | 0.23 | 1.34 |
| Avian host phylogeny | 0.32 | 0.09 | 0.16 | 0.50 |

Table 4: Parameter estimates, standard errors, and credible intervals for the Bayesian model testing the differences in weighted closeness of avian hosts from distinct migratory categories. (Residents only = reference category)

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | **Estimate** | **Std. error** | **Cred. Inter (95%)** | |
| Intercept | -4.48 | 0.31 | -5.50 | -4.23 |
| Non-resident host species | 0.30 | 0.10 | 0.10 | 0.49 |
| Biomes | 0.57 | 0.30 | 0.24 | 1.39 |
| Avian host phylogeny | 0.32 | 0.09 | 0.16 | 0.50 |

Table 5: Degrees of freedom, sum and mean square and F and P value for permutational multivariate analysis of variance (PERMANOVA) testing the difference in parasite taxonomic composition among avian host from distinct migratory categories. (Residents only = reference category)

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  | **Degrees of Freedom** | **Sum Square** | **Mean Square** | **F value** | **P value** |
| Groups | 2 | 0.003365 | 0.0016823 | 0.783 | 0.46 |
| Residuals | 16 | 0.034376 | 0.0021485 |  |  |

Table 6: Degrees of freedom, sum and mean square and F and P value for permutational multivariate analysis of variance (PERMANOVA) testing the difference in parasite taxonomic composition among resident and non-resident avian species. (Residents only = reference category)

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  | **Degrees of Freedom** | **Sum Square** | **Mean Square** | **F value** | **P value** |
| Groups | 1 | 0.000212 | 0.000212 | 0.0745 | 0.79 |
| Residuals | 12 | 0.034095 | 0.002841 |  |  |