

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

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19

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

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

44 **Introduction**

45 Migration, i.e. long distance and periodical roundtrip movement of animals between  
46 distinct habitats, can alter interaction dynamics among parasites and their hosts by serving  
47 as an escape mechanism from some pathogens but also increasing parasite prevalence and  
48 richness of certain other pathogens within migrant host species (Altizer et al. 2011;  
49 Satterfield et al. 2015; de Angeli Dutra et al. 2021a; Poulin and de Angeli Dutra 2021).  
50 Migratory behavior can also modify the availability of hosts for parasites across regions  
51 since migrant individuals do not inhabit the same habitat year-round (Bauer and Hoye  
52 2014). At the same time, migrants can represent an opportunity for parasites to increase  
53 their distribution worldwide, as infected migrant individuals transport their pathogens  
54 through their routes and stopovers, therefore, providing new opportunities for host  
55 switching into new environments and resident species (Altizer et al. 2011; de Angeli Dutra  
56 et al. 2021b; Poulin and de Angeli Dutra 2021). Indeed, the presence of migratory  
57 individuals can also affect local parasite transmission, altering parasite prevalence and  
58 richness within resident host communities (Bauer and Hoye 2014; de Angeli Dutra et al.  
59 2021b; Fecchio et al. 2021). However, despite the fact migration can modulate parasite-host  
60 interaction, only a few studies have addressed the implications of host migration for  
61 parasite ecology and evolution (Poulin and de Angeli Dutra 2021).

62 Intrinsic characteristics of host-parasite interactions could be altered by host  
63 migratory behavior, including traits such as virulence (i.e. pathogenicity level) or partner  
64 fidelity, i.e. the species specificity in pairwise host-parasite associations. In this context,  
65 network analysis can be a powerful tool to explore the roles of particular species in host-  
66 parasite interactions (Runghen et al. 2021). Previous research suggests antagonistic

67 interactions display lower partner fidelity than mutualistic ones, indicating host-parasite  
68 interaction networks are evolutionarily malleable (Fortuna et al. 2020) and hosts traits can  
69 drive network descriptors (Campião and Dátilo 2020). Additionally, infecting migratory  
70 individuals may pose a challenge to parasites due to the need to adapt to novel resources  
71 and conditions, which could lead to looser fidelity among parasites and their migrant hosts.  
72 For example, for malaria parasites infecting migratory birds to be transmitted into their  
73 hosts' new habitats, they must be able to infect and complete their cycle in new vector  
74 species under distinct environmental characteristics (Valkiūnas 2005). Hence, the exposure  
75 of parasites to abrupt environmental and vector changes may impact the ecological and  
76 evolutionary relationship between parasites and their migratory hosts since host migrations  
77 represent repeated, predictable, and directional selective pressures (Møller and Szép 2011;  
78 Poulin and de Angeli Dutra 2021). Therefore, it is essential to study how host shifts  
79 between migratory and resident hosts occurring in sympatry and under different  
80 environmental conditions can alter parasite-host dynamics. This is necessary to elucidate  
81 how parasite life-history traits evolve under repeated and predictable changes.

82 Avian haemosporidian parasites, i.e. malaria and malaria-like vector borne  
83 protozoan parasites, are some of the most prevalent, diverse and studied wildlife pathogens.  
84 These parasites are an excellent ecological and evolutionary model to study host-parasite  
85 relationships due to their high prevalence, diversity, cosmopolitan distribution and variable  
86 levels of specificity to their hosts (Valkiūnas 2005). This is particularly relevant for South  
87 America, which harbors the highest diversity of birds, vectors and haemosporidian parasites  
88 worldwide (Remsen et al.; Santiago-Alarcon et al. 2012; Ellis et al. 2019). This region is  
89 also characterized by great vector abundance and considerable haemosporidian prevalence

90 (Braga et al. 2011; Santiago-Alarcon et al. 2012). Furthermore, avian community  
91 composition seems to impact parasite composition as well, with avian community turnover  
92 driving both haemosporidian and ornithophilic mosquito turnover across the Amazon  
93 region (De La Torre et al. 2021). All those features together make South America an ideal  
94 region to investigate ecological and evolutionary dynamics of avian haemosporidian  
95 interaction.

96 For the above reasons, studying the role of host migratory behavior in shaping  
97 parasite taxonomic composition (i.e. the set of distinct parasite lineages infecting a given  
98 host species), network centrality (i.e. the position a species occupies in the host-parasite  
99 interaction network) and partner fidelity is fundamental to understand the impact of host  
100 migration on life-history traits for parasites. Here, we hypothesize that resident species  
101 show higher partner fidelity to their parasites due to the greater stability of environmental  
102 conditions and vector species they face. Additionally, since migrants harbor higher richness  
103 of haemosporidians (de Angeli Dutra et al. 2021a) and because the more unstable  
104 environmental conditions and vectors they encounter may favor their infection by generalist  
105 parasites, we also expect them to occupy more central positions in host-parasite networks.  
106 Moreover, since migrants are exposed to more parasite lineages as they visit regions that  
107 harbor different parasite communities, our second hypothesis is that parasite taxonomic  
108 composition differs between resident and migratory avian hosts species. In this study, we  
109 computed and compared partner fidelity and network centrality levels between  
110 haemosporidians and their resident and partially and fully migratory avian hosts using  
111 Bayesian multilevel models. Further, using permutational multivariate analyses of variance

112 (PERMANOVA) we evaluated whether resident and migratory hosts harbor similar  
113 haemosporidian assemblages.

114

115 **Methods**

116 *Dataset*

117 All analyses were performed using a dataset comprising ~15200 individual birds  
118 representing 974 avian species. Avian communities were sampled in 85 different localities  
119 across seven different South American biomes - Amazonia, Atlantic Rain Forest, Cerrado,  
120 Temperate Grassland, Caatinga, Pantanal and Andean Forest (Fig. 1). The birds were  
121 sampled from 2005 to 2018 with a subset of those samples having previously been used in  
122 published research (Lacorte et al. 2013; Ferreira et al. 2017; Fecchio et al. 2019a, 2020;  
123 Anjos et al. 2021) and the rest consisting of unpublished data. This large dataset was  
124 combined with data available from MalAvi (<http://130.235.244.92/Malavi/>) and represents  
125 a total of 2758 sequenced parasites representing 752 distinct lineages, all belonging to one  
126 of three genera: *Plasmodium*, *Haemoproteus* and *Leucocytozoon*. Haemosporidian infection  
127 was estimated using PCR protocols described previously (Fallon et al., 2003; Hellgren et  
128 al., 2004; Bell et al., 2015). All lineages were identified by sequencing a DNA fragment  
129 obtained using PCR protocols described by Hellgren et al. (2004) that amplify a  
130 cytochrome b fragment of 478 base pairs. Hosts were classified into three migratory  
131 categories: (1) resident; (2) partial migrant and (3) full migrant, according to the Brazilian  
132 Committee of Ornithology Records - CRBO 2014, Somenzari et al., 2018 and BirdLife  
133 International (<https://www.birdlife.org/>).

134

135 *Haemosporidian-Host Partner Fidelity and Network Centrality Analyses*

136 All analyses were conducted in R version 4.0 (R Core Team, 2019). For  
137 haemosporidian-bird partner fidelity and network centrality analyses, we considered only  
138 biomes with at least 10 distinct parasite lineages, which involved 249 distinct avian host  
139 species and 40 parasite lineages from five biomes – Amazonia, Andean Forest, Cerrado,  
140 Caatinga and Atlantic Rain Forest (Supplementary Table S1). We created incidence  
141 matrices between avian host species and parasite lineages for each biome. Using the  
142 “specieslevel” function from the “bipartite” package (Dormann et al. 2008) in R, we  
143 computed normalized degree and weighted closeness and betweenness values for hosts  
144 infected by parasites in each biome. The first value represents the number of distinct  
145 realized interactions between hosts and parasites in each biome divided by the total number  
146 of distinct potential partners (i.e. parasites) in that same region. Normalized degree values  
147 can be employed as measures of partner fidelity, with hosts presenting higher values being  
148 less specific to their partners than hosts with lower values (Fortuna et al. 2020). On the  
149 other hand, weighted closeness and betweenness are measures of centrality in a network.  
150 Weighted closeness is calculated as the inverse minimum sum of the paths between a  
151 species (i.e. hosts) and all their partners (i.e. parasites) through the network, with hosts  
152 presenting higher closeness values being more central. In contrast, weighted betweenness  
153 represents the degree to which a species is positioned on the paths linking other species, i.e.  
154 the degree to which a species connects other species in an ecological network. We then  
155 combined the values obtained for birds in all biomes into one single dataset and ran a

156 Bayesian model to compare partner fidelity and network centrality among migratory  
157 categories.

158 In order to run our Bayesian analyses, we employed the function “`brm`” from the  
159 “`brms`” package (Bürkner 2017). In the first model, we considered normalized degree as the  
160 response variable and avian host migratory category (resident; partial migrant and full  
161 migrant, reference level = resident) as our population-level effect and used biome as  
162 random effect. Likewise, for our second model we employed weighted closeness as the  
163 response variable, avian host migratory category (resident; partial migrant and full migrant,  
164 reference level = resident) as our population-level effect and again biome as random effect.  
165 Then, we ran a third model with weighted betweenness as our response variable, again host  
166 migratory category (resident; partial migrant and full migrant, reference level = resident) as  
167 our population-level effect and biome as random effect. We downloaded the full avian  
168 phylogeny file from the AllBirdsHackett1.tre website (<https://birdtree.org/>), selected only  
169 the species used for our analyses and created a matrix with phylogenetic distances between  
170 bird species. This matrix was also added to all our model as random effect to account for  
171 host phylogenetic influence on partner fidelity and network centrality. Priors were  
172 determined using the “`get_prior`” function. We ran the Bayesian models using 4 chains with  
173 4000 total iterations per chain (2000 for warmup, 2000 for sampling) and employed zero-  
174 one inflated beta distributions, since normalized degree and weighted closeness and  
175 betweenness represent rate data. Further, we subsequently combined partial and full  
176 migrants into one single category and repeated our Bayesian analyses. Afterwards, we  
177 applied the “`bip_ggnet`” function from the “`ggnet`” package ([briatte.github.io/ggnet/](https://briatte.github.io/ggnet/)) to plot

178 a bipartite net representing the relationships among haemosporidian lineages and avian  
179 hosts from different migratory categories.

180

181 *Haemosporidian Taxonomic Composition Analyses*

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

196

197 **Results**

198 Among the 249 avian species included in the Bayesian analyses, 227 bird species  
199 were classified as resident whereas 16 and six were considered to be partially and fully

200 migratory species, respectively. In these analyses, we assessed 81 bird species from  
201 Amazonia, 89 from Andean Forest, 73 from Cerrado, 68 from Atlantic Rain Forest and 34  
202 from Caatinga. Our first Bayesian model revealed avian hosts display similar normalized  
203 degree (i.e. partner fidelity) among host migratory categories (Table 1) with normalized  
204 degree values around 0.10 (Fig. 2). Likewise, no difference was observed for partner  
205 fidelity when comparing resident versus non-resident (i.e. partial and full migrant hosts  
206 combined, Table 2).

207 For our next Bayesian models evaluating weighted closeness (i.e. network  
208 centrality), we observed that only partially migratory hosts present higher values of  
209 network centrality compared to residents (Table 3). On the other hand, when combining  
210 fully and partially migratory hosts into a single category, we observed that non-resident  
211 avian hosts present higher network centrality than resident species (Fig. 3, Table 4).  
212 Betweenness values were similar among host migratory categories in both models  
213 (Supplementary Tables S3, S4). Furthermore, only 51 hosts species had weighted  
214 betweenness values higher than 0, consisting of two full migratory, five partial migratory  
215 and 44 resident species. In all our Bayesian models phylogeny and biome had significant  
216 effects on partner fidelity (Tables 1-4, Supplementary Tables S3, S4). Similarly, our  
217 network plot demonstrates most hosts and parasites are found within one main component  
218 (i.e. subgroup of vertices within a graph in which there is a path possible between all  
219 vertices) and that non-resident hosts are more centrally distributed in our parasite-host  
220 network system (Fig. 4). Moreover, we can also observe that most parasites infect multiple  
221 hosts while avian hosts seem mainly infected by one or a few distinct haemosporidian  
222 lineages.

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

232

### 233   **Discussion**

234           Avian hosts can disperse haemosporidians across their flyways and are also able to  
235   modify local patterns of infections (de Angeli Dutra et al. 2021b), thus, migrants can play  
236   major roles into host-parasite networks. In this study, we observed that non-resident species  
237   display greater closeness centrality in host-parasites networks, which indicates they play a  
238   disproportionate role in overall network connectance (i.e. the proportion of realized  
239   interactions in a network out of the all possible interactions). However, we found no  
240   difference between resident and non-resident hosts in betweenness centrality and that most  
241   species are not network connectors (betweenness centrality = 0). This result suggests that,  
242   despite the fact migrants drive overall network connectance, these hosts do not necessarily  
243   act as key connectors between species within the network. Additionally, we also observed  
244   that resident and non-resident hosts show similar partner fidelity and parasite taxonomic  
245   composition, demonstrating that similar parasites infect resident and non-resident hosts and

246 that there is no difference in pairwise parasite specificity among migratory and non-  
247 migratory species.

248 By connecting more species within the network, migratory hosts can act as keystone  
249 species (i.e. species with disproportionate importance in keeping the structure and  
250 ecological services and functions within a community; *sensu* Paine 1969) since they  
251 interact with more distinct parasite lineages and are more closely associated with further  
252 hosts. Therefore, the presence of migrants in a community could impact local parasite-host  
253 dynamics. Indeed, previous research has associated the presence of migratory birds with  
254 variation in tick prevalence and haemosporidian prevalence and richness within the local  
255 community in South America (de Angeli Dutra et al. 2021b; Fecchio et al. 2021). In  
256 contrast, despite the fact that only partially migratory hosts presented higher closeness  
257 centrality when evaluated separately, de Angeli Dutra et al. (2021a) observed that only  
258 fully migratory birds harbor higher prevalence and richness of haemosporidian parasites.  
259 Nevertheless, no difference was observed here with respect to betweenness centrality,  
260 suggesting resident and non-resident hosts play similar roles in connecting parasites and  
261 other hosts. Thus, since migrants show higher closeness centrality and are involved in  
262 disproportionately more interactions within the network, they are influential in shaping  
263 parasite transmission within the community.

264 We also demonstrated that migration does not impact partner fidelity for  
265 haemosporidian parasites and their avian hosts. Hence, it is possible the predictability of  
266 migration patterns allows parasites to co-adapt to these hosts as successfully as they do for  
267 resident species. Furthermore, the trade-off between adapting to multiple environments and  
268 vectors may be compensated by the opportunities to colonize new habitats and host species

269 provided by host migration. Concomitantly, haemosporidian parasites tend to infect wide  
270 subsets of phylogenetically related avian hosts (Pinheiro et al. 2016; Huang et al. 2018).  
271 Thus, parasite host specificity patterns may remain similar within subsets of hosts which  
272 include resident and non-resident species, leading to similar parasite fidelity and taxonomic  
273 composition among distinct migratory categories. Indeed, we observed a host phylogenetic  
274 effect in all our Bayesian models, indicating that host phylogeny may be associated with  
275 multiple factors shaping host-parasite networks. Furthermore, similarity in environmental  
276 conditions also seems to affect network structure for parasites and their hosts as biome  
277 category (included as a random factor) also influenced partner fidelity and centrality in all  
278 our models. Likewise, previous research suggests that climate variation is an important  
279 driver of haemosporidian parasite specificity in South America (Fecchio et al. 2019b).  
280 Therefore, host phylogeny and environment may be better predictors of parasite fidelity and  
281 taxonomic compositions than host migratory behavior.

282 Antagonistic interactions are generally characterized by lower partner fidelity  
283 patterns and, therefore, more malleability than mutualistic interactions (Fortuna et al.  
284 2020). Therefore, parasites may be associated with looser evolutionary pressures for  
285 specialization favoring colonization of new habitats and spillover events. Indeed, a recent  
286 spillover of *Plasmodium juxtanucleare* from domestic and exotic hosts (chickens) to wild  
287 passerine birds has been reported in Brazil (Ferreira-Junior et al. 2018), demonstrating  
288 haemosporidian parasites can adapt to new hosts when placed in alien habitats. Moreover,  
289 Krasnov et al. (2012) argued that parasites can infect unrelated hosts when phylogenetically  
290 close hosts are exploited by too many pathogens. These findings suggest that parasites are  
291 malleable enough to exploit unfamiliar hosts in response to adverse resource conditions.

292 This plasticity could lead to looser interaction patterns in avian-haemosporidian networks  
293 and similar dynamics for resident and non-resident birds. Nevertheless, host-parasite  
294 networks tend to be compartmentalized into modules (Bascompte 2010; Krasnov et al.  
295 2012), which may reflect an ongoing arms race between parasites and their hosts  
296 (Bascompte 2010) and consequential convergence of traits among distinct parasites  
297 (Krasnov et al. 2012).

298 In summary, we show migratory hosts may be keystone species within host-parasite  
299 networks and their presence could putatively shape bird-haemosporidian interactions by,  
300 for example, impacting local prevalence and richness of parasites (de Angeli Dutra et al.  
301 2021b). Additionally, most birds are not important connectors in this network, with resident  
302 and non-resident hosts playing similar parts in connecting hosts and parasites. However, it  
303 is important to note that, despite the fact most avian hosts are not network connectors, most  
304 species belong to a single network component. Moreover, no difference in partner fidelity  
305 or parasite taxonomic composition was detected in this study between migrant and non-  
306 migrant birds, indicating parasite specificity may be associated with other traits of avian  
307 and vector hosts. Further, biome and phylogeny seem to play important roles in  
308 determining network characteristics of hosts in avian-haemosporidian networks, an effect  
309 already demonstrated in systems involving trophically transmitted parasites (Poulin et al.  
310 2013). We conclude that migrants may play fundamental roles in shaping host-parasite  
311 interactions, and encourage further research into other potential implications of host  
312 migration for disease dynamics.

313

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325

326 **Availability of data and material**

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

331

332 **Authors' contribution**

333 Daniela Dutra and Robert Poulin conceived the idea and designed the study. Daniela Dutra  
334 performed the data analyses. Daniela Dutra, Érika Braga and Alan Fecchio collected the

335 data. Daniela Dutra wrote the manuscript with input from all other authors. All authors  
336 contributed critically to the drafts and gave final approval for publication.

337

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445

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

448

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

452

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

456

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

460

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

464

465

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

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

469

470

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

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

474

475 Table 3: Parameter estimates, standard errors, and credible intervals for the Bayesian model  
476 testing the differences in closeness centrality to haemosporidian parasites among avian  
477 hosts from distinct migratory categories. (Residents only = reference category)

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

478

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

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

482

483 Table 5: Results of the permutational multivariate analysis of variance (PERMANOVA)  
484 testing the difference in parasite taxonomic composition among avian hosts from distinct  
485 migratory categories. (Residents only = reference category)

	<i>Degrees of Freedom</i>	<i>Sum Square</i>	<i>Mean Square</i>	<i>F value</i>	<i>P value</i>
<i>Groups</i>	2	0.003365	0.0016823	0.783	0.46
<i>Residuals</i>	16	0.034376	0.0021485		

486

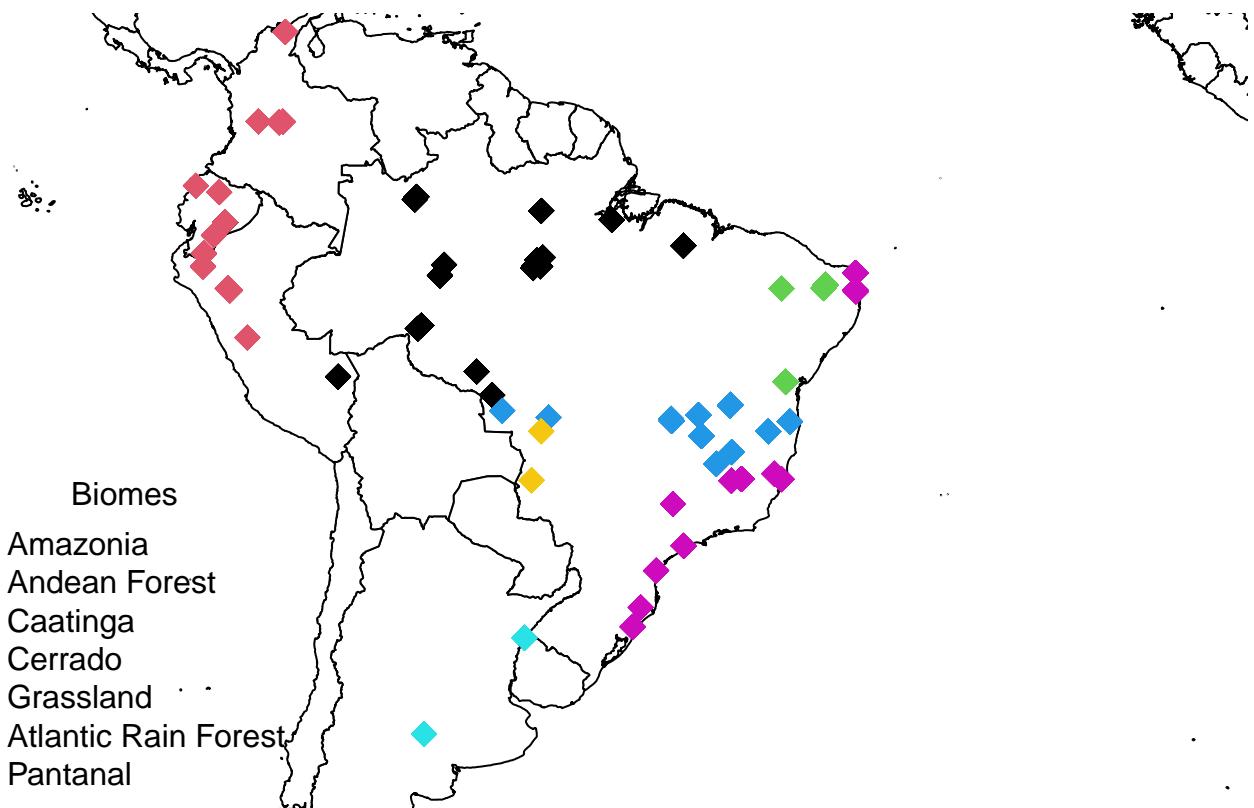
487

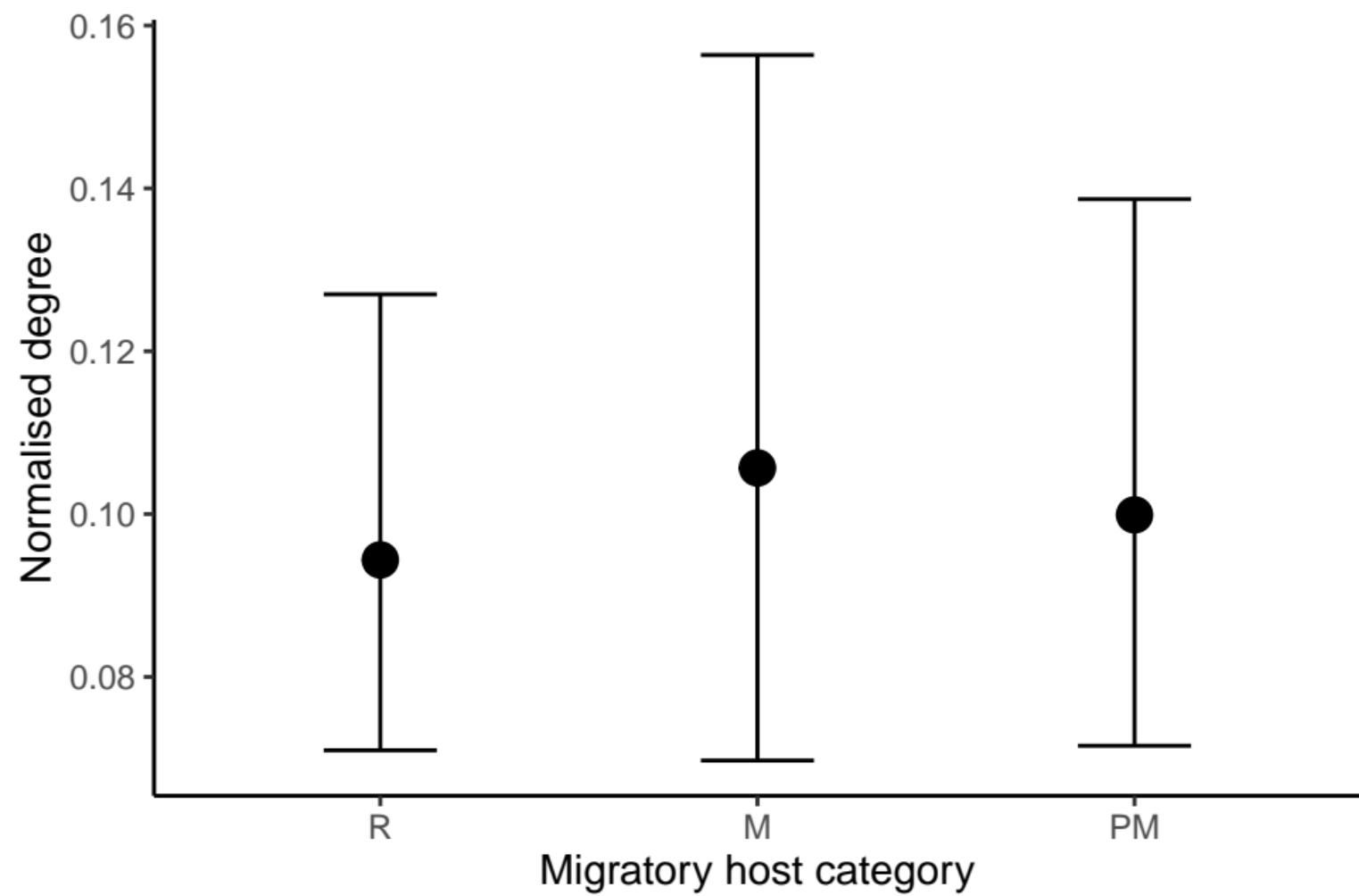
488 Table 6: Results of the permutational multivariate analysis of variance (PERMANOVA)  
489 testing the difference in parasite taxonomic composition among resident and non-resident  
490 avian species. (Residents only = reference category)

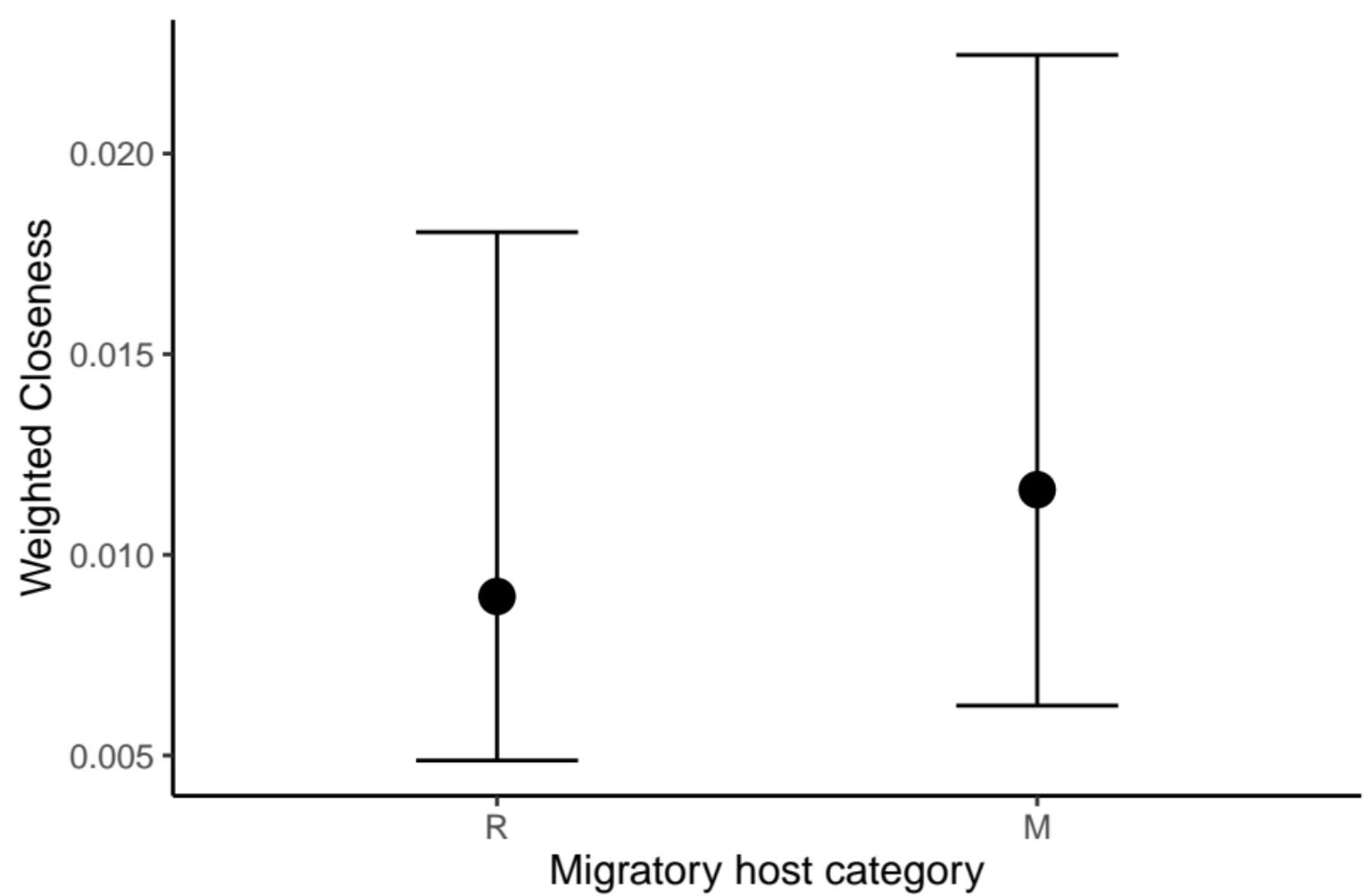
	<i>Degrees of Freedom</i>	<i>Sum Square</i>	<i>Mean Square</i>	<i>F value</i>	<i>P value</i>
<i>Groups</i>	1	0.000212	0.000212	0.0745	0.79
<i>Residuals</i>	12	0.034095	0.002841		

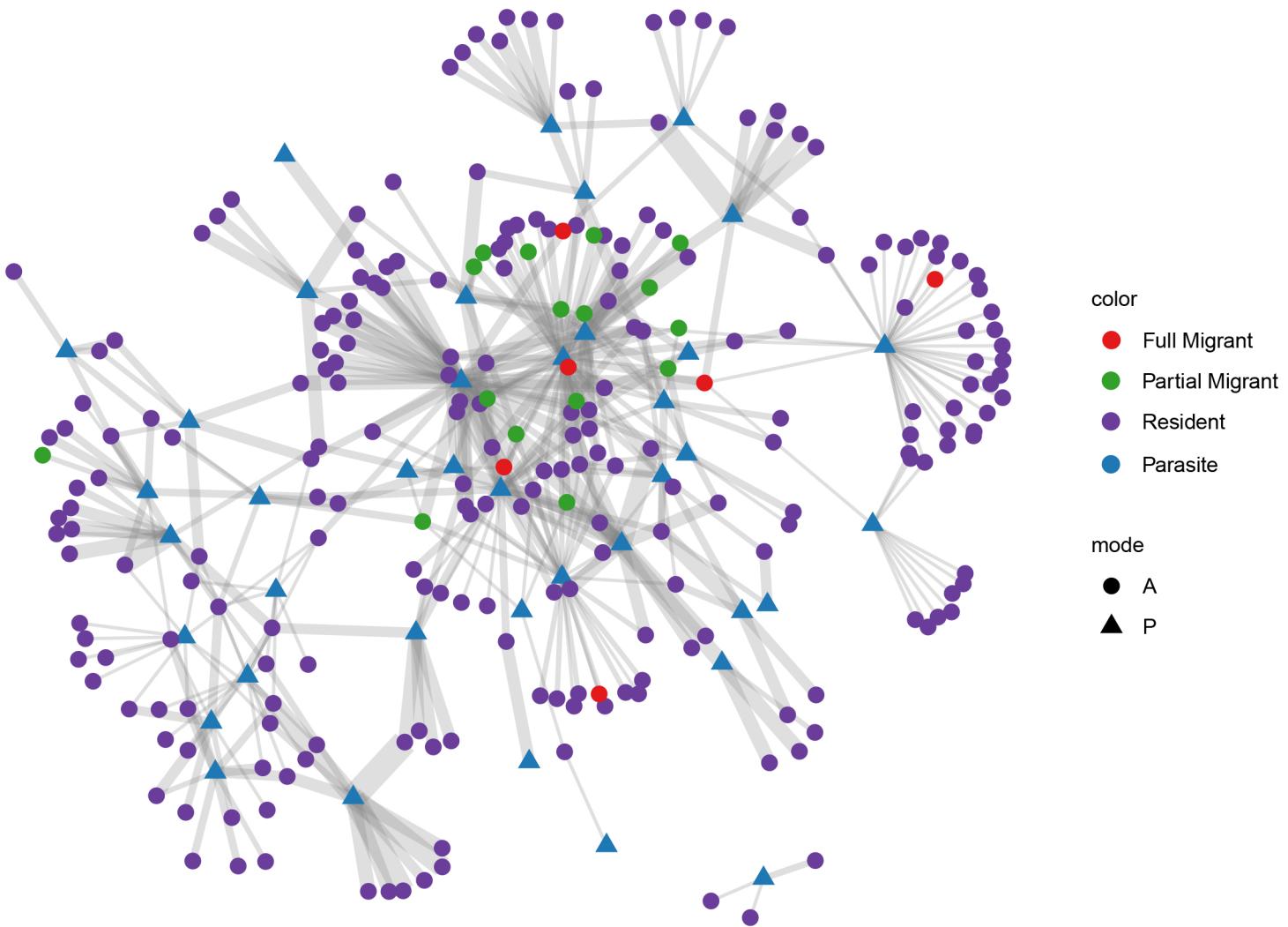
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492









PCoA 2

-0.3 -0.1 0.1 0.3

-0.5

PCoA 1

