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# Climate variation influences host specificity in avian malaria parasites

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48

49 **Abstract**

50 Parasites with low host specificity (e.g. infecting a large diversity of host species) are of special  
51 interest in disease ecology, as they are likely more capable of circumventing ecological or  
52 evolutionary barriers to infect new hosts than are specialist parasites. Yet for many parasites,  
53 host specificity is not fixed and can vary in response to environmental conditions. Using data on  
54 host associations for avian malaria parasites (Apicomplexa: Haemosporida), we develop a  
55 hierarchical model that quantifies this environmental dependency by partitioning host specificity  
56 variation into region- and parasite-level effects. Parasites were generally phylogenetic host  
57 specialists, infecting phylogenetically clustered subsets of available avian hosts. However, the  
58 magnitude of this specialization varied biogeographically, with parasites exhibiting higher host  
59 specificity in regions with more pronounced rainfall seasonality and wetter dry seasons.  
60 Recognizing the environmental dependency of parasite specialization can provide useful  
61 leverage for improving predictions of infection risk in response to global climate change.

62

## 63 INTRODUCTION

64 Global disease burdens commonly reflect host range expansions (termed herein as ‘host  
65 shifting’) by multi-host parasites (Han *et al.* 2015; Wells *et al.* 2018a). Host specificity (e.g. the  
66 diversity of host species a parasite is capable of infecting) is a useful metric to describe  
67 differences among parasites in their capacity to infect novel hosts or trigger parasitic disease  
68 emergence events (Poulin *et al.* 2011). With the majority of emerging infectious diseases thought  
69 to result from shifting host associations by parasites with low host specificity, a major goal in  
70 disease ecology is to apply host specificity metrics using observed host association data to  
71 identify ‘generalist’ parasites before they cause disease outbreaks (Cooper *et al.* 2012; Brooks *et*  
72 *al.* 2014; Dallas *et al.* 2017). However, mounting experimental and theoretical evidence suggests  
73 that host specificity is not a fixed trait (Poulin & Mouillot 2005; Brooks & Hoberg 2007; Agosta  
74 *et al.* 2010; Nylin *et al.* 2018). Instead, a parasite’s local host specificity (herein termed ‘realized  
75 host specificity’) can be considered the product of a hierarchical process involving both regional  
76 and evolutionary forces (Wells *et al.* 2018b). For host range expansions to occur, a parasite must  
77 first be exposed to a novel host species. This exposure will be influenced by environmental  
78 conditions that determine host community composition, as spatiotemporal variation in host  
79 occurrences alters host-parasite contact rates (Canard *et al.* 2004). Second, adaptation to a new  
80 host is required to facilitate transmission. For many parasites, this process is expected to adhere  
81 to the principle of ‘ecological fitting’ (Janzen 1985), which states that sharing certain  
82 characteristics with previous host species is necessary for successful infection (Brooks *et al.*  
83 2006; Davies & Pedersen 2008; Poulin *et al.* 2011; Clark & Clegg 2017). Yet host traits that  
84 influence susceptibility, such as clutch size or breeding behavior, can fluctuate in response to  
85 environmental conditions (Møller *et al.* 2013). Despite an accelerated focus on describing host  
86 specificity for a multitude of parasites (de Vienne *et al.* 2009; Hellgren *et al.* 2009; Farrell *et al.*  
87 2013; Clark *et al.* 2018; Doña *et al.* 2018; Park *et al.* 2018), few empirical studies recognize this  
88 environmental dependency by treating specificity as a geographically labile trait (but see  
89 Krasnov *et al.* 2004a, b; Well *et al.* 2018b).

90 The challenge of assessing variation in realized host specificity is understandable. This  
91 requires detailed information about the host distributions of parasites across climatically variable  
92 bioregions, which is difficult to acquire for many parasites (Murray *et al.* 2015). Nevertheless,  
93 the lack of a comprehensive assessment of how climate variation influences host specificity

94 presents an impediment for both predicting the emergence of infectious diseases and developing  
95 mitigation strategies (Altizer *et al.* 2013; Brooks *et al.* 2014). We address this gap by using a  
96 hierarchical modelling approach to test whether the realized host specificity of multi-host  
97 parasites varies across biogeographical regions. Focusing on a cosmopolitan group of avian  
98 blood parasites, we partition variation in realized host specificity into regional and parasite-level  
99 effects.

100 Avian haemosporidians (including the genera *Plasmodium* and *Haemoproteus*, termed  
101 hereafter as avian malaria parasites) are protozoan parasites that infect bird blood cells and are  
102 transmitted by hematophagous dipteran vectors (Valkiūnas 2005; Santiago-Alarcon *et al.* 2012a).  
103 These parasites are globally distributed, abundant and diverse in most bird clades, and their  
104 estimated host specificities are highly variable, ranging from infecting a single host species to  
105 many unrelated species (Valkiūnas 2005; Clark *et al.* 2014; Moens & Pérez-Tris 2016). Previous  
106 studies have revealed that the distributions and community compositions of avian malaria  
107 parasites are the outcome of host switching events over macroevolutionary timescales (Ricklefs  
108 *et al.* 2014; Fecchio *et al.* 2018b) and recent ecological forces such as variation in host dispersion  
109 capability (Pérez-Tris & Bensch 2005; Ellis *et al.* 2015; Clark *et al.* 2017; Fecchio *et al.* 2018b).  
110 Yet mechanisms that contribute to the large observed variation in host specificity are largely  
111 unknown, although environmental forces may play substantial roles (Clark *et al.* 2017). For  
112 example, risk of *Plasmodium* infection in birds is expected to increase with increasing  
113 temperatures on a global scale (Garamszegi 2011). Despite not being able to directly link  
114 climatic conditions to parasite specialization, Garamszegi (2011) demonstrated that the impact of  
115 climate change on avian *Plasmodium* prevalence varies on a continental scale, with the strongest  
116 effects found for Europe and Africa. Climate variation also influences rates of parasite  
117 reproduction and development within vector hosts, which could in turn affect parasite  
118 transmission and the exposure of parasites to novel host species (LaPointe *et al.* 2010; Santiago-  
119 Alarcon *et al.* 2012a).

120 The search for general processes governing host specificity should assess both ecological  
121 and phylogenetic relationships of potential host species in efforts to identify barriers to host  
122 range expansions (Poulin & Mouillot 2005; Hoberg & Brooks 2008; Clark *et al.* 2017). We  
123 present our framework using a database comprising infection data for 154 multi-host avian  
124 malaria parasites sampled from 15,541 individual birds in South America and the Australia-

125 Pacific. Samples cover 109 sites, which we group into 10 biogeographical regions to delineate  
126 communities with similar environmental conditions and avian compositions (Fig. 1 and Table 1).  
127 We consider variation in pairwise distances between infected (i.e. observed to carry a parasite)  
128 and potential (i.e. hosts occurring in the same region but not found to be infected) host species to  
129 represent a signal of realized host specificity. We test whether magnitudes of realized  
130 phylogenetic and ecological host specificity vary across regions using a multilevel model that  
131 includes parameters reflecting region-level and parasite-level contributions. We then test whether  
132 environmental (rainfall and temperature) and biotic (host and parasite species diversity) factors  
133 explain regional differences in host specificity.

134

## 135 **MATERIAL AND METHODS**

### 136 **Parasite database**

137 All parasite lineages in our dataset were identified using PCR-based detection methods targeting  
138 a 477 cytochrome-*b* (*cyt-b*) barcoding fragment of the haemosporidian mitochondrial genome.  
139 The majority of observations came from field studies led by the authors from the period of 2005  
140 - 2016, with remaining observations extracted from published studies that took place in the study  
141 region (see Clark *et al.* 2017 for details). Protocols detailing reactions, reagents, primer names,  
142 cycling conditions, and how lineages were determined can be found in (Hellgren *et al.* 2004;  
143 Bensch *et al.* 2009; Bell *et al.* 2015). As evidence indicates that avian malaria lineages differing  
144 by one *cyt-b* nucleotide may be reproductively isolated entities (Bensch *et al.* 2004), we use the  
145 standard practice of referring to each unique *cyt-b* lineage as a unique parasite.

146

### 147 **Climate variable extraction and biogeographic region delineation**

148 Our study region was delineated to represent a diversity of habitats, avian compositions, and  
149 climate envelopes so that we had robust statistical power to estimate associations between  
150 regional conditions and host ranges of parasites. We extracted 19 climate variables (based on  
151 average values from the years 1970 - 2000) for each site (n = 109) from [www.worldclim.org](http://www.worldclim.org)  
152 (accessed March 2018; see Appendix S1 in Supporting Information). We chose WorldClim  
153 records as such lower resolution climate data are more appropriate for predicting species'  
154 distributions across large bioregions (i.e. the distributions of potential and realized hosts), which  
155 higher resolution climate data may fail to detect due to localized weather events or stochastic

156 variation. Records of avian occurrences for sites were extracted from species distribution maps  
157 acquired from [www.datazone.birdlife.org](http://www.datazone.birdlife.org) (BirdLife International and NatureServe, 2017). We  
158 grouped sites into 10 biogeographical regions using hierarchical clustering of a Gower's matrix  
159 (Gower 1971) capturing dissimilarity in avian community composition and climate variables  
160 (Table 1, Fig. 1, Appendix S1). We chose this method for grouping sites into regions based on  
161 mounting evidence that variation in avian composition and long-term climate variables both have  
162 major influences on the assembly, prevalence, and host specificity of avian malaria parasites  
163 (e.g., Sehgal 2010; Clark *et al.* 2017; Clark 2018; Fecchio *et al.* 2018a). Our clustering method  
164 therefore presents a data-driven approach designed to delineate regions that are biologically  
165 meaningful at the parasite level.

166

### 167 **Avian host phylogenetic and ecological relationships**

168 Distributions for a total of 5,450 avian species overlapped our sample area according to BirdLife  
169 species range maps. We extracted phylogenetic and ecological data for these species to generate  
170 estimates of historical and functional relationships of potential host species. Note that only  
171 species sampled for avian malaria parasites were considered as potential hosts (957 species).  
172 Phylogenetic distances were calculated as mean pairwise distance across 100 phylogenetic trees  
173 sampled from a global avian supertree distribution (Jetz *et al.* 2012; accessed at  
174 <http://birdtree.org/subsets/>). We extracted species' proportional use of ten diet categories and  
175 seven foraging habitats (traits likely to impact parasite exposure) from EltonTraits v1.0 (Wilman  
176 *et al.* 2014). We quantified pairwise ecological distances using a Gower's distance matrix  
177 (Gower 1971) following methods in Pavoine *et al.* (2009). Host phylogenetic and ecological  
178 distance matrices were scaled (dividing by the maximum for each matrix; see Appendix S2).

179

### 180 **Statistical analysis**

#### 181 *Parasite- and region-specific host specificity*

182 Lists of potential avian host species (i.e. species sampled for avian malaria parasites) were  
183 generated for parasites in each region where the parasite was recorded. This resulted in parasite-  
184 and region-specific potential host pools for which associations were recorded as binary variables  
185 (i.e. '1' if the potential host was infected, '0' if uninfected). Vectors of potential host pairwise  
186 distances were response variables in hierarchical linear regressions of the form



187  $distance \sim \mathcal{N}(\mu_{region} + \beta_{region*parasite} host.pair, \sigma^2)$   
188  $\mu_{region} \sim \mathcal{N}(H_{\mu}, \sigma_{\mu}^2); \beta_{region*parasite} \sim \mathcal{N}(\mu_{\beta} + \beta_{parasite} + \beta_{region}, \sigma_{\beta}^2)$   
189  $\mathcal{N}(\mu, \sigma^2)$  denotes normal distributions with mean  $\mu$  and variance  $\sigma^2$ .  $\mu_{region}$  denotes regional  
190 averages (corresponding to the intercept of linear models) of either ecological or phylogenetic  
191 pairwise distances (*distance*) for potential host pools, drawn from a hyperprior  $H_{\mu}$  with Gaussian  
192 error  $\sigma_{\mu}^2$  representing ‘global’ averages. Coefficients  $\beta_{region*parasite}$  represent parasite- and region-  
193 specific estimates of differences between observed and potential host distances (i.e. the binary  
194 indicator variable *host.pair* where ‘1’ indicates the pair of potential host species that is infected;  
195 ‘0’ indicates that they are uninfected). This was modelled with intercept  $\mu_{\beta}$  and coefficients  
196  $\beta_{parasite}$  and  $\beta_{region}$  to capture expectations that host specificity is a function of both parasite  
197 identity and environmental conditions.

198 We used Gibbs Variable Selection (GVS) to pull  $\beta_{parasite}$  and  $\beta_{region}$  estimates towards zero  
199 when support was limited (O’Hara & Sillanpää 2009). We sampled *Bernoulli* indicator variables,  
200 in this case  $I$ , to control whether the effect  $\beta$  was included in the model. By specifying a low  
201 prior probability of drawing 1 for indicator variable  $I$ , we only estimated  $\beta$  if sufficient data  
202 existed to warrant its inclusion. If  $I = 0$ , indicating little support for sampling  $\beta$  according to  
203 likelihood estimates, we sampled instead from a ‘pseudo-prior’ that resulted in zero-effects. This  
204 ensured avoidance of over-parameterization (Wells *et al.* 2016).  $\beta_{parasite}$  estimates were sampled  
205 from normal hyperpriors ( $H_{genus}$ ), which were based on the average specificity for the parasite’s  
206 respective genus (*Plasmodium* or *Haemoproteus*), using parasite-specific variance components  
207 ( $\sigma_{parasite}^2$ ). Estimates for  $\beta_{region}$  were drawn from a ‘global’ normal distribution. Parameters were  
208 estimated independently for phylogenetic and ecological specificity (Appendix S3).

209 We estimated  $\beta$  coefficients for each parasite and each region using Markov Chain Monte  
210 Carlo (MCMC) sampling based on the Gibbs sampler in the open-source software JAGS  
211 (Plummer 2003). Priors for coefficients were specified with  $H \sim \mathcal{N}(0, 10)$  and  $\sigma \sim \text{dexp}(0.5)$ . We  
212 ran two MCMC chains for 50,000 iterations for parameter adaptation and sampled 1,000  
213 posterior estimates. Mixing of chains was inspected visually and with the Gelman-Rubin  
214 diagnostic (all values < 1.2). We compared magnitudes of  $\beta_{region}$  and  $\beta_{parasite}$  coefficients to gather  
215 evidence that particular parasites and/or regions showed different host specificities in  
216 comparison to other parasites/regions. Distances between infected host species that differ from  
217 draws from potential host pools indicate specificity; lower values (i.e. 95% credible intervals <

218 0) indicate higher similarity between observed hosts than expected; values  $> 0$  suggest that  
219 parasites infect more distantly related hosts than expected (Clark & Clegg 2017).

220 Many parasites were only recorded infecting a single host species ( $n = 468$  single-host  
221 parasites) and for some hosts we sampled only a few individuals (289 host species). Because our  
222 estimate of host specificity is based on pairwise distances from potential and realized host pools,  
223 detecting significant effects is only possible with reasonable sample sizes. We filtered the dataset  
224 by keeping (1) host species with at least eight samples in each region and (2) parasites that  
225 infected at least one of the included host species and were recorded at least three times overall.  
226 This allowed us to assess host species that have been sufficiently sampled to detect relatively  
227 rare parasites (i.e. a sample size of eight translates to an  $\sim 80\%$  probability of detecting a parasite  
228 with a true prevalence of 20%) and to assess parasites for which we have adequate information  
229 on observed host ranges. This dataset included 154 parasite lineages (71 *Plasmodium*, 83  
230 *Haemoproteus*; Appendix S3 and S4), which were recorded in 2 – 24 different avian host species  
231 and across 1 – 4 different biogeographical regions (Fig. 2). A total of 289 avian species were  
232 included as potential host species across the final dataset. We did not record whether avian  
233 species were native or introduced, as their occurrence within a region (regardless of how they  
234 came to be there) should still make them suitable as potential host species.

### 235 236 *Predictors of regional variation in host specificity*

237 We explored potential predictors of regional variation in host specificity using posterior modes  
238 of  $\beta_{region}$  coefficients as response variables in a multiple linear regression with assumed Gaussian  
239 error distribution. We tested six climate variables (all related to temperature and precipitation) as  
240 continuous covariates. Indices of region-specific host phylogenetic and ecological diversity were  
241 calculated using a metric that captured host species richness and average pairwise distances  
242 within each region ( $\mu_{region}$  estimates). These were also included as covariates to assess whether  
243 increased host diversity (in terms of either phylogenetic or functional diversity) leads to  
244 increased parasite specialization. To account for sampling bias, we included parasite richness,  
245 the number of birds screened (sample size), and the GVS support for  $\beta_{region}$  estimates as  
246 covariates. Collinearity was accounted for by removing the more highly correlated variable (i.e.  
247 the variable that showed a higher number of strong pairwise correlations) from those pairs with  
248 Pearson correlations  $> 0.7$ . Remaining covariates were: minimum rainfall of the driest quarter,

249 maximum rainfall of the wettest quarter, rainfall seasonality, minimum temperature of the  
250 coldest quarter, temperature seasonality, parasite species richness, sample size, and host  
251 diversity. We used LASSO variable selection (where the important predictors are retained by  
252 iteratively regularizing coefficients for less important predictors toward zero) and leave-one-out  
253 cross-validation to test within-sample model fit (Friedman *et al.* 2010). This was repeated 1,000  
254 times to minimize cross-validated error and identify important predictors (i.e. those retained in at  
255 least 90% of cross-validation runs). We calculated proportions of explained variance for retained  
256 predictors following Nakagawa and Schielzeth (2013; see Appendix S3).

257 Analyses were conducted in R version 3.3.3 (R Core Team, 2017) and primarily used  
258 functions in packages *ade4* (Dray & Dufour 2007), *dplyr* (Wickham *et al.* 2017), *glmnet*  
259 (Friedman *et al.* 2010), *readxl* (Wickham & Bryan 2017), and *rjags* (Plummer 2016). Tutorials  
260 to replicate analyses are included in the Appendices. GenBank accession numbers for the 154  
261 modelled parasites are presented in Appendix S4.

262

## 263 RESULTS

264 Our hierarchical regression is formulated to test the extent to which parasite identity ( $\beta_{parasite}$ ) and  
265 regional environmental conditions ( $\beta_{region}$ ) contribute to a parasite's realized host specificity.  
266 Applying this framework to observed host association data for 154 multi-host avian malaria  
267 parasites, we find that realized host specificity varies across biogeographical regions (Fig. 1).  
268 Patterns are similar regardless of whether we assess ecological or phylogenetic  $\beta_{region}$  specificity,  
269 suggesting the presence of general biogeographical forces influencing the host ranges of avian  
270 malaria parasites (Fig. 1). Cross-validated linear regressions to explore environmental predictors  
271 of host specificity variation show a strong influence of precipitation heterogeneity: regions with  
272 more pronounced rainfall seasonality harbor more specialized parasites (smaller  $\beta_{region}$   
273 estimates), with the coefficient of rainfall variation accounting for 53% of explained variance in  
274  $\beta_{region}$  estimates ( $t = -0.56$ ; Appendix S3). Although seasonality is important, rainfall in the dry  
275 season also correlates with variation in host specificity: minimum rainfall of the driest quarter  
276 accounted for a further 35% of explained variance, with parasites becoming more specialized in  
277 regions with wetter dry seasons ( $t = -0.45$ ; Fig. 3, Appendix S3).

278 Inferences on climate-driven effects were robust to potential sampling bias, which we  
279 accounted for by focusing on adequately sampled hosts and parasites to minimize underestimates

280 of host ranges (see ‘Parasite- and region-specific host specificity’ in Material and Methods and  
281 Appendix 3 for details). Moreover, parameters capturing variation in sample sizes, the diversity  
282 of sampled avian hosts and numbers of recovered parasites in a region all had little influence on  
283 realized host specificity. This identification of important climate predictors allows delineation of  
284 biogeographical areas with greater potential for ongoing host range expansions by generalist  
285 parasites. For instance, sites in Brazilian Amazonia, Peruvian Andes, and tropical / sub-tropical  
286 islands in Malaysia and Melanesia contain very distinct avian communities (Holt *et al.* 2013) and  
287 exhibit considerable variation in sampling effort and diversity of recovered parasites (Table 1).  
288 Yet these regions contained some of the least specialized parasite communities in our dataset, in  
289 correspondence with relatively low levels of average rainfall in the dry season (Fig. 3). In  
290 contrast, parasite communities in New Zealand, The Philippines, and southeastern Australia were  
291 more specialized than expected according to potential host species pools (Table 1, Fig. 1 and 3).

292         Assessing host specialization components at the parasite level ( $\beta_{\text{parasite}}$ ) indicates whether  
293 parasites are infecting clustered subsets of available hosts. If host range expansions are  
294 predominately driven by vector feeding patterns, parasites should infect hosts that are more  
295 ecologically similar (i.e. occupying more similar habitats). However, we would also expect  
296 parasites to show some level of host phylogenetic specialization, as different physiological  
297 characteristics among unrelated hosts can impose barriers to parasite transmission or within-host  
298 development. These mechanisms are not mutually exclusive. By estimating parasite-level  
299 specificity components, we find that parasite specialization was generally driven by host  
300 phylogeny, not by host ecological similarity. Phylogenetic  $\beta_{\text{parasite}}$  estimates were consistently  
301 negative for both parasite genera, indicating that most parasites infected hosts that were  
302 phylogenetically clustered within the community (Fig. 4). Ecological  $\beta_{\text{parasite}}$  estimates generally  
303 centered around zero.

304         To account for possible influences of biogeographical region delineation on our  
305 inferences, we tested the robustness of our results by repeating the analysis using a second  
306 grouping scheme (grouping into nine regions rather than 10 and giving more weight to avian  
307 composition and climate variables; see Appendix S6 for details). Results were broadly equivalent  
308 (strong influences of minimum rainfall in the driest quarter and rainfall seasonality on  $\beta_{\text{region}}$   
309 estimates), with the exception that ecological  $\beta_{\text{parasite}}$  estimates were also generally negative.

310

## 311 **DISCUSSION**

312 Niche specialization for a multitude of organisms is not fixed but is predicted to vary in response  
313 to environmental heterogeneity (Dobzhansky 1950; Janz & Nylin 2008; Schemske *et al.* 2009). A  
314 growing body of anecdotal and theoretical evidence suggests parasites are no exception (Agosta  
315 *et al.* 2010; Araujo *et al.* 2015; Hoberg & Brooks 2015; Nylin *et al.* 2018). Using a hierarchical  
316 model, we provide empirical evidence that the magnitude of realized host specificity for multi-  
317 host parasites varies in response to environmental conditions. While most avian malaria parasites  
318 generally infect phylogenetically clustered subsets of available hosts, realized host specificity  
319 increases in regions with higher rainfall during the dry season and more pronounced rainfall  
320 seasonality. This may reflect pulses in vector feeding activities or local host contact rates acting  
321 as selective barriers to host range expansions. These findings underscore the importance of  
322 treating host specificity as a geographically labile trait, contingent on both historical host-  
323 parasite interactions and environmental conditions (Hoberg & Brooks 2015). Climate change  
324 may have unforeseen consequences on the emergence potential of multi-host pathogens.

325

### 326 **Influences of precipitation heterogeneity on realized host specificity**

327 Climate change and biotic homogenization are major forces acting on the distributions of species  
328 (Wilson *et al.* 2016; Poisot *et al.* 2017). Efforts to determine how such forces influence  
329 distributions of parasites, and the ranges of host species they infect, are needed to understand and  
330 predict disease emergence (Poulin *et al.* 2011; Altizer *et al.* 2013; Brooks *et al.* 2014; Wells *et al.*  
331 *et al.* 2015; Dallas *et al.* 2017; Wells *et al.* 2018a). We show that pronounced seasonality in rainfall  
332 and higher rainfall during the dry season correlate with increased host specificity for multi-host  
333 avian malaria parasites. This link with seasonality goes against expectations of increased  
334 specialization under stable conditions (Futuyma & Moreno 1988). An understanding of vector-  
335 vertebrate host interactions is necessary to explain this discrepancy. Successful host range  
336 expansions by parasites will predominately be driven by variation in opportunity (exposure to  
337 novel host species) and host-parasite compatibility (driven by ecological fitting; Janzen 1968;  
338 Araujo *et al.* 2015). For the incredible diversity of vector-transmitted parasites, including avian  
339 malaria, opportunistic contact with novel host species depends on vector feeding patterns. Birds  
340 in seasonal areas typically breed near the start of the wet season, relying on energy reserves  
341 accrued during the dry season (Sinclair 1978; Rubenstein & Lovette 2007). Vector reproduction

342 and larval development, both of which affect parasite transmission, are positively correlated with  
343 rainfall and synchronized with vertebrate reproduction (LaPointe *et al.* 2010; Santiago-Alarcon  
344 *et al.* 2012a). Seasonality drives pulses in food, water, and habitat availability, which increases  
345 breeding densities and perhaps concentrates organisms near available water bodies (Chesson *et*  
346 *al.* 2004; Tonkin *et al.* 2017). This is especially true for birds, which often concentrate in high  
347 densities at the start of the breeding season (Karr 1976; Levey 1988). These water bodies could  
348 therefore serve as source locations for parasite transmission, as has been shown for West Nile  
349 virus transmission to greater sage-grouse (*Centrocercus urophasianus*) (Zou *et al.* 2006; Walker  
350 *et al.* 2007). Concordance between avian breeding behavior and peak vector activity in  
351 concentrated areas could also direct parasites to concentrated sets of ecologically similar avian  
352 species. This may impose selective pressure toward vertebrate specialization. In such an  
353 environment, where vectors are concentrated and host-vector encounter rates and resource  
354 competition are high, one would expect parasites that are more specialized to be more successful.  
355 In contrast, if vertebrate hosts are scattered throughout the environment (which may occur in less  
356 seasonal environments) indiscriminant vector feeding could increase opportunities for novel  
357 host-parasite interactions and perhaps lead to less specialized parasites.

358         Variation in transmission rates may also occur under seasonal conditions. The  
359 supposition that disease outbreaks are more prominent in seasonal environments than in constant  
360 ones has received strong theoretical and empirical support (Altizer *et al.* 2006; Lisovski *et al.*  
361 2017; Huber *et al.* 2018). A number of explanatory mechanisms have been proposed, including  
362 seasonal variation in host sociality, breeding behavior or immune investment (Altizer *et al.*  
363 2006). Regardless of underlying processes, higher frequencies of disease outbreaks suggest  
364 parasites in seasonal areas may benefit from increased infection prevalence. This could also  
365 select against range expansions to phylogenetically or functionally distant potential host species,  
366 which require costly adaptation to new defences but may be necessary when overall transmission  
367 rates are low (Poulin 1998).

368         Importantly, we did not test for associations between specialization and prevalence or  
369 infection intensity here, and the idea that vectors are the limiting step in avian malaria  
370 distributions or specialization has received mixed support. For example, some work  
371 demonstrates preferential feeding of vectors on certain avian species (Apperson *et al.* 2004) and  
372 tight evolutionary links between *Haemoproteus* lineages and vector species (Martínez de la

373 Puente *et al.* 2011), both of which support our idea that exposure of parasites to new hosts could  
374 be limited in seasonal environments. Other studies provide conflicting evidence by suggesting  
375 that vector feeding specificity is not important in structuring haemosporidian communities,  
376 particularly for *Plasmodium* parasites (Njabo *et al.* 2010; Medeiros *et al.* 2013). Furthermore, a  
377 recent work suggests that although a parasite lineage may be found infecting a wide diversity of  
378 hosts, they are actually better adapted to key host species as indicated by their infection  
379 intensities (Huang *et al.* 2018). Collectively, this evidence could indicate that other forces  
380 besides vector feeding may limit rates of novel host encounters for parasites. Assessing whether  
381 vector feeding specificity or activity rates change across regions with differing seasonality  
382 patterns would help interpret our findings and generate future research directions.

383

#### 384 **Phylogenetic barriers to host range expansions**

385 Many parasites and pathogens can disperse widely across geographical realms and infect  
386 distantly related host species, and avian malaria parasites are no exception (Pérez-Tris & Bensch  
387 2005; Hellgren *et al.* 2007; Ellis *et al.* 2015; Ricklefs *et al.* 2017; Fecchio *et al.* 2018a, b). Global  
388 distributions of several common and potentially invasive *Plasmodium* lineages (Bensch *et al.*  
389 2009; Marzal *et al.* 2014; Clark *et al.* 2015; Ellis *et al.* 2018) could be interpreted as evidence  
390 that these parasites are indiscriminant host-generalists capable of infecting an enormous diversity  
391 of host species in any given environment. We challenge this assertion by showing that multi-host  
392 avian malaria parasites, even those that infect a high number of avian host species, generally  
393 infect phylogenetically clustered subsets of available hosts. This has important ramifications for  
394 our understanding of how host range expansions occur. Local co-occurrence of primary host  
395 species is sometimes necessary to facilitate survival of parasites that have encountered novel host  
396 species but have not yet locally co-adapted to the new host's immune defenses (Fox *et al.* 1997,  
397 Best *et al.* 2010). For avian malaria parasites, phylogenetic relationships between primary and  
398 potential avian host species clearly play a central role in determining host associations and  
399 community assembly (Ellis *et al.* 2015; Clark *et al.* 2017; Fecchio *et al.* 2018a), despite their  
400 reliance on arthropod vectors that may feed on a diversity of avian species (Santiago-Alarcon *et*  
401 *al.* 2012b). However, although our study agrees with suggestions that breaking phylogenetic host  
402 barriers is an evolutionarily rare event (Hellgren *et al.* 2007; Agosta *et al.* 2010), this must  
403 nevertheless be a key process for generating parasite biodiversity. Host switching is a major

404 macroevolutionary event shaping avian malaria evolution and community turnover (Ricklefs *et*  
405 *al.* 2014; Alcalá *et al.* 2017; Fecchio *et al.* 2018b). Importantly, we here only study  
406 contemporary host ranges of parasites, rather than inferring patterns of historical host switching.  
407 However, our findings could indicate that rainfall seasonality plays a role in the likelihood of  
408 host switching over evolutionary timescales. Climate variation should be jointly considered with  
409 historical factors in understanding the ecology and evolution of vector-borne pathogens.

410

### 411 **Study limitations**

412 Some limitations of our modelling approach should be recognized. First, we concentrate only on  
413 multi-host avian malaria parasites. This ignores the many parasite lineages that only infect a  
414 single host species, which may limit our ability to draw conclusions on the biogeography of  
415 realized host specificity. Our estimates of realized host specificity rely on adequate support from  
416 the data, meaning that precisely estimating coefficients for parasites occurring in a small number  
417 of hosts will, in many cases, be limited. Delineating larger biogeographical regions can improve  
418 sample sizes, albeit at the cost of resolution. For example, our sensitivity analysis, which used  
419 only nine rather than 10 regions, identified a greater tendency for ecological specialization  
420 among parasites. This suggests that the added sample sizes within groups may have provided the  
421 extra data necessary to tease apart ecological specialists. Finally, because we constrain estimates  
422 with insufficient support to the overall average (through hyperprior specifications and Bayesian  
423 variable selection), effects can be considered conservative and should be revisited following  
424 acquisition of additional data.

425

### 426 **Extending our models to other host-parasite systems under the emerging *Stockholm***

#### 427 ***Paradigm***

428 Our findings can broadly be interpreted under principles of *The Stockholm Paradigm*, which  
429 postulates that host range expansions by parasites are the product of an interplay between (a)  
430 novel host-parasite opportunities occurring across dynamic host landscapes and (b) phylogenetic  
431 and/or ecological barriers that limit adaptation by parasites to these opportunistic hosts (Araujo  
432 *et al.* 2015; Hoberg & Brooks 2015). Multi-host parasites exhibit a *Sloppy Fitness Space*  
433 whereby realized host ranges are a subset of larger potential host ranges, including the full  
434 diversity of host species that a parasite is capable of infecting (Hoberg & Klassen 2002; Agosta



435 & Klemens 2008). Our findings suggest that variation in the realized host specificity of avian  
436 malaria parasites follows a hierarchical process consisting first of heterogeneity in potential host  
437 pools (occurring most notably across regions characterized by different precipitation patterns)  
438 and evolutionarily conserved host traits or behaviours that limit successful infection (Wells *et al.*  
439 2018b). Biogeographical structure in host specificity likely reflects prominent roles of vector  
440 feeding patterns or shifts in host compositions in response to regional climatic conditions.

441 Recognizing that host specificity is not fixed, as we have shown here, provides new  
442 leverage for outlining region-specific predictions of infectious disease risk by emerging  
443 parasites, particularly in areas undergoing rapid climate change. Given that an enormous  
444 diversity of macro- and micro-parasites depend on external climate conditions during at least part  
445 of the life cycles (Patz *et al.* 2000; Brooks & Hoberg, 2007), our approach can provide new  
446 insights into host association patterns for many host-parasite systems. Related models have  
447 already been successfully used to uncover global variation in realized host specificity for  
448 important zoonotic helminth parasites (Wells *et al.* 2018b). We have extended the flexibility of  
449 these models by incorporating group-level hyperpriors to capitalize on the added power that  
450 partial pooling can provide in mixed effects regressions (Gelman & Hill 2007). Used in  
451 combination with the increasing availability of remote-sensed environmental variables and host-  
452 parasite association datasets (Wardeh *et al.* 2015; Stephens *et al.* 2017), our approach can play a  
453 key role in determining whether the magnitude of parasite specialization varies in response to  
454 climate patterns. For example, incorporating data on host migration patterns (to provide finer  
455 estimates of local host composition) or landscape features (to more adequately describe regional  
456 ecological variation) could be a valuable next step to ground-truthing our models for other  
457 systems. Improving surveillance regimes and the spatial resolutions of open-source host-parasite  
458 databases will enhance our ability to disentangle biological signals of host specificity from  
459 inherent noise associated with low resolution data. This is imperative to identify which biotic and  
460 abiotic conditions increase risks for parasitic disease emergence and pathogen spillover events.

461

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475 **Statement of authorship:**

476 A.F. and N.J.C. designed research and wrote the first draft; N.J.C., and K.W. analyzed data;  
477 A.F., J.A.B., V.V.T., H.L.L., J.D.W., S.M.C., and N.J.C. conducted field/lab research; all authors  
478 interpreted results and contributed to writing.

479

480 **Data accessibility statement:**

481 R code and raw datasets will be uploaded as supplements and to the Dryad digital repository  
482 upon acceptance.

483

484

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753 Table 1. Sample sizes (sites, individual birds, host species, and parasite lineages sampled/modelled), bird species  
754 specificity coefficients (**Phylo  $\beta_{region}$**  and **Eco  $\beta_{region}$** ) for biogeographical regions. Regions were delineated based  
755 avian community composition and climate variables. Diversity metrics (**phylo diversity**, **eco diversity**) were calculated  
756 multiplying host species richness by posterior modes of regression intercepts ( $\mu_{region}$ ), which represent the average  
757 between potential host species in a region. PNG: Papua New Guinea

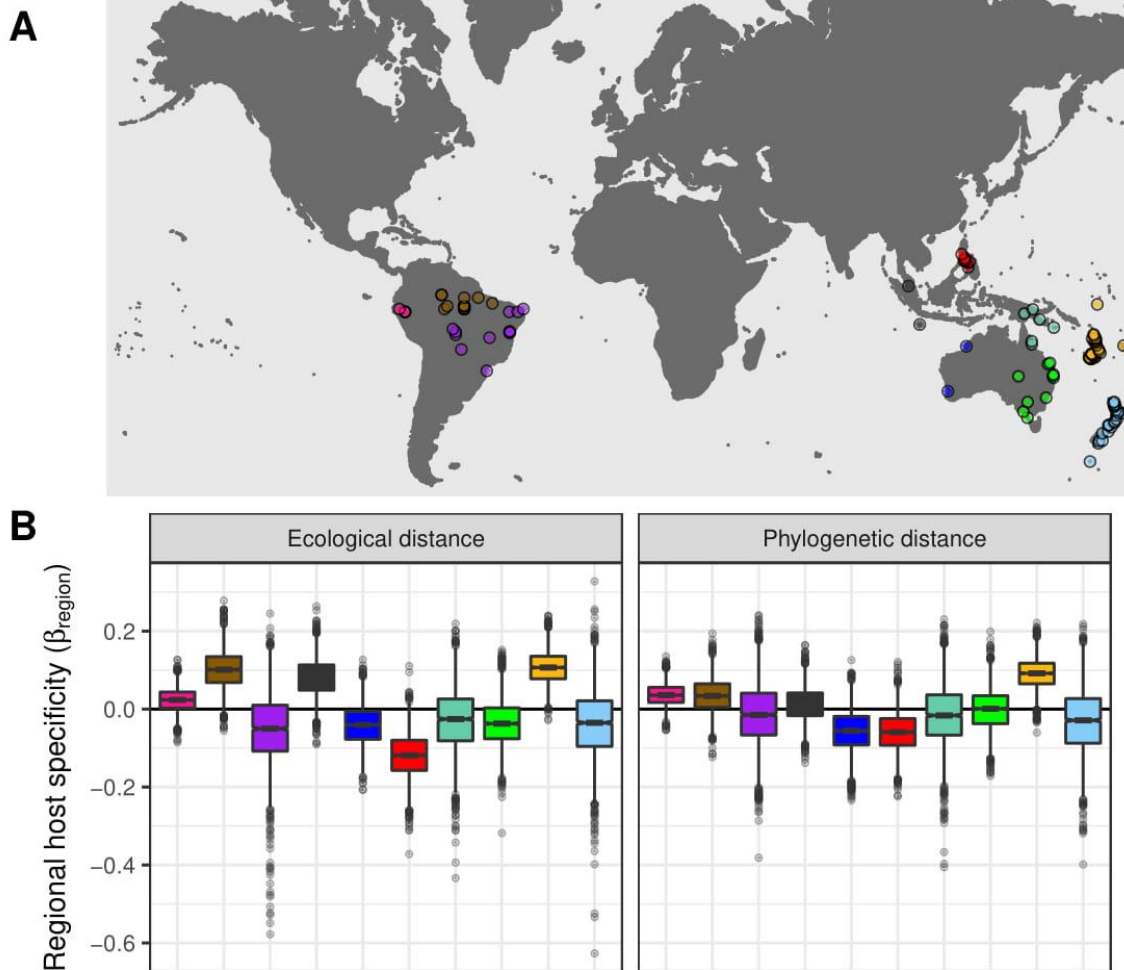
Bioregion	Latitude (mean)	Longitude (mean)	Phylo Beta (mean)	Host phylo diversity	Eco Beta (mean)	Host eco diversity	# sample sites	# samples	# host species	# pa
<b>Australia N / PNG</b>	-15	145.97	-0.02	62.48	-0.02	70.38	6	1336	115	1
<b>Australia SE</b>	-31.19	148.1	0.01	40.61	-0.05	46.74	10	3926	73	4
<b>Australia W</b>	-28.02	117.65	-0.06	5.18	-0.03	6.34	2	191	10	1
<b>Brazil Amazonia</b>	-2.75	-56.28	0.04	188.73	0.1	172.68	14	2251	308	20
<b>Brazil Central / E</b>	-13.71	-48.15	-0.03	102.75	-0.06	128.93	12	1757	210	9
<b>Malaysia</b>	-2.85	103.45	0.01	19.17	0.08	20.59	2	143	36	1
<b>Melanesia</b>	-17.36	167.63	0.1	20.42	0.1	22.19	28	1947	44	5
<b>New Zealand</b>	-40.2	174.25	-0.03	15.43	-0.02	16.7	23	2544	29	1

<b>Peru</b>	-5.87	-77.27	0.03	154.22	0.03	170.78	4	1174	270	72
<b>Philippines</b>	12.57	121.79	-0.06	17.31	-0.12	21.4	7	245	37	55

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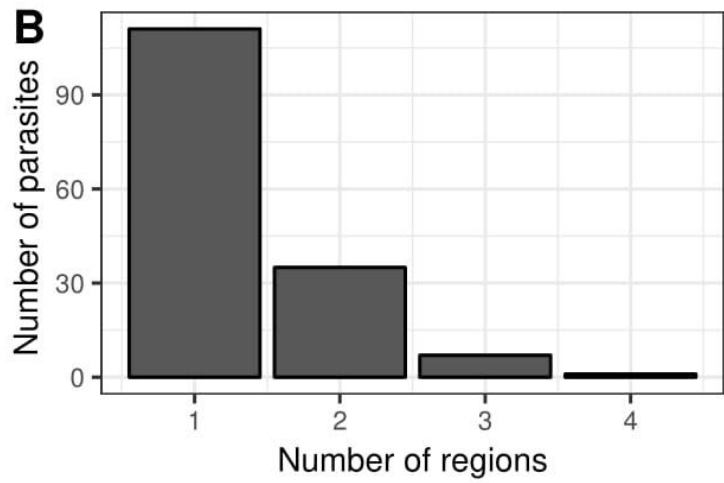
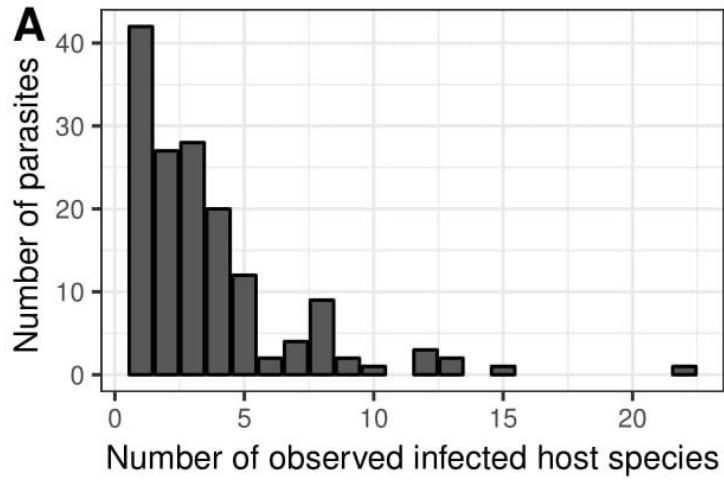


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763 **Figure 1.** (A) Sample coordinates for study sites, colors depict their classification into ten  
764 biogeographical regions. Regions were delineated based on dissimilarities in avian community  
765 composition and climate variables. (B) Posterior distributions of host specificity  $\beta_{region}$   
766 coefficients for phylogenetic host specificity and ecological host specificity. Lower  $\beta_{region}$  values  
767 indicate higher similarity between infected host species than expected by chance, indicating  
768 higher parasite host specificity in a region (relative to remaining regions). Higher  $\beta_{region}$  values  
769 suggest parasites infect more distantly related host species, indicating a greater tendency towards  
770 host generalism. Boxplots show median (lines), interquartile range (hinges) and 90% quantiles of  
771 posterior  $\beta_{region}$  estimates. Point and boxplot colors correspond to regional names in Table 1.

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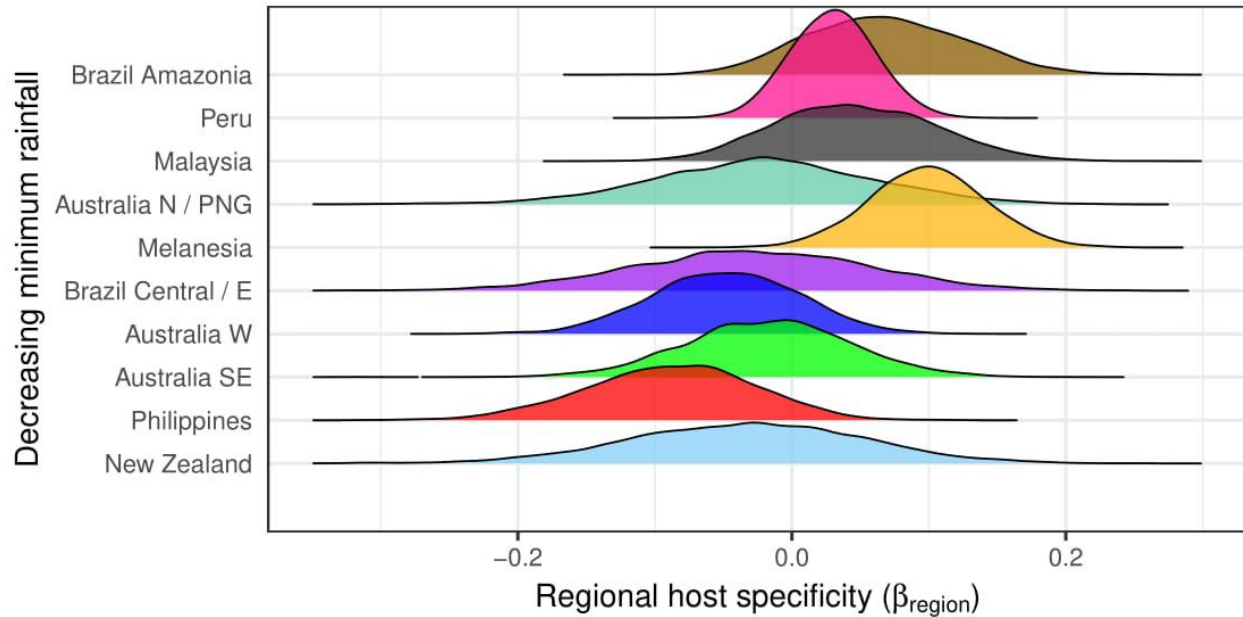
773

774 **Figure 2.** Distribution of the observed numbers of infected host species (A) and numbers of  
 775 biogeographical regions (B) for the 154 avian malaria parasites (71 *Plasmodium*, 83  
 776 *Haemoproteus*) included in the host specificity analyses.

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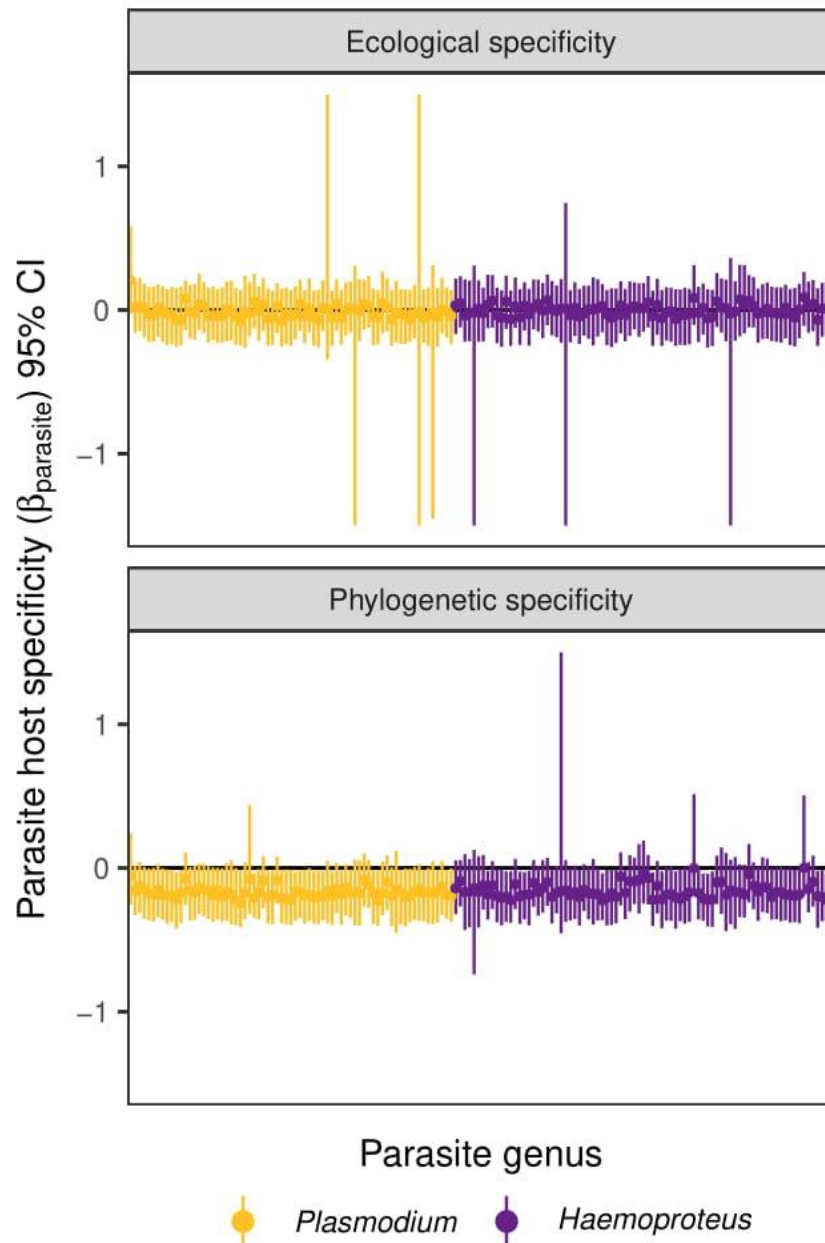
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**Figure 3.** Density distributions of regional host specificity ( $\beta_{region}$ ) coefficients, arranged by decreasing minimum rainfall of the driest quarter. Lower  $\beta_{region}$  values indicate higher similarity between infected host species than expected by chance, suggesting higher host specificity in a region (relative to remaining regions). Higher  $\beta_{region}$  values suggest parasites infect more distantly related host species than expected, indicating a greater tendency towards host generalism. Minimum rainfall variation accounted for 44% of explained variance in  $\beta_{region}$  values, with more specialized parasites in regions with wetter dry seasons. Polygon colors correspond to region names in Table 1.





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802 **Figure 4.** Parasite host specificity regression coefficients ( $\beta_{parasite}$ ) presented as 95% highest  
 803 posterior density credibility intervals. Each vertical bar indicates a parasite species' ecological  
 804 (upper panel) and phylogenetic (lower panel) specificity, respectively. Negative (i.e. not  
 805 overlapping with zero)  $\beta_{parasite}$  values indicate that pairs of host species tend to be more similar  
 806 than by chance according to regional host species pools.

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