



Swansea University
Prifysgol Abertawe



Cronfa - Swansea University Open Access Repository

This is an author produced version of a paper published in:

Ecology Letters

Cronfa URL for this paper:

<http://cronfa.swan.ac.uk/Record/cronfa46171>

Paper:

Fecchio, A., Wells, K., Bell, J., Tkach, V., Lutz, H., Weckstein, J., Clegg, S. & Clark, N. (2019). Climate variation influences host specificity in avian malaria parasites. *Ecology Letters*

<http://dx.doi.org/10.1111/ele.13215>

This item is brought to you by Swansea University. Any person downloading material is agreeing to abide by the terms of the repository licence. Copies of full text items may be used or reproduced in any format or medium, without prior permission for personal research or study, educational or non-commercial purposes only. The copyright for any work remains with the original author unless otherwise specified. The full-text must not be sold in any format or medium without the formal permission of the copyright holder.

Permission for multiple reproductions should be obtained from the original author.

Authors are personally responsible for adhering to copyright and publisher restrictions when uploading content to the repository.

<http://www.swansea.ac.uk/library/researchsupport/ris-support/>

Climate variation influences host specificity in avian malaria parasites

Authors:

Alan Fecchio, Konstans Wells, Jeffrey A. Bell, Vasyl V. Tkach, Holly L. Lutz, Jason D. Weckstein, Sonya M. Clegg, Nicholas J. Clark

A. Fecchio, Laboratório de Evolução e Biogeografia, Universidade Federal da Bahia, Rua Barão de Jeremoabo 147, Salvador, BA 40170115, Brazil, alanfecchio@gmail.com, <https://orcid.org/0000-0002-7319-0234>.

K. Wells, Department of Biosciences, Swansea University, Swansea SA2 8PP, UK, k.l.wells@swansea.ac.uk

J. A. Bell, Department of Biology, University of North Dakota, 1 Campus Drive and Cornell Street, Grand Forks, ND 58202, USA, jeffrey.bell@und.edu

V. V. Tkach, Department of Biology, University of North Dakota, 10 Cornell Street, Grand Forks, ND 58202, USA, vasyl.tkach@und.edu

H. L. Lutz, Department of Surgery, University of Chicago, 5812 S. Ellis Ave., Chicago, IL 606372 and Integrative Research Center, Field Museum of Natural History, 1400 S. Lake Shore Drive, Chicago, IL 60605, USA, hlutz@fieldmuseum.org

J. D. Weckstein, Department of Ornithology, Academy of Natural Sciences and Department of Biodiversity, Earth, and Environmental Sciences, Drexel University, 1900 Benjamin Franklin Parkway, Philadelphia, PA 19103, USA, jdw342@drexel.edu

S. M. Clegg, Edward Grey Institute of Field Ornithology, Department of Zoology, University of Oxford, Oxford, OX1 3PS, UK, sonya.clegg@zoo.ox.ac.uk

N. J. Clark, School of Veterinary Science, University of Queensland, Gatton, Queensland, Australia, nicholas.j.clark1214@gmail.com

Running title:

Host specificity of avian malaria parasites

31 **Keywords:**

32 avian malaria, climate change, disease ecology, disease emergence, host shifting, host
33 specificity, infectious disease, niche specialization, parasite specialization, vector borne disease

34

35

36

37 **Corresponding author:**

38 Alan Fecchio

39 Universidade Federal da Bahia

40 Laboratório de Evolução e Biogeografia

41 Rua Barão de Jeremoabo 147

42 Salvador, BA 40170115, Brazil.

43 Phone number: +55 (71) 3283-6519

44 Fax: +55 (71) 3283-6511

45 E-mail: alanfecchio@gmail.com

46

47

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
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 (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 μ and variance σ^2 . μ_{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_{μ} with Gaussian
 192 error σ_{μ}^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 μ_{β} and coefficients
 196 $\beta_{parasite}$ and β_{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 β_{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 β was included in the model. By specifying a low
 201 prior probability of drawing 1 for indicator variable I , we only estimated β if sufficient data
 202 existed to warrant its inclusion. If $I = 0$, indicating little support for sampling β 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 β_{region} were drawn from a ‘global’ normal distribution. Parameters were
 208 estimated independently for phylogenetic and ecological specificity (Appendix S3).

209 We estimated β 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 β_{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 β_{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 (μ_{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 β_{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 (β_{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 β_{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 β_{region}
273 estimates), with the coefficient of rainfall variation accounting for 53% of explained variance in
274 β_{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 (β_{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 β_{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 β_{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 β_{region}
309 estimates), with the exception that ecological β_{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

462 **ACKNOWLEDGEMENTS**

463 Our work would not have been possible without the field assistance of several local residents and
464 ornithologists. We thank the curators from the following museums who loaned part of the

465 samples used in this study: Instituto Nacional de Pesquisas da Amazônia, Museu Paraense
466 Emílio Goeldi, Field Museum of Natural History, and Academy of Natural Sciences of Drexel
467 University. Eric Schall and Therese Catanach carried out GIS work to extract host occurrence
468 lists. We thank governmental agencies which provided all permits necessary for collection and
469 exportation of tissue samples. We also thank four anonymous referees for their comments on
470 earlier versions of the manuscript. This work was funded in part by US National Science
471 Foundation grants DEB-1503804 to JDW and DEB-1120734 to VVT and a National Geographic
472 Society Committee for Research and Exploration Grant (9383-13) to SMC. During the project,
473 AF was supported by a postdoctoral fellowship (PNPD scholarship) from Coordenação de
474 Aperfeiçoamento de Pessoal de Nível Superior (CAPES).

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

485 **REFERENCES**

486 Agosta S.J., Janz, N. & Brooks, D.R. (2010). How specialists can be generalists: resolving the
487 "parasite paradox" and implications for emerging infectious disease. *Zoologia*, 27, 151-
488 162.

489 Agosta, S.J. & Klemens, J.A. (2008). Ecological fitting by phenotypically flexible genotypes:
490 implications for species associations, community assembly and evolution. *Ecol. Lett.*, 11,
491 1123-1134.

492 Alcala, N., Jenkins, T., Christe, P., & Vuilleumier, S. (2017). Host shift and cospeciation rate
493 estimation from co-phylogenies. *Ecol. Lett.*, 20, 1014-1024.

494 Altizer, S., Dobson, A., Hosseini, P., Hudson, P., Pascual, M. & Rohani, P. (2006). Seasonality
495 and the dynamics of infectious diseases. *Ecol. Lett.*, 9, 467-84.

496 Altizer, S., Ostfeld, R.S., Johnson, P.T., Kutz, S. & Harvell, C. (2013). Climate change and
497 infectious diseases: from evidence to a predictive framework. *Science*, 341, 514-519.

498 Apperson, C.S., Hassan, H.K., Harrison, B.A., Savage, H.M., Aspen, S.E., Farajollahi, A. *et al.*
499 (2004). Host Feeding Patterns of Established and Potential Mosquito Vectors of West Nile
500 Virus in the Eastern United States. *Vector Borne Zoonotic Dis*, 4, 71-82.

501 Araujo, S.B., Braga, M.P., Brooks, D.R., Agosta, S.J., Hoberg, E.P., von Hartenthal, F.W. *et al.*
502 (2015). Understanding host-switching by ecological fitting. *PLoS ONE*, 10, e0139225.

503 Bell, J.A., Weckstein, J.D., Fecchio, A. & Tkach, V.V. (2015). A new real-time PCR protocol
504 for detection of avian haemosporidians. *Parasit. Vectors*, 8, 383.

505 Bensch, S., Hellgren, O. & Pérez-Tris, J. (2009). MalAvi: a public database of malaria parasites
506 and related haemosporidians in avian hosts based on mitochondrial cytochrome b lineages.
507 *Mol. Ecol. Res.*, 9, 1353-1358.

508 Bensch, S., Pérez-Tris, J., Waldenström, J. & Hellgren, O. (2004). Linkage between nuclear and
509 mitochondrial DNA sequences in avian malaria parasites: Multiple cases of cryptic
510 speciation? *Evolution*, 58, 1617-1621.

511 Best, A., White, A., Kisdi, E., Antonovics, J., Brockhurst, M.A. & Boots, M. (2010). The
512 evolution of host-parasite range. *Am. Nat.*, 176, 63-71.

513 BirdLife International and NatureServe (2017). Bird species distribution maps of the world.
514 Version 7.0. BirdLife International, Cambridge, UK and NatureServe, Arlington, USA.

515 Brooks, D.R. & Hoberg, E.P. (2007). How will global climate change affect parasite-host
516 assemblages? *Trends in Parasitol.*, 23, 571-574.

517 Brooks, D.R., Hoberg, E.P., Boeger, W.A., Gardner, S.L., Galbreath, K.E., Herczeg, D. *et al.*
518 (2014). Finding them before they find us: informatics, parasites, and environments in
519 accelerating climate change. *Comp. Parasitol.*, 81, 155-164.

520 Brooks, D.R., León-Règagnon, V., McLennan, D.A. & Zelmer, D. (2006). Ecological fitting as a
521 determinant of the community structure of platyhelminth parasites of anurans. *Ecology*, 87,
522 S76-S85.

523 Canard, E.F., Mouquet, N., Mouillot, D., Stanko, M., Miklisova, D. & Gravel, D. (2014).
524 Empirical evaluation of neutral interactions in host-parasite networks. *Am. Nat.*, 183, 468-
525 479.

526 Chesson, P., Gebauer, R.L.E., Schwinning, S., Huntly, N., Wiegand, K., Ernest, M.S.K. *et al.*
527 (2004). Resource pulses, species interactions, and diversity maintenance in arid and semi-
528 arid environments. *Oecologia*, 141, 236-253.

529 Clark, N.J. & Clegg, S.M. (2017). Integrating phylogenetic and ecological distances reveals new
530 insights into parasite host-specificity. *Mol. Ecol.*, 26, 3074-3086.

531 Clark, N.J. (2018). Phylogenetic uniqueness, not latitude, explains the diversity of avian blood
532 parasite communities worldwide. *Global Ecol. Biogeogr.*, 27, 744-755.

533 Clark, N.J., Clegg, S.M. & Lima, M.R. (2014). A review of global diversity in avian
534 haemosporidians (*Plasmodium* and *Haemoproteus*: Haemosporida): new insights from
535 molecular data. *Int. J. Parasitol.*, 44, 329-338.

536 Clark, N.J., Clegg, S.M., Sam, K., Goulding, W., Koane, B. & Wells, K. (2017). Climate, host
537 phylogeny and the connectivity of host communities govern regional parasite assembly.
538 *Divers. Distrib.*, 24, 13-23.

539 Clark, N.J., Olsson-Pons, S., Ishtiaq, F. & Clegg, S.M. (2015). Specialist enemies, generalist
540 weapons and the potential spread of exotic pathogens: malaria parasites in a highly invasive
541 bird. *Int. J. Parasitol.*, 45, 891-899.

542 Clark, N.J., Seddon, J.M., Šlapeta, J. & Wells, K. (2018). Parasite spread at the domestic animal
543 - wildlife interface: anthropogenic habitat use, phylogeny and body mass drive risk of cat
544 and dog flea (*Ctenocephalides* spp.) infestation in wild mammals. *Parasit. Vectors*, 11, 8

545 Cooper, N., Griffin, R., Franz, M., Omotayo, M. & Nunn, C.L. (2012). Phylogenetic host
546 specificity and understanding parasite sharing in primates. *Ecol. Lett.*, 15, 1370-1377.

547 Dallas, T., Huang, S., Nunn, C., Park, A.W. & Drake, J.M. (2017). Estimating parasite host
548 range. *Proc. Biol. Sci.*, 284, 20171250.

549 Davies, T.J. & Pedersen, A.B. (2008). Phylogeny and geography predict pathogen community
550 similarity in wild primates and humans. *Proc. Biol. Sci.*, 275, 1695-1701.

551 de Vienne, D.M., Hood, M.E. & Giraud, T. (2009). Phylogenetic determinants of potential host
552 shifts in fungal pathogens. *J. Evol. Biol.*, 22, 2532-2541.

553 Dobzhansky, T. (1950). Evolution in the tropics. *Am. Sci.*, 38, 209-221.

554 Doña, J., Proctor, H., Mironov, S., Serrano, D. & Jovani, R. (2018). Host specificity, infrequent
555 major host switching and the diversification of highly host-specific symbionts: The case of
556 vane-dwelling feather mites. *Global Ecol. Biogeogr.*, 27, 188-198.

557 Dray, S. & Dufour, A.B. (2007). The ade4 package: implementing the duality diagram for
558 ecologists. *J. Stat. Softw.*, 22, 1-20.

559 Ellis, V.A., Collins, M.D., Medeiros, M.C.I., Sari, E.H.R., Coffey, E.D., Dickerson, R.C. *et al.*
560 (2015). Local host specialization, host-switching, and dispersal shape the regional
561 distributions of avian haemosporidian parasites. *Proc. Natl. Acad. Sci. USA*, 112, 11294-
562 11299.

563 Ellis, V.A., Sari, E.H.R., Rubenstein, D.R., Dickerson, R.C., Bensch, S. & Ricklefs, R.E. (2018).
564 The global biogeography of avian haemosporidian parasites is characterized by local
565 diversification and intercontinental dispersal. *Parasitology*, 1-7,
566 doi:10.1017/S0031182018001130

567 Farrell, M.J., Berrang-Ford, L. & Davies, T.J. (2013). The study of parasite sharing for
568 surveillance of zoonotic diseases. *Environ. Res. Lett.*, 8, 015036.

569 Fecchio, A., Bell, J.A., Collins, M.D., Farias, I.P., Trisos, C.H., Tobias, J.A. *et al.* (2018b).
570 Diversification by host switching and dispersal shaped the diversity and distribution of
571 avian malaria parasites in Amazonia. *Oikos*, 127, 1233-1242

572 Fecchio, A., Pinheiro, R., Felix, G., Faria, I.P., Pinho, J.B., Lacorte, G.A. *et al.* (2018a). Host
573 community similarity and geography shape the diversity and distribution of
574 haemosporidian parasites in Amazonian birds. *Ecography*, 41, 505-515.

575 Fox, C.W., Nilsson, J.A. & Mousseau, T.A. (1997). The ecology of diet expansion in a seed-
576 feeding beetle: Pre-existing variation, rapid adaptation and maternal effects? *Evol. Ecol.*,
577 11, 183-194.

578 Friedman, J., Hastie, T. & Tibshirani, R. (2010). Regularization Paths for Generalized Linear
579 Models via Coordinate Descent. *J. Stat. Softw.*, 33, 1-22.

580 Futuyma, D.J. & Moreno, G. (1988). The Evolution of Ecological Specialization. *Ann. Rev. Ecol.*
581 *Syst.*, 19, 207-233.

582 Garamszegi, L.Z. (2011). Climate change increases the risk of malaria in birds. *Glob. Chang.*
583 *Biol.*, 17, 1751-1759.

584 Gelman, A. & Hill, J. (2007). Data analysis using regression and multilevel/hierarchical models.
585 Cambridge University Press Cambridge, New York, NY.

586 Gower, J.C. (1971). A general coefficient of similarity and some of its properties. *Biometrics*, 27,
587 857-871.

588 Han, B.A., Schmidt, J.P., Bowden, S.E. & Drake, J.M. (2015). Rodent reservoirs of future
589 zoonotic diseases. *Proc. Natl. Acad. Sci. USA*, 112, 7039-7044.

590 Hellgren, O., Pérez-Tris, J. & Bensch, S. (2009). A jack-of-all-trades and still a master of some:
591 prevalence and host range in avian malaria and related blood parasites. *Ecology*, 90, 2840-
592 2849.

593 Hellgren, O., Waldenström, J. & Bensch, S. (2004). A new PCR assay for simultaneous studies
594 of *Leucocytozoon*, *Plasmodium*, and *Haemoproteus* from avian blood. *J. Parasitol.*, 90,
595 797-802.

596 Hellgren, O., Waldenström, J., Pérez-Tris, J., Szollosi, E., Hasselquist, D., Krizanauskiene, A. *et al.*
597 (2007). Detecting shifts of transmission areas in avian blood parasites - a phylogenetic
598 approach. *Mol. Ecol.*, 16, 1281-1290.

599 Hoberg, E.P. & Brooks, D.R. (2008). A macroevolutionary mosaic: episodic host-switching,
600 geographical colonization and diversification in complex host-parasite systems. *J.*
601 *Biogeogr.*, 35, 1533-1550.

602 Hoberg, E.P. & Brooks, D.R. (2015). Evolution in action: climate change, biodiversity dynamics
603 and emerging infectious disease. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 370, 20130553.

604 Hoberg, E.P. & Klassen, G.J. (2002). Revealing the faunal tapestry: co-evolution and historical
605 biogeography of hosts and parasites in marine systems. *Parasitology*, 124, 3-22.

606 Holt, B.G., Lessard, J-P., Borregaard, M.K., Fritz, S.A., Araújo, M.B., Dimitrov, D. *et al.* (2013).
607 An update of Wallace's zoogeographic regions of the world. *Science*, 39, 74-78.

608 Huang, X., Ellis, V.A., Jönsson, J. & Bensch, S. (2018) Generalist haemosporidian parasites are
609 better adapted to a subset of host species in a multiple host community. *Mol. Ecol.*, 27,
610 4336-4346.

611 Huber, J.H., Childs, M.L., Caldwell, J.M. & Mordecai, E.A. (2018). Seasonal temperature
612 variation influences climate suitability for dengue, chikungunya, and Zika transmission.
613 *PLoS Negl. Trop. Dis.*, 12, e0006451.

614 Janz, N. & Nylin, S. (2008). The Oscillation Hypothesis of Host-Plant Range and Speciation. In:
615 *Specialization, Speciation, and Radiation: The Evolutionary Biology of Herbivorous*
616 *Insects* (ed Tilmon, K.J.). University of California Press, Berkeley, CA, pp. 203-215.

617 Janzen, D.H. (1968). Host plants as islands in evolutionary and contemporary time. *Am. Nat.*,
618 102, 592-595.

619 Janzen, D.H. (1985). On ecological fitting. *Oikos*, 45, 308-310.

620 Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O. (2012). The global diversity of
621 birds in space and time. *Nature*, 491, 444-448.

622 Karr, J.R. (1976). Seasonality, resource availability, and community diversity in tropical bird
623 communities. *Am. Nat.*, 110, 973-994.

624 Krasnov, B.R., Mouillot, D., Shenbrot, G.I., Khokhlova, I.S. & Poulin, R. (2004b). Geographical
625 variation in host specificity of fleas (Siphonaptera) parasitic on small mammals: the
626 influence of phylogeny and local environmental conditions. *Ecography*, 27, 787-797.

627 Krasnov, B.R., Poulin, R., Shenbrot, G.I., Mouillot, D. & Khokhlova, I.S. (2004a). Ectoparasitic
628 ‘jacks-of-all-trades’: relationship between abundance and host specificity in fleas
629 (Siphonaptera) parasitic on small mammals. *Am. Nat.*, 164, 506-516.

630 LaPointe, D.A., Goff, M.L. & Atkinson, C.T. (2010). Thermal constraints to the sporogonic
631 development and altitudinal distribution of avian malaria *Plasmodium relictum* in Hawaii.
632 *J. Parasitol.*, 96, 318-324.

633 Levey, D.J. (1988). Spatial and temporal variation in Costa Rican fruit and fruit-eating bird
634 abundance. *Ecol. Monogr.*, 58, 251-269.

635 Lisovski, S., Hoyer, B.J. & Klaassen, M. (2017). Geographic variation in seasonality and its
636 influence on the dynamics of an infectious disease. *Oikos*, 126, 931-936.

637 Martínez-de la Puente, J., Martínez, J., Rivero-de Aguilar, J., Herrero, J. & Merino, S. (2011).
638 On the specificity of avian blood parasites: revealing specific and generalist relationships
639 between haemosporidians and biting midges. *Mol. Ecol.*, 20, 3275-3287.

640 Marzal, A., García-Longoria, L., Cárdenas Callirgos, J.M. & Sehgal, R.N.M. (2015). Invasive
641 avian malaria as an emerging parasitic disease in native birds of Peru. *Biol. Invasions*, 17,
642 39-45.

643 Medeiros, M.C.I., Hamer, G.L. & Ricklefs, R.E. (2013). Host compatibility rather than vector-
644 host encounter rate determines the host range of avian *Plasmodium* parasites. *Proc. Biol.*
645 *Sci.*, 280, 20122947.

646 Moens, M.A.J. & Pérez-Tris, J. (2016). Discovering potential sources of emerging pathogens:
647 South America is a reservoir of generalist avian blood parasites. *Int. J. Parasitol.*, 46, 41-
648 49.

649 Møller, A.P., Merino, S., Soler, J.J., Antonov, A., Badás, E.P., Calero-Torralbo, M.A. *et al.*
650 (2013). Assessing the Effects of Climate on Host-Parasite Interactions: A Comparative
651 Study of European Birds and Their Parasites. *PLoS ONE*, 8, e82886.

652 Murray, K.A., Preston, N., Allen, T., Zambrana-Torrel, C., Hosseini, P.R. & Daszak, P. (2015).
653 Global biogeography of human infectious diseases. *Proc. Natl. Acad. Sci. USA*, 112,
654 12746-12751.

655 Nakagawa, S. & Schielzeth, H. (2013). A general and simple method for obtaining R^2 from
656 generalized linear mixed-effects models. *Methods Ecol. Evol.*, 4, 133-142.

657 Njabo, K.Y., Cornel, A.J., Bonneaud, C., Toffelmier, E., Sehgal, R.N.M., Valkiūnas G. *et al.*
658 (2010). Nonspecific patterns of vector, host and avian malaria parasite associations in a
659 central African rainforest. *Mol. Ecol.*, 20, 1049-1061.

660 Nylin, S., Agosta, S., Bensch, S., Boeger, W., Braga, M.P., Brooks, R.D. *et al.* (2018). Embracing
661 Colonizations: A New Paradigm for Species Association Dynamics. *Trends Ecol. Evol.*, 33,
662 4-14.

663 O'Hara, R.B. & Sillanpää, M.J. (2009). A review of Bayesian variable selection methods: what,
664 how and which. *Bayesian Analysis*, 4, 85-117.

665 Olival, K.J., Hosseini, P.R., Zambrana-Torrel, C., Ross, N., Bogich, T.L. & Daszak, P. (2017).
666 Host and viral traits predict zoonotic spillover from mammals. *Nature*, 546, 646-650.

667 Park, A.W., Farrell, M.J., Schmidt, J.P., Huang, S., Dallas, T.A., Pappalardo, P. *et al.* (2018).
668 Characterizing the phylogenetic specialism–generalism spectrum of mammal parasites.
669 *Proc. Biol. Sci.*, 285, 20172613.

670 Patz, J.A., Graczyk, T.K., Geller, N. & Vittor, A.Y. (2000). Effects of environmental change on
671 emerging parasitic diseases. *Int. J. Parasitol.*, 30, 1395-1406.

672 Pavoine, S., Vallet, J., Dufour, A.B., Gachet, S. & Daniel, H. (2009). On the challenge of
673 treating various types of variables: application for improving the measurement of
674 functional diversity. *Oikos*, 118, 391-402.

675 Pérez-Tris, J. & Bensch, S. (2005). Dispersal increases local transmission of avian malarial
676 parasites. *Ecol. Lett.*, 8, 838-8845.

677 Plummer, M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs
678 sampling. Proceedings of the 3rd International Workshop on Distributed Statistical
679 Computing.

680 Plummer, M. (2016). rjags: Bayesian Graphical Models using MCMC. R package version 4-6.
681 <https://CRAN.R-project.org/package=rjags>.

682 Poisot, T., Guéveneux-Julien, C., Fortin, M-J., Gravel, D. & Legendre, P. (2017). Hosts,
683 parasites and their interactions respond to different climatic variables. *Global Ecol.*
684 *Biogeogr.*, 26, 942-951.

685 Poulin R. & Mouillot, D. (2005). Combining phylogenetic and ecological information into a new
686 index of host specificity. *J. Parasitol.*, 91, 511-514.

687 Poulin, R. (1998). Large-scale patterns of host use by parasites of freshwater fishes. *Ecol. Lett.*,
688 1, 118-128.

689 Poulin, R., Krasnov, B.R. & Mouillot, D. (2011). Host specificity in phylogenetic and
690 geographic space. *Trends Parasitol.*, 27, 355-361.

691 Ricklefs, R.E., Medeiros, M., Ellis, V.A., Svensson-Coelho, M., Blake, J.G., Loiselle, B.A. *et al.*
692 (2017). Avian migration and the distribution of malaria parasites in New World passerine
693 birds. *J. Biogeogr.*, 44, 1113-1123.

694 Ricklefs, R.E., Outlaw, D.C., Svensson-Coelho, M., Medeiros, M.C.I., Ellis, V.A. & Latta, S.
695 (2014). Species formation in avian malaria parasites. *Proc. Natl. Acad. Sci. USA*, 111,
696 14816-14821.

697 Rubenstein, D.R. & Lovette, I.J. (2007). Temporal environmental variability drives the evolution
698 of cooperative breeding in birds. *Curr. Biol.*, 17, 1414-1419.

699 Santiago-Alarcon, D., Havelka, P., Schaefer, H.M., Segelbacher, G. (2012b). Blood meal
700 analysis reveals avian *Plasmodium* infections and broad host preferences of *Culicoides*
701 (Diptera: Ceratopogonidae) vectors. *PLoS ONE*, 7, e31098.

702 Santiago-Alarcon, D., Palinauskas, V. & Schaefer, H. M. (2012a). Diptera vectors of avian
703 Haemosporidian parasites: untangling parasite life cycles and their taxonomy. *Biol. Rev.*,
704 87, 928-964.

705 Santiago-Alarcon, D., Rodríguez-Ferraro, A., Parker, P.G. & Ricklefs, R.E. (2014). Different
706 meal, same flavor: cospeciation and host switching of haemosporidian parasites in some
707 non-passerine birds. *Parasit. Vectors*, 7, 286.

708 Schemske, D.W., Mittelbach, G.G., Cornell, H.V., Sobel, J.M. & Roy, K. (2009). Is there a
709 latitudinal gradient in the importance of biotic interactions? *Annu. Rev. Ecol. Evol. Syst.*,
710 40, 245-269.

711 Sehgal, R.N.M. (2010). Deforestation and avian infectious diseases. *J. Exp. Biol.*, 213, 955-960.

712 Sinclair, A.R.E. (1978). Factors affecting the food supply and breeding season of resident birds
713 and movements of Palaearctic migrants in a tropical African savannah. *Ibis*, 120, 480-497.

714 Stephens, P.R., Pappalardo, P., Huang, S., Byers, J.E., Farrell, M.J., Gehman, A. *et al.* (2017).
715 Global Mammal Parasite Database version 2.0. *Ecology*, 98, 1476-1476.

716 Tonkin, J.D., Bogan, M.T., Bonada, N., Rios-Touma, B. & Lytle, D.A. (2017). Seasonality and
717 predictability shape temporal species diversity. *Ecology*, 98, 1201-1216.

718 Valkiūnas, G. (2005). Avian Malaria Parasites and Other Haemosporidia. CRC Press, Boca
719 Raton, FL.

720 Walker, B.L., Naugle, D.E., Doherty, K.E. & Cornish, T.E. (2007). West Nile virus and greater
721 sage-grouse: estimating infection rate in wild bird population. *Avian Dis.*, 51, 691-696.

722 Wardeh, M., Risley, C., McIntyre, M.K., Setzkorn, C. & Baylis, M. (2015). Database of host-
723 pathogen and related species interactions, and their global distribution. *Scientific Data*, 2,
724 150049.

725 Weckstein, J.D. (2004). Biogeography Explains Cophylogenetic Patterns in Toucan Chewing
726 Lice. *Syst. Biol.*, 53, 154-164.

727 Wells, K., Gibson, D.I. & Clark, N.J. (2018b). Global patterns in helminth host specificity:
728 phylogenetic and functional diversity of regional host species pools matter. *Ecography*, in
729 press (accepted). doi:10.1111/ecog.03886.

730 Wells, K., Gibson, D.I., Clark, N.J., Ribas, A., Morand, S. & McCallum, H.I. (2018a). Global
731 spread of helminth parasites at the human–domestic animal–wildlife interface. *Glob.*
732 *Chang. Biol.*, 24, 3254-3265.

733 Wells, K., O'Hara, R.B., Cooke, B.D., Mutze, G.J., Prowse, T.A.A. & Fordham, D.A. (2016).
734 Environmental effects and individual body condition drive seasonal fecundity of rabbits:
735 identifying acute and lagged processes. *Oecologia*, 181, 853-864.

736 Wells, K., O'Hara, R.B., Morand, S., Lessard, J., Ribas, A. & Beggs, J. (2015). The importance
737 of parasite geography and spillover effects for global patterns of host-parasite associations
738 in two invasive species. *Divers. Distrib.*, 21, 477-486.

739 Wickham, H. & Bryan, J. (2017). readxl: Read Excel Files. R package version 1.0.0.
740 <https://CRAN.R-project.org/package=readxl>.

741 Wickham, H., Francois, R., Henry, L. & Müller, K. (2017). dplyr: A Grammar of Data
742 Manipulation. R package version 0.7.4. <https://CRAN.R-project.org/package=dplyr>

743 Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M. & Jetz, W. (2014).
744 EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals.
745 *Ecology*, 95, 2027-2027.

746 Wilson, L.J., Fulton, C.J., Hogg, A.M., Joyce, K.E., Radford, B.T.M. & Fraser, C.I. (2016).
747 Climate-driven changes to ocean circulation and their inferred impacts on marine dispersal
748 patterns. *Global Ecol. Biogeogr.*, 25, 923-939.

749 Zou, L., Miller, S.N. & Schmidtman, E. T. (2006). Mosquito larval habitat mapping using
750 remote sensing and GIS: implications of coalbed methane development and West Nile
751 virus. *J. Med. Entomol.*, 43, 1034-1041.

752

753 Table 1. Sample sizes (sites, individual birds, host species, and parasite lineages sampled/modelled), bird species
754 specificity coefficients (**Phylo β_{region}** and **Eco β_{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 (μ_{region}), which represent the average
757 between potential host species in a region. PNG: Papua New Guinea

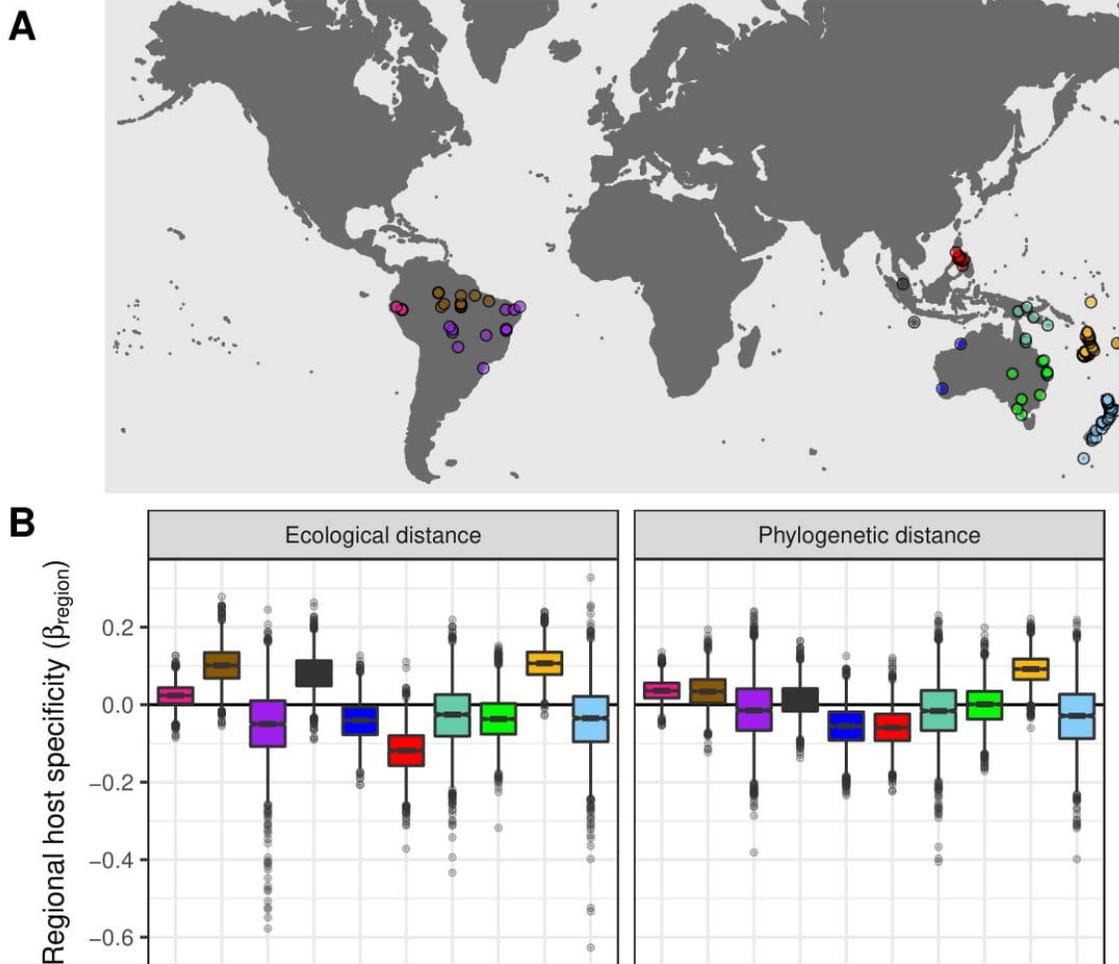
Bioregion	Latitude (mean)	Longitude (mean)	Phylo Beta (mean)	Host phylo diversity	Eco Beta (mean)	Host eco diversity	# sample sites	# samples	# host species	# pa
Australia N / PNG	-15	145.97	-0.02	62.48	-0.02	70.38	6	1336	115	1
Australia SE	-31.19	148.1	0.01	40.61	-0.05	46.74	10	3926	73	4
Australia W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

Peru	-5.87	-77.27	0.03	154.22	0.03	170.78	4	1174	270	72
Philippines	12.57	121.79	-0.06	17.31	-0.12	21.4	7	245	37	59

758

759

760

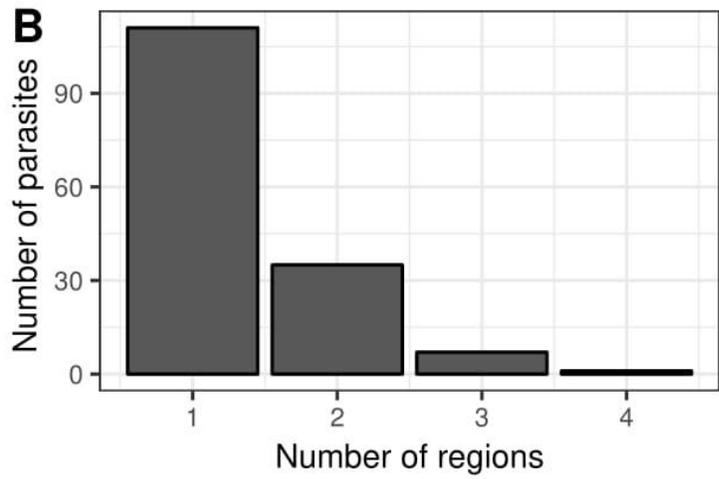
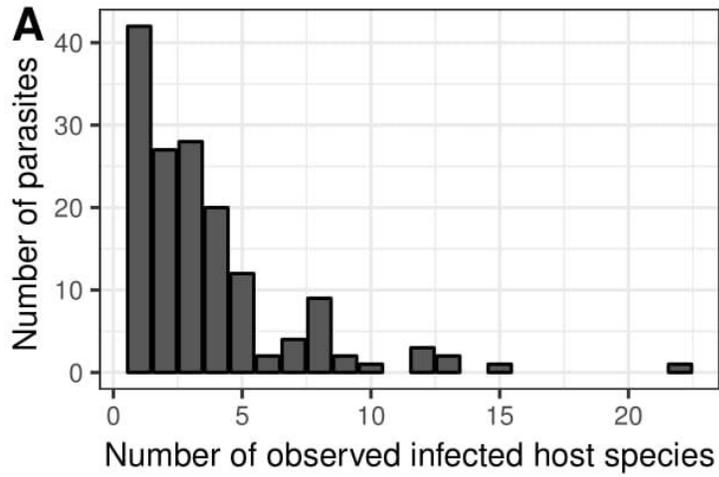


761

762

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 β_{region}
766 coefficients for phylogenetic host specificity and ecological host specificity. Lower β_{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 β_{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 β_{region} estimates. Point and boxplot colors correspond to regional names in Table 1.

772



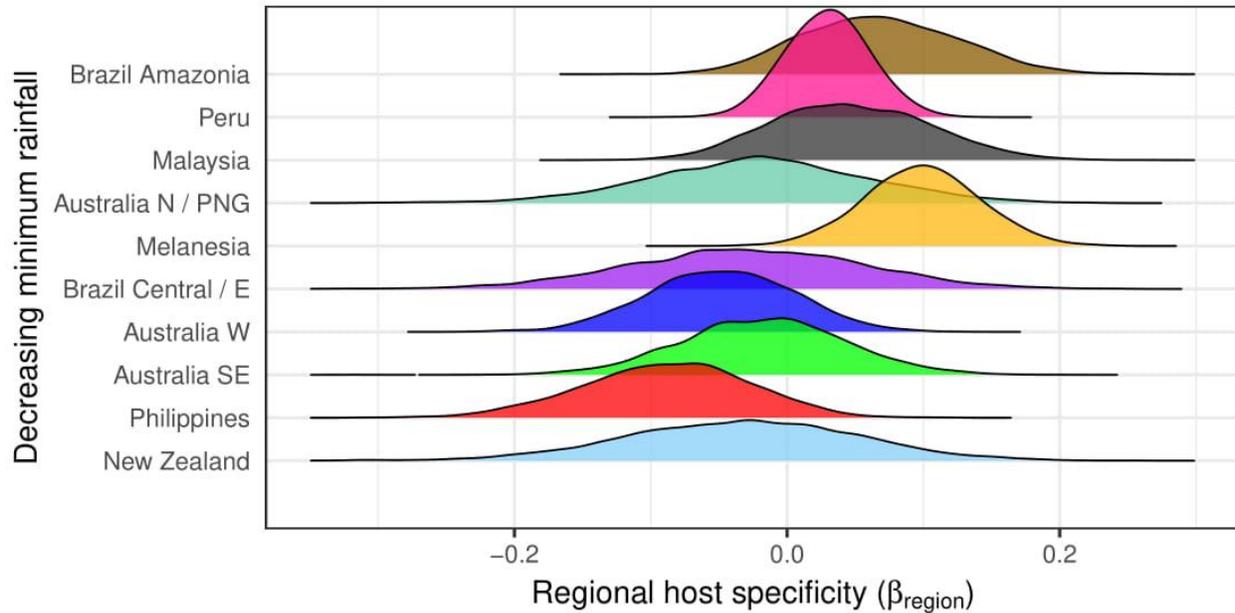
773

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.

777

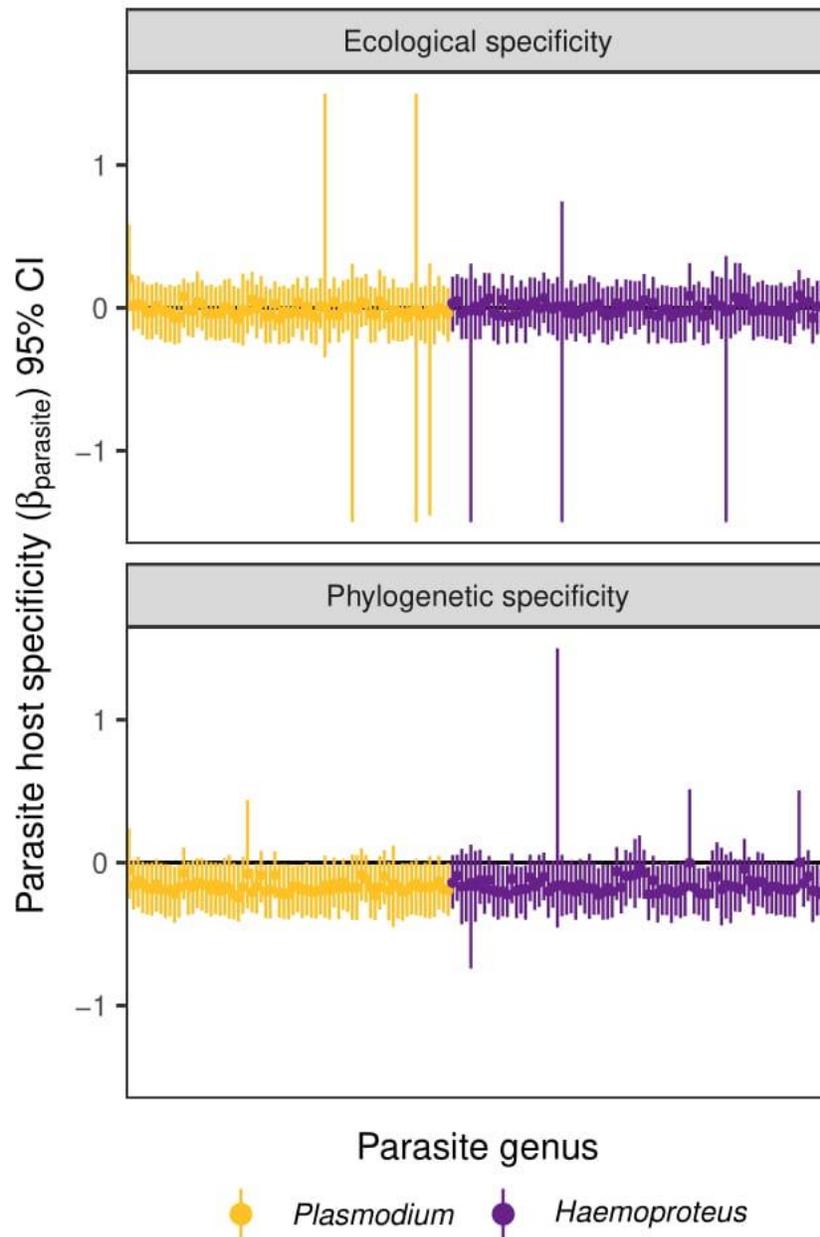
778

779



780
781
782
783
784
785
786
787
788
789
790
791
792
793
794
795
796
797
798
799

Figure 3. Density distributions of regional host specificity (β_{region}) coefficients, arranged by decreasing minimum rainfall of the driest quarter. Lower β_{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 β_{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 β_{region} values, with more specialized parasites in regions with wetter dry seasons. Polygon colors correspond to region names in Table 1.



801

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.

807