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1 **Climate, host phylogeny and the connectivity of host communities govern**
2 **regional parasite assembly**

3

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37 **ABSTRACT**

38 **Aim** Identifying barriers that govern parasite community assembly and parasite
39 invasion risk is critical to understand how shifting host ranges impact disease
40 emergence. We studied regional variation in the phylogenetic compositions of
41 bird species and their blood parasites (*Plasmodium* and *Haemoproteus* spp.) to
42 identify barriers that shape parasite community assembly.

43 **Location** Australasia and Oceania

44 **Methods** We used a dataset of parasite infections from >10,000 host individuals
45 sampled across 29 bioregions. Hierarchical models and matrix regressions were
46 used to assess the relative influences of interspecies (host community
47 connectivity and local phylogenetic distinctiveness), climate and geographic
48 barriers on parasite local distinctiveness and composition.

49 **Results** Parasites were more locally distinct (co-occurred with distantly related
50 parasites) when infecting locally distinct hosts, but less distinct (co-occurred
51 with closely related parasites) in areas with increased host diversity and
52 community connectivity (a proxy for parasite dispersal potential). Turnover and
53 the phylogenetic symmetry of parasite communities were jointly driven by host
54 turnover, climate similarity and geographic distance.

55 **Main conclusions** Interspecies barriers linked to host phylogeny and dispersal
56 shape parasite assembly, perhaps by limiting parasite establishment or local
57 diversification. Infecting hosts that co-occur with few related species decreases a
58 parasite's likelihood of encountering related competitors, perhaps increasing
59 invasion potential but decreasing diversification opportunity. While climate
60 partially constrains parasite distributions, future host range expansions that
61 spread distinct parasites and diminish barriers to host shifting will likely be key
62 drivers of parasite invasions.

63

64 **Key words:** community assembly, host shifting, host specificity, interspecies
65 barriers, parasite invasion, *Plasmodium*

66

67 **INTRODUCTION**

68 Regional variation in community composition is a central property in nature
69 (Wallace, 1876; Kraft *et al.*, 2007). With increasing environmental destabilisation
70 and biotic homogenisation, predicting how ecosystems will function following
71 disturbance relies on identifying processes that govern **community assembly**
72 (Ricklefs, 1987; Barnagaud *et al.*, 2014; see Table 1 for bold term definitions).
73 Understanding parasite community assembly is crucial, as changes to parasite
74 composition or the frequency of host-parasite interactions can alter risks of
75 parasite invasions and emerging disease (Brooks & Hoberg, 2007; Hoberg &
76 Brooks, 2008; Lafferty, 2009; Agosta *et al.*, 2010; Adlard *et al.*, 2015).

77 A strong incentive exists to identify barriers to species establishment and
78 determine how these barriers modulate invasion risk (Hoberg, 2010; Kelly *et al.*,
79 2009; Springborn *et al.*, 2015). For parasites, **geographic barriers** (such as
80 distance or mountain ranges) are known to constrain species' distributions
81 (Brooks & Ferrao, 2005; Lafferty, 2009; Warburton *et al.*, 2016; Krasnov *et al.*,
82 2016). In addition, **environmental barriers** (such as temperature and
83 precipitation) drive development or transmission rates for many parasites,
84 especially vector-borne parasites such as those causing malaria and lyme disease
85 (Githeko *et al.*, 2000; Epstein, 2001; Patz *et al.*, 2005). However, parasite
86 distributions are also linked to host life histories and distributions (Poulin *et al.*,
87 2011; Olsson-Pons *et al.*, 2015; Fecchio *et al.*, 2017). Such **interspecies barriers**
88 are increasingly recognised to govern local assembly (HilleRisLambers *et al.*,
89 2012; Wisz *et al.*, 2013; Mayfield & Stouffer, 2017). Predicting how parasite
90 composition may change in the future relies on defining a consistent framework
91 to identify patterns that improve knowledge of assembly and elucidate

92 underlying mechanisms acting as barriers. Such patterns may be driven by a
93 hierarchical process, where parasites must first break through geographic
94 and/or environmental barriers to initially colonise a new range (Brooks &
95 Hoberg, 2007; Agosta *et al.*, 2010). Following colonisation, assembly may be
96 limited by interspecies barriers that govern parasite spread and diversification
97 (Fig. 1). This process, termed ‘ecological fitting’ (Janzen, 1985), suggests many
98 parasites are capable of infecting a broader range of hosts than is currently
99 realised, with changes to host and/or parasite distributions producing new
100 associations that may be limited by host phylogenetic relationships (Brooks &
101 Ferrao, 2005; Radtke *et al.*, 2007; Araujo *et al.*, 2015).

102 For parasites that rely on host dispersal to colonise new areas, regions
103 comprising a diversity of host species whose ranges overlap with other potential
104 hosts (i.e. high distributional connectivity to other regions; **host community**
105 **connectivity**) should support broader parasite diversity due to increased niche
106 space (Hector *et al.*, 2001) and a higher likelihood for parasites to break
107 geographic and/or environmental barriers (Fig. 1). However biotic barriers
108 could still limit parasite invasions in phylogenetically diverse systems,
109 particularly if invasion success is positively related to the invader’s **local**
110 **phylogenetic distinctiveness** (i.e. more locally distinct invaders are less likely
111 to be limited by related competitors; HilleRisLambers *et al.*, 2012). Yet while host
112 community connectivity can overcome geographic dispersal barriers, few studies
113 recognise this aspect as a potential driver of parasite assembly (but see Buckee
114 *et al.*, 2007).

115 Parasites are often restricted to hosts with phylogenetically conserved
116 ecological or physiological traits (Janzen, 1968; Rohde, 1980; Streicker *et al.*,

117 2010; Schulze-Lefert & Panstruga, 2011), a phenomenon that has powerful
118 consequences for species interactions and ecosystem functioning (Ehrlich &
119 Raven, 1964; Hoberg & Brooks, 2008). As parasites with high **host specificity**
120 may be unable to shift hosts, the local availability of suitable hosts can present an
121 invasion barrier following initial dispersal, especially if parasites are adapted to
122 hosts that do not commonly co-occur with closely related species (Brooks, 1979;
123 Ewen *et al.*, 2012; Clark & Clegg, 2015; Ellis *et al.*, 2015; Mata *et al.*, 2015; Fig. 1).

124 While ecological fitting (governed at least partly by parasite host
125 specificity and host evolutionary history) and host dispersal potential are clearly
126 important mechanisms impacting parasite establishment and diversification,
127 identifying their roles in natural host-parasite systems is challenging. We
128 develop a framework to identify relative influences of barriers to regional
129 parasite community assembly, and apply this framework to naturally-occurring
130 parasite infections from Australasian bird communities. Haemosporidians
131 (genera *Plasmodium* and *Haemoproteus*) are vector-borne blood parasites that
132 display a range of host specificities (Križanauskienė *et al.*, 2006). Due to limited
133 vector dispersal (Ejiri *et al.*, 2011), avian hosts are the primary vehicles by which
134 these parasites disperse (Pérez-Tris & Bensch, 2005). Avian haemosporidians
135 have been introduced to numerous bioregions, sometimes with devastating
136 effects on native birds, raising questions about how interspecies and geographic
137 barriers regulate parasite assembly and invasion potential (van Riper III *et al.*,
138 1986; Hellgren *et al.*, 2014).

139 We assess barriers that may govern parasite local coexistence at the
140 species level by estimating effects of host community connectivity and
141 interspecies barriers (host phylogeny and parasite host specificity) on parasite

142 local phylogenetic distinctiveness. We then address barriers at the community
143 level by (1) exploring effects of host **phylogenetic turnover**, environmental
144 variation and geographic distance on parasite turnover and (2) testing if host
145 connectivity or environmental variation influence parasite **phylogenetic**
146 **community skewness**. We expect that increased host community connectivity
147 reduces barriers to parasite establishment, leading to phylogenetically
148 homogenised parasite communities. If host phylogeny acts as a relatively strong
149 interspecies barrier to parasite assembly, we expect that distinct hosts carry
150 distinct parasites and that between-region host turnover predicts parasite
151 turnover. We also expect host-specialist parasites to be more locally distinct than
152 generalists, as specialists may have less opportunity to diversify through host
153 range expansions. Alternatively, if higher diversities of host specialists are able
154 to co-occur through extensive niche packing (Ricklefs, 2010), then we expect
155 specialists to be less distinct than generalists.

156

157 **METHODS**

158 **Host-parasite occurrence data and avian community connectivity**

159 We surveyed published literature and queried the MalAvi database
160 (<http://mbio-serv2.mbioekol.lu.se/Malavi/>; accessed September 2016; Bensch
161 *et al.*, 2009) to compile data from >10,000 sampled host individuals (from 297
162 avian species) across 83 sites, ranging across latitudes -50.77 to 14.27 and
163 longitudes -159.78 to 178.07 (Fig. 2). In all cases, parasite lineages were
164 identified using PCR targeting the cytochrome-*b* (*cyt-b*) gene (Hellgren *et al.*,
165 2004; Waldenström *et al.*, 2004). Evidence indicates lineages differing by as little
166 as one base pair may be reproductively isolated (Bensch *et al.* 2004). We thus

167 regard each unique sequence as a parasite 'species'. Low numbers of recovered
168 parasites at some sites meant we could not assess within-site composition. We
169 thus grouped sites into 29 regions. Australian mainland sites were grouped by
170 climate zone using the Bureau of Meteorology's Köppen classification, which
171 defines zones using temperature, precipitation and vegetation data
172 (http://www.bom.gov.au/jsp/ncc/climate_averages/climate-classifications/;
173 accessed November 2016). Papua New Guinea mainland sites were grouped
174 based on elevation (highlands, mean altitude = 2500m; and lowlands, mean
175 altitude = 60m). Island sites were either grouped by island (if at least three
176 parasite species were recovered) or into regions representing nearby islands in
177 an archipelago (Fig. 2; Supplementary Dataset 1).

178 We downloaded range maps for all avian species occurring in the study
179 area (N = 3,024 species) from BirdLife International and NatureServe
180 (<http://www.birdlife.org/datazone>; accessed October 2016). For each region, we
181 obtained lists of occurring avian species (defined as the 'total' assemblage) by
182 recording all species whose ranges overlapped 111 km buffers (1° at the
183 equator) around sites. Bird range sizes were calculated as the total area of range
184 polygons. Range sizes varied from 1km² (island endemics) to 28,000km² (wide
185 ranging seabirds).

186 Avian community connectivity was calculated as an inverse Simpson
187 diversity index (Simpson 1949) using species' range sizes as weights (instead of
188 using species abundances). Here increased species richness, larger species range
189 sizes and more even range size distributions all lead to increased collective
190 mobility of a local host assemblage. Two connectivity indices were created, one
191 using sampled hosts (***Sampled.Con_H***) and a second using total assemblages (all

192 occurring avian species; **Total.Con_H**). We included *Total.Con_H* because many
193 haemosporidians infect a diversity of avian species (Ewen *et al.* 2012; Olsson-
194 Pons *et al.* 2015), suggesting unsampled but present host species impact parasite
195 assembly. This will be especially relevant for generalist parasites, whereas
196 sampled hosts should be representative for specialised parasites that are
197 unlikely to occur in unsampled host species.

198

199 **Parasite and host phylogenetic reconstructions**

200 Parasite *cyt-b* sequences (205 *Haemoproteus* and 80 *Plasmodium* parasites) were
201 used to reconstruct phylogenetic relationships in BEAST v1.8.1 (Drummond &
202 Rambaut, 2007; See Fig. S1 in Supplementary Material). We identified the best
203 evolutionary model (HKR+G) using maximum likelihood in MEGA v7.0 (Tamura
204 *et al.*, 2007). We specified a Yule speciation prior and ran two chains of
205 17,500,000 iterations, sampling every 100,000 and removing 2,500,000 samples
206 as burn-in. Chains were examined visually for stationarity and convergence.

207 Avian phylogenies were gathered from Birdtree.org (<http://birdtree.org>;
208 accessed September 2016), which contains a Bayesian posterior distribution of
209 phylogenies for 9,993 avian species (Jetz *et al.*, 2012). We gathered 100 trees
210 from the 'Ericsson All Species Trees' dataset for the 297 sampled host species,
211 and another 100 trees for the 3,024 avian species occurring in the sample area.
212 For all trees, branch lengths represented substitutions per site and were scaled
213 (dividing branch lengths by the maximum) prior to analyses.

214

215 **Species level analyses**

216 *Host and parasite phylogenetic distinctiveness*

217 For sampled host species, local phylogenetic distinctiveness (***Sampled.Dis_H***) was
218 calculated as mean pairwise phylogenetic distance between a focal species and
219 all other sampled host species in a region. This distance was divided by the mean
220 of all pairwise distances in the region, resulting in region-specific distinctiveness
221 (higher values indicating more distinct species). We calculated total host
222 distinctiveness (***Total.Dis_H***) using mean phylogenetic distance between a
223 sampled host and all occurring avian species (sampled and unsampled) in a
224 region. Parasite distinctiveness (***Dis_P***) was calculated separately for each parasite
225 genus.

226

227 *Parasite host specificity*

228 Two indices described parasite host specificity. First, we built bipartite networks
229 (using numbers of infected individuals for each host species) and calculated the
230 ***d'*** specialisation index using Kullback-Leibler distances (Blüthgen *et al.*, 2006).
231 Ranging from zero (no specialisation; i.e. using all available hosts) to one (perfect
232 specialist), ***d'*** quantifies how strongly a parasite is 'specialised' compared to
233 other parasites in terms of host range and interaction frequencies. We calculated
234 phylospecificity for each parasite (***STD****; Poulin & Mouillot, 2005), which
235 accounts for the number of infected host species and their phylogenetic
236 distances. Because ***STD**** ranges from one (specialist) to greater than one, we
237 used inverse ***STD**** so both metrics could be interpreted in the same scale and
238 direction. Parasite ***STD**** and ***d'*** were uncorrelated (Pearson correlation; $t = -1.41$,
239 $p = 0.16$), suggesting they capture different aspects of parasite host specificity (***d'***
240 capturing the level of host sharing by parasites and ***STD**** capturing phylogenetic
241 relationships of infected hosts).

242

243 *Influences of host community connectivity, host phylogeny and host specificity on*244 *parasite distinctiveness*

245 We tested whether interspecies barriers influenced parasite distinctiveness

246 (Dis_P) with a hierarchical linear model, using 548 unique parasite*host*region247 combinations as data points (Supplementary Dataset 2). Because Dis_P indices

248 were non-negative and positively skewed, we log transformed values and

249 specified a Gaussian error distribution. Continuous predictors were the two host

250 distinctiveness metrics ($Sampled.Dis_H$, $Total.Dis_H$), the two host connectivity251 metrics ($Sampled.Con_H$, $Total.Con_H$), host geographic range and both parasite host252 specificity metrics (d' , STD^*). Because parasite genera showed different253 phylogenetic patterns (see Results) and $Total.Dis_H$ explained a significant254 proportion of variance in Dis_P in preliminary analyses, we tested a255 $Total.Dis_H$ *parasite genus interaction. To decompose variation among covariates

256 and account for underlying phylogeographic structure, host phylogeny and

257 sample region were included as random grouping terms, allowing inferences for

258 group-specific slopes whilst estimating between-group variation (Gelman & Hill,

259 2007).

260 The model was fitted in a Bayesian framework using R package

261 MCMCglmm (Hadfield, 2010). We used a flat prior for residual variance and

262 parameter expansion (redundant multiplicative reparameterisation of the linear

263 model) for grouping terms, which reduces dependence among parameters and

264 improves mixing (Gelman, 2006). To account for phylogenetic uncertainty, we

265 ran separate models across 50 host trees (Guillerme & Healy, 2014). Models

266 were run using two chains of 100,000 iterations with burn-in of 10,000 and

267 thinning interval of 300. Chains were inspected for mixing/convergence both
268 visually and with the Gelman-Rubin diagnostic (Gelman & Rubin, 1992).
269 Autocorrelations were calculated to ensure independence of coefficient
270 estimates (all autocorrelations < 0.1).

271

272 **Community analyses**

273 *Interspecies and geographic barriers to parasite phylogenetic turnover*

274 To describe shifts in diversity among regions, parasite phylogenetic turnover
275 (β_P) was calculated (using binary occurrence data; Tsirogiannis & Sandel, 2015)
276 between regions where three or more parasites occurred. Host turnover was
277 calculated using either sampled hosts (***Sampled. β_H***) or total avian assemblages
278 (***Total. β_H***). Distances between paired regions were calculated as beeline distance
279 (km) between central points (mean latitude and longitude of regions). Regional
280 climate dissimilarity was captured by three Gower's distance matrices (Gower,
281 1971) to describe temperature and precipitation variation (both of which are
282 thought to influence haemosporidian distributions; Sehgal *et al.*, 2010; Sehgal,
283 2015). We used minimum temperature of the coldest month and mean
284 temperature of the coldest quarter in a *min.temp* matrix, while a *max.temp*
285 matrix included maximum temperature of the warmest month and mean
286 temperature of the warmest quarter. Mean yearly precipitation and
287 precipitations of the wettest and driest quarters were included in a *precip*
288 matrix. For climate matrices, variables were sourced from (www.worldclim.org;
289 accessed November 2016) and were continuous, unweighted and scaled by
290 range (dividing by the maximum).

291 We tested if β_P was correlated with *Sampled. β_H* , *Total. β_H* , geographic

292 distance or climate dissimilarity matrices using multiple regressions on distance
293 matrices (MRM; Goslee & Urban, 2007). Phylogenetic uncertainty was captured
294 by repeating regressions over 1,000 iterations, where β values were re-
295 calculated in each iteration using randomly sampled (with replacement) trees.
296 To account for sampling variation that could bias turnover estimates (rare
297 species may be more likely to be observed with larger sample sizes), we
298 randomly removed subsets of species from well-sampled regions (>8 observed
299 parasite species) prior to regression. We arbitrarily allowed the proportion of
300 removed species to vary across a uniform distribution from zero to 30% in each
301 iteration. Regression coefficients and R^2 values were gathered from the 1,000
302 iterations.

303

304 *Barriers to parasite phylogenetic community skewness*

305 Host and parasite phylogenetic community skewness were calculated using
306 pairwise phylogenetic distance distributions. A measure of symmetry, this index
307 will be less than zero (right skewed) if communities are made up of relatively
308 more closely than distantly related species (Schweiger *et al.*, 2008), suggesting
309 future colonising parasites have a greater likelihood of being locally distinct.
310 Thus, regions with right skewed communities may be more vulnerable to
311 invasions by distantly related species if parasites are able to overcome
312 environmental barriers and colonise. Skewness was calculated for regions where
313 three or more parasites occurred.

314 We tested if parasite skewness was predicted by host connectivity
315 (*Sampled.Con_H*, *Total.Con_H*) using linear regression with Gaussian error
316 distribution. Mean annual precipitation and mean temperatures of the warmest

317 and coldest quarters were included as continuous covariates to account for
318 possible climate influences, while sampled and total host skewness were
319 included to account for influences of host phylogenetic symmetry. Parasite genus
320 was included as a categorical covariate. The model was fitted using MCMCglmm
321 with a flat prior for residual variance. We ran two chains of 100,000 iterations
322 with burn-in of 10,000 and thinning interval of 300, following procedures above
323 to examine convergence and estimate autocorrelations.

324 For all phylogenetic metrics (skewness, distinctiveness and *STD**), we
325 accounted for phylogenetic uncertainty by calculating median indices across
326 1,000 randomly sampled host and parasite trees. Significance of model effects
327 was determined by examining if 95% quantiles (for MRM models) or 95%
328 credible intervals (CI; for Bayesian models) of regression coefficients did not
329 overlap zero. Continuous predictors were scaled (centred and divided by one
330 standard deviation), and variances explained were calculated following
331 Nakagawa & Schielzeth (2013). Data was analysed in R v3.2.1 (R Core Team,
332 2016; R: A language and environment for statistical computing). Data and R code
333 are presented in Supplementary Data and the Dryad Digital Repository: (doi:
334 XXXXX XXXXX).

335

336 **RESULTS**

337 **Host phylogeny, local distinctiveness and connectivity drive parasite**

338 **distinctiveness**

339 Parasite distinctiveness (*Dis_P*) was strongly related to host phylogeny (variance
340 explained = 46.8 to 78.3%), with hosts from certain clades more likely to carry
341 distinct parasites (Fig. 3). These included carriers of distinct *Haemoproteus* spp.

342 such as doves (Columbidae), kingfishers (Alcedinidae) and corvids such as
 343 crows (Corvidae) and whistlers (Pachycephalidae; Fig. 3), all of which occupy a
 344 range of regions yet rarely co-occur with sympatric sister species (Dutson, 2012;
 345 Jønsson *et al.*, 2014). After accounting for the strong influence of host phylogeny,
 346 Dis_P was also positively predicted by local host total distinctiveness ($Total.Dis_H$;
 347 coefficient 95%CI = 0.04 to 0.12; variance explained = 2.48 to 6.38%; Fig. 3),
 348 suggesting host relatedness to the local avian assemblage acts as an interspecies
 349 barrier to parasite assembly. This relationship varied between parasite genera,
 350 as increases in $Total.Dis_H$ lead to a 1.95 times higher increase in Dis_P for
 351 *Haemoproteus* than for *Plasmodium* parasites.

352 Dis_P decreased with increasing total host connectivity ($Total.Con_H$;
 353 coefficient = 0.01 to 0.09; variance explained = 0.04 to 7.7%; See Fig. S2 in
 354 Supplementary Material), indicating greater host diversity and collective
 355 mobility increases a parasite's chance of encountering related parasites.
 356 $Total.Con_H$ was highest in Malaysia (509 avian species; $Total.Con_H = 83.60$) and
 357 southeast Australia (468 avian species; $Total.Con_H = 80.42$), moderate in Papua
 358 New Guinea where many endemic avian species occur (mean species = 520.5;
 359 mean $Total.Con_H = 42.62$) and lowest in Vanuatu and New Caledonia (mean
 360 species = 115 and 110; mean $Total.Con_H = 32.3$ and 31.6 , respectively). Dis_P was
 361 not influenced by $Sampled.Con_H$, $Sampled.Dis_H$ or individual host range
 362 (coefficient CIs overlapped zero).

363 We observed considerable variation in host specificity for both parasite
 364 genera, though neither specificity metric influenced Dis_P (coefficients overlapped
 365 with zero). For both genera, STD^* (phylospecificity) ranged from 0.41 to 1 (mean
 366 = 0.79 and 0.87 for *Plasmodium* and *Haemoproteus*, respectively), while d'

367 (network specificity) ranged from 0 to 1 (means = 0.65 and 0.67). In total, fixed
 368 effects (d' , STD^* , host range size, $Total.Con_H$, $Sampled.Con_H$, $Total.Dis_H$,
 369 $Sampled.Dis_H$) explained 5.7 to 13.2% of variance in Dis_P while the full model
 370 (including host phylogeny and region grouping terms) explained 69.8 to 88.9%.
 371

372 **Host phylogeny and climate shape parasite community structure**

373 We found evidence that both environmental and interspecies barriers influence
 374 parasite turnover. For *Plasmodium*, β_P was positively correlated with $Sample.\beta_H$
 375 (MRM coefficient = 1.01 to 1.86), indicating host phylogeny influences shifts in
 376 parasite diversity. *Plasmodium* β_P also correlated positively with geographic
 377 distance (0.56 to 1.21), but negatively with $max.temp$ (-0.09 to -0.18). For
 378 *Haemoproteus*, β_P correlated positively with both host turnover metrics
 379 ($Sampled.\beta_H$ coefficient = 0.30 to 0.61; $Total.\beta_H$ = 0.58 to 1.13), and with
 380 geographic distance and $max.temp$ (0.04 to 1.37; 0.16 to 0.45, respectively), but
 381 negatively with $min.temp$ (-0.11 to -0.28). Variance explained by predictors
 382 ranged from 47 to 57% for *Haemoproteus* β_P and from 4 to 11% for *Plasmodium*
 383 β_P .

384 Mainland communities such as Papua New Guinea and eastern Australia
 385 showed low mean parasite turnover among paired regions (low average
 386 pairwise β_P after accounting for geographic distance; Fig. 2; Supplementary
 387 Dataset 3), suggesting these assemblages were less phylogenetically unique
 388 within the study area. Parasite assemblages on Melanesian islands (New
 389 Caledonia and Vanuatu) showed moderate mean turnover, while relatively
 390 isolated and less well-sampled communities such as Christmas Island and
 391 northwest Australia showed high turnover (Fig. 2). *Plasmodium* communities in

392 New Zealand and Micronesia, where many occurring parasites are known to be
393 introduced (Beadell *et al.* 2006; Ewen *et al.*, 2012), showed high mean turnover
394 (Fig. 2).

395 Parasite community skewness indices were predominantly negative
396 (right-skewed; Fig. 4), with assemblages generally made up of more closely than
397 distantly related parasites. Parasite skewness was not influenced by host
398 community connectivity or host skewness, but was driven by mean temperature
399 of the coldest quarter (coefficient = 0.02 to 2.98; variance explained = 0.2 to
400 10.6%), with colder regions harbouring more negatively skewed communities
401 (Fig. 4). Parasite skewness also differed between genera (coefficient = -0.91 to -
402 0.02; variance explained = 7.5 to 27.10%), with *Plasmodium* more negatively
403 skewed than *Haemoproteus* communities (Fig. 4). Interestingly, *Haemoproteus*
404 communities in Papua New Guinea were positively skewed, while those in
405 eastern Australian were negatively skewed (Fig. 4), suggesting neighbouring
406 parasite assemblages with low phylogenetic turnover (Fig. 2) can vary
407 substantially in community structure.

408

409 **DISCUSSION**

410 We illustrate a framework for identifying relative influences of interspecies,
411 environmental and geographic barriers to parasite community assembly. Using
412 this framework, we show that host phylogeny is a key driver of local parasite
413 assembly, while climate and the regional connectivity of host assemblages play
414 lesser but nonetheless important roles. Moreover, host phylogeny and
415 geographic distance were more important than environmental barriers in
416 shaping parasite turnover, indicating alterations to host movement and

417 community composition may strongly affect parasite dispersal and invasion
418 potential across biogeographic scales.

419

420 **Barriers to parasite community assembly and their roles in parasite spread**

421 Host phylogeny was an important driver of parasite distinctiveness and species
422 turnover, supporting suggestions that host identity drives shifts in
423 haemosporidian diversity and implicating host evolutionary history as a
424 determinant of regional parasite assembly (Scordato & Kardish, 2014; Fecchio *et*
425 *al.*, 2017). Phylogenetic signals are a proxy for physical (i.e physiological,
426 morphological, biochemical) and ecological traits, where closely related species
427 resemble each other more than random pairs, indicating conserved attributes
428 likely play a role in modulating interspecies barriers to regional parasite
429 assembly (Huang *et al.* 2014). Yet an important consideration here is that we do
430 not know which shared host traits influence blood parasite assembly patterns.
431 Determining underlying interspecies barriers to parasite composition will
432 require additional interdisciplinary work, combining data on host traits with
433 methods that can decompose phylogenetic and ecological similarity to improve
434 inference (Cadotte *et al.*, 2013; Clark & Clegg, 2017).

435 Future host range shifts may considerably impact parasite spread and
436 disease emergence, both by breaking down existing barriers to host shifting and
437 by increasing parasite dispersal (Atkinson & LaPointe 2009; Young *et al.*, 2017).
438 Here, a positive relationship between host and parasite distinctiveness indicates
439 that diminishing phylogeographic barriers (where host range shifts may alter
440 local host distinctiveness) could present more opportunities for parasites to shift
441 between related hosts. Yet a strong host phylogenetic signal, where distinct

442 parasites are more strongly associated with certain host clades, suggests
443 alterations to host species' distributions may have different effects on parasite
444 spread depending on host evolutionary history. For instance, we identified
445 multiple host clades as prominent carriers of distinct parasites, including non-
446 passerines (kingfishers and doves) as well as certain passerine groups (crows
447 and whistlers), indicating that future range shifts for these host groups could
448 lead to novel parasite introductions. Our work therefore corroborates a large
449 body of literature to show that interactions between ecological fitting and
450 shifting geographic distributions will have powerful influences on parasite
451 assembly and emergence potential (Brooks & Hoberg, 2007; Hoberg & Brooks,
452 2008; Hoberg, 2010; Agosta *et al.*, 2010; Araujo *et al.*, 2015). However, a
453 significant influence of host community connectivity suggests that parasite
454 distinctiveness is not only driven by host phylogeny, but also by forces that limit
455 host diversity and distributional overlap (i.e. competitive exclusion or dispersal
456 barriers; Ricklefs, 2010; Ewen *et al.*, 2012). This finding generates exciting new
457 avenues for studying parasite assembly, particularly since few studies relate the
458 connectivity of host communities to parasite dispersal opportunity (but see
459 Buckee *et al.*, 2007).

460 Our findings that environmental effects influence parasite turnover and
461 community skewness agree with previous studies to suggest that even if
462 dispersal barriers break down, climate and perhaps other environmental
463 conditions may constrain parasite distributions (Kutz *et al.*, 2014; Sehgal, 2015;
464 Clark *et al.*, 2016a,b). Indeed, regional temperature similarity impacted shifts in
465 diversity for both parasite genera, albeit with different directional relationships.
466 One possible explanation could be that haemosporidians are subject to

467 influences of external temperature changes on ectothermic vectors (Paaijmans *et*
468 *al.*, 2010), and *Plasmodium* and *Haemoproteus* parasites are transmitted by
469 different arthropods (mosquitoes from family Culicidae and midges from family
470 Ceratopogonidae, respectively; Santiago-Alarcon *et al.*, 2012). However, little is
471 known about the particular vector species transmitting avian haemosporidians
472 in the South Pacific (but see Ishtiaq *et al.*, 2008), and so drawing conclusions
473 from these different patterns remains challenging. Intriguingly, regions with
474 colder temperatures harboured more closely related communities for both
475 parasite genera, perhaps indicating minimum temperatures act as a strong filter
476 for haemosporidian diversity, a finding that warrants future study. Regardless of
477 the biological mechanism, accounting for interspecies interactions and
478 environmental conditions can improve predictions of species distributions
479 following climate shifts (Choler *et al.*, 2001; Wells *et al.*, 2014; Mayfield &
480 Stouffer, 2017).

481 Determining which species are likely to be introduced and become
482 invasive are prominent ecological questions (Wiens, 2011; Springborn *et al.*,
483 2015). Our results suggest that parasites introduced to regions with low host
484 community connectivity, high host turnover and low minimum temperatures
485 may be more likely to invade the community. These patterns highlight that New
486 Zealand, which showed high rates of host and parasite turnover and contained
487 distantly related (phylogenetically left skewed) *Plasmodium* communities, may
488 be particularly vulnerable to invasions. Distinct invaders can have key
489 competitive advantages and a greater chance of becoming invasive
490 (HilleRisLambers *et al.*, 2012), as has been the case in the Galapagos where the
491 invasive fly, *Philornis downsi*, parasitizes a diversity of endemic bird species

492 (Fessl *et al.* 2006). Indeed, invasive avian malaria parasites have already been
493 recorded infecting a diversity of native New Zealand birds, with evidence
494 suggesting that introduced birds play key roles in driving parasite spread (Ewen
495 *et al.*, 2012; Schoener *et al.*, 2013). Parasites introduced to highly connected host
496 regions, on the other hand, may be more likely to experience competition with
497 closely related parasites, perhaps curbing invasion potential. Under this
498 consideration, areas such as eastern Australia and mainland Papua New Guinea
499 may be less vulnerable to parasite invasions (though not immune; see Clark *et*
500 *al.*, 2015), as these regions contain a relatively balanced phylogenetic diversity of
501 parasites and experience high host community connectivity.

502

503 **Accounting for unsampled host species in parasite assembly studies**

504 Our study raises a critical point for assessing parasite composition, as measures
505 of host relationships were more important in driving parasite assembly when
506 considering the total host assemblage rather than only sampled hosts. A host's
507 distinctiveness with respect to the entire avian community positively predicted
508 parasite distinctiveness, while considering only sampled hosts had no influence
509 on parasite distinctiveness. Phylogenetic turnover of the total avian assemblage
510 was also a stronger predictor of *Haemoproteus* turnover than was sampled host
511 turnover. These findings imply that variation in unsampled but locally present
512 host species are important for driving parasite establishment. Inferences beyond
513 those obtained from sampled hosts are clearly needed, a process which is rarely
514 considered in host-parasite interactions (but see Wells *et al.*, 2012), despite
515 being a well-known problem in the sample survey literature (Little, 2004).

516

517 **Caveats and conclusions**

518 There are several ways in which our study framework can be improved. First, we
519 did not consider individual sites in our study as our data was limited by small
520 sample sizes for many sites. Inclusion of site-specific species and climate data
521 could be used as an additional source of information to examine possible impacts
522 of sampling bias on regional community inferences. Second, consideration of
523 sampling distribution across regions may have an impact on community
524 turnover estimates, as regions such as Christmas Island and Micronesia had a
525 relatively high turnover that could have been influenced by low overall sample
526 sizes and large geographic distances to many other study regions. Future studies
527 that sample smaller and more regular geographic intervals could help to address
528 this drawback. Finally, our phylogenetic metrics relied only on binary species
529 occurrences (present or absent), and may be improved with better consideration
530 of species' relative abundances, since host abundance plays a role in host
531 reservoir potential and cross-species parasite transmission (Kilpatrick *et al.*,
532 2006). Unfortunately, such data for host abundance were not available and
533 would require additional field survey efforts.

534 In summary, our study agrees with previous work to suggest that in
535 addition to identifying environmental barriers, considering host phylogenetic
536 relationships and dispersal abilities is key to understanding regional parasite
537 assembly (Brooks & Ferrao, 2005; Agosta *et al.*, 2010; Wells *et al.*, 2015; Sehgal,
538 2015). Moreover, we show that accounting for the overall connectivity of the
539 host community, rather than solely focussing on individual host species'
540 dispersal potentials, may be crucial to predicting future parasite invasions. With
541 the pervasive need to understand how interspecies interactions shape species

542 distributions (Wisz *et al.*, 2013), our study represents an important step towards
543 predicting how parasite assemblages will be shaped following future global
544 change.

545

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562

563 **SUPPLEMENTARY MATERIAL**

564 **Fig. S1:** Phylogenetic relationships of *Haemoproteus* and *Plasmodium*
565 cytochrome-*b* sequences.

566 **Fig. S2:** Relationship between regional total host community connectivity
567 (*Total.Con_H*) and parasite local phylogenetic distinctiveness (*Dis_P*).

568 **Dataset 1:** Sample locations, host species sample sizes and parasite infection
569 prevalence across regions.

570 **Dataset 2:** Raw data used to analyse parasite local phylogenetic distinctiveness
571 (*Dis_P*)

572 **Dataset 3:** Turnover estimates and avian species richness metrics across
573 regions.

574

575 **DATA ACCESSIBILITY**

576 Newly reported parasite sequences will be uploaded to GenBank and the MalAvi
577 avian malaria database upon acceptance. R code and raw datasets will be
578 uploaded as supplements and to the Dryad digital repository upon acceptance.

579

580 **BIOSKETCH**

581 Nicholas Clark is a disease ecologist interested in evolutionary ecology and the
582 biogeography of wildlife pathogens. His research interests concern topics in
583 computational phylogenetics, biodiversity and host-pathogen interactions, as
584 well as large-scale patterns in community assembly.

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868 TABLES

869

870 **Table 1:** Glossary of definitions for proposed community assembly barriers and
871 metrics used in analyses.

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Community assembly: the establishment and maintenance of local communities through arrival of potential colonists from external species pools.

Environmental barriers: environmental differences between regions that may govern species' distributions, including variation in macroclimate, habitat and altitude.

Geographic barriers: physical barriers to between-region parasite dispersal, including geographic distance, mountain ranges, and water barriers.

Host community connectivity: the distributional overlap of host communities among regions, taking into account host species richness and host geographic range sizes. Here, *Sampled.Con_H* describes host community connectivity while considering only sampled avian host species, and *Total.Con_H* describes connectivity for all occurring avian species within a local assemblage.

Host specificity: the range and diversity of hosts a parasite is observed to infect. Here, *d'* describes parasite host specificity using host-parasite interaction networks, while *STD** describes phylogenetic host specificity using host phylogenetic distances.

Interspecies barriers: for parasites, interspecies barriers relate to variation in host species attributes that prevent parasite spread and diversification. These may include host phylogenetic relatedness and ecological similarity (e.g. microhabitat use, nesting behaviour, and feeding behaviour).

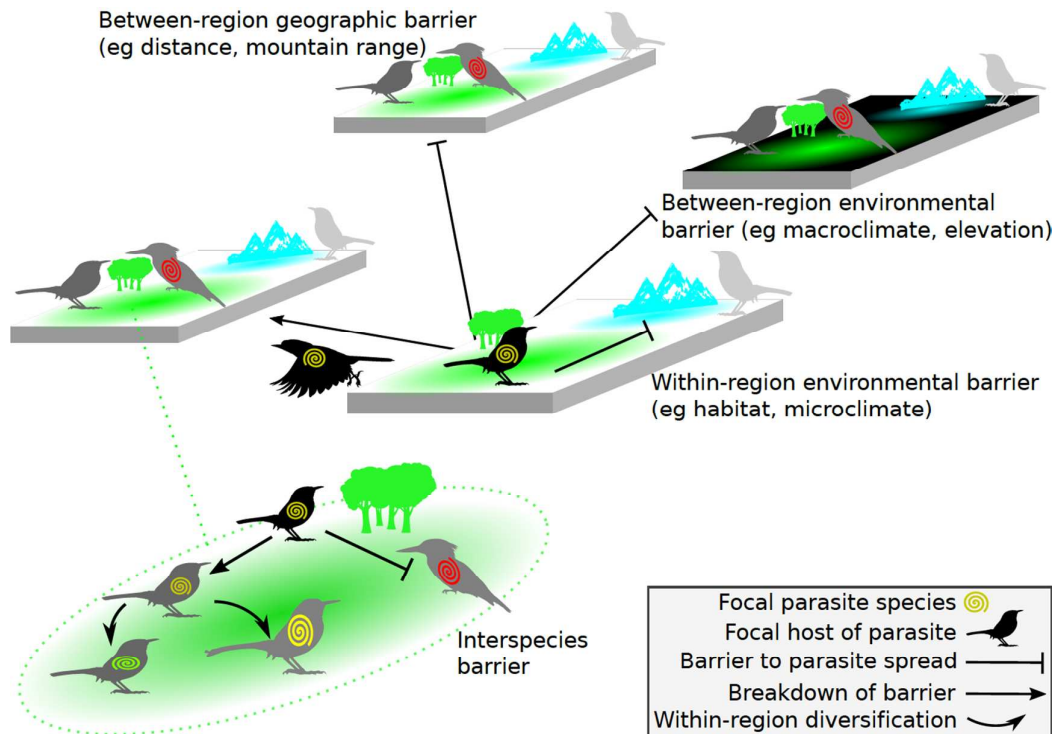
Local phylogenetic distinctiveness: the average pairwise phylogenetic distance between a focal taxon and co-occurring taxa within a local assemblage. Here, *Dis_P* describes parasite species distinctiveness, *Sampled.Dis_H* describes host species distinctiveness with respect to co-occurring sampled host species, and *Total.Dis_H* describes host species distinctiveness with respect to all co-occurring sampled avian species.

Phylogenetic community skewness: a measure of the asymmetry of species' pairwise phylogenetic distances, where a left-skew indicates relatively more distantly than closely related species in a community, while a right-skew indicates the opposite.

Phylogenetic turnover (β): shifts in phylogenetic diversity between communities. Here, β_P describes parasite phylogenetic turnover, *Sampled. β_H* describes turnover of sampled host assemblages, and *Total. β_H* describes turnover of total avian assemblages.

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875 **FIGURES**

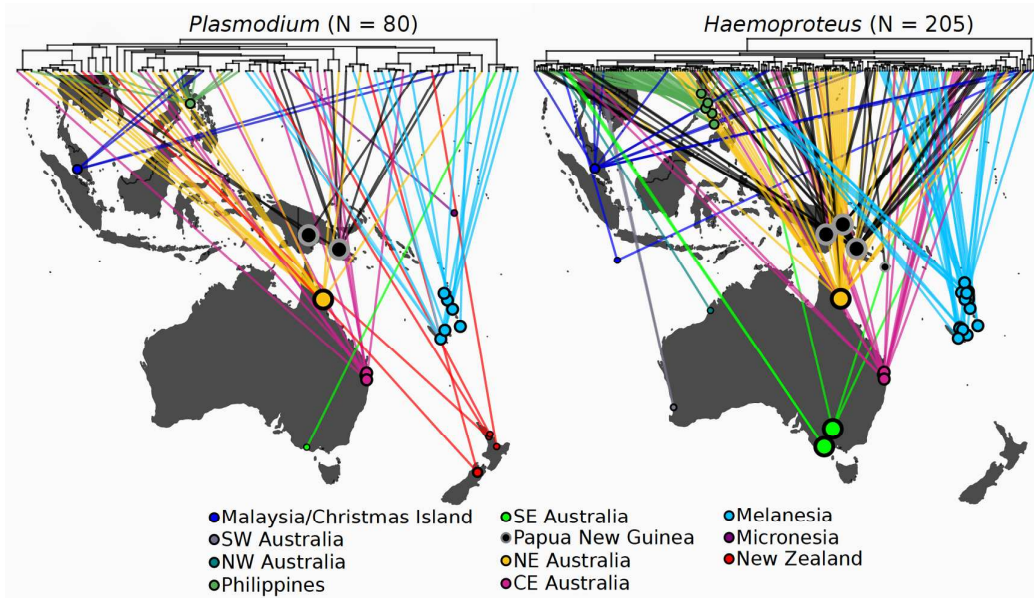
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878 **Fig. 1:** Schematic illustrating potential barriers to regional spread and
 879 diversification for parasites that rely on host movement for dispersal. Plates
 880 represent different bioregions, while zones (forest, mountain) within plates
 881 represent different habitat types. At the bottom left is a sectional zoom of the
 882 forested habitat in the left-hand plate, illustrating within-region parasite
 883 diversification where closely related host species enable the breakdown of
 884 interspecies barriers. Shown in black is the focal host of a given parasite species,
 885 with ecologically or phylogenetically similar host species depicted as similar
 886 shapes in varying shades of grey. A distantly related host species is depicted as a
 887 different body shape. Concentric oval shapes represent parasites, with different
 888 shapes and colours representing different parasite species.

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Fig. 2: Distribution of parasites across the study area. Lines connect phylogenetic parasite lineages to the region where they were most frequently observed. Circle sizes are inversely proportional to mean phylogenetic turnover (β_P) between the region and remaining regions, accounting for geographic distance. Hence, larger circles show communities with lower mean turnover to surrounding regions, which can be thought of as having more 'connected' parasite communities. Lines and circles are coloured according to region, with closely situated regions grouped to improve clarity.

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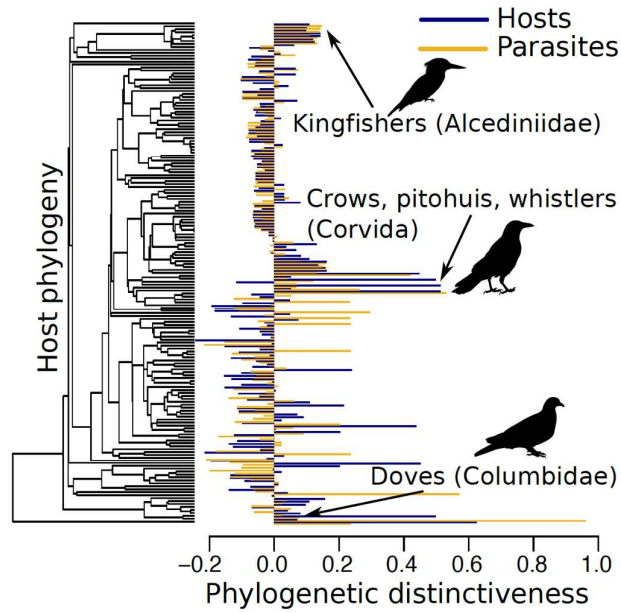
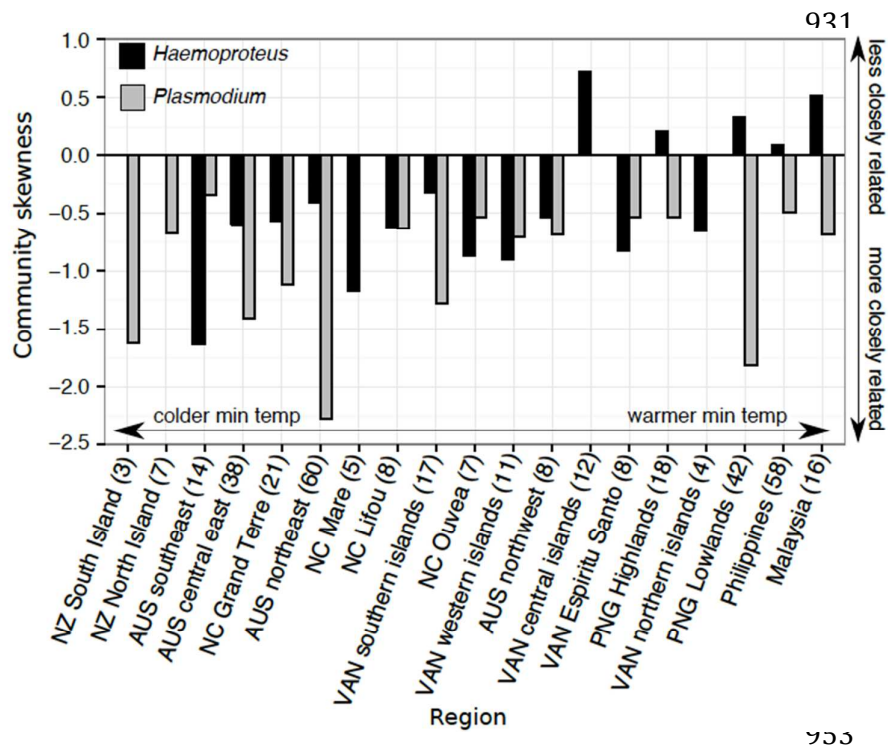


Fig. 3: Distribution of local phylogenetic distinctiveness for hosts ($Total.Dis_H$) and their parasites (Dis_P) across the host phylogeny. Distinctiveness represents mean phylogenetic distance between the focal species and all co-occurring species within a region. Values are scaled so values > 0 indicate taxa that are more distinct, while those < 0 indicate less distinct taxa.



954 **Fig. 4:** Parasite phylogenetic community skewness across regions. Skewness >
 955 zero indicates co-occurring parasites are relatively distantly related (left skewed
 956 pairwise distance distribution), while < zero indicates parasites are relatively
 957 closely related (right skewed distance distribution). Regions are ordered based
 958 on mean temperature of the coldest quarter, with numbers in parentheses
 959 indicating the number of parasites recovered in each region. NZ, New Zealand;
 960 AUS, Australia; NC, New Caledonia; VAN, Vanuatu; PNG, Papua New Guinea.
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