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1 **Global patterns in helminth host specificity: phylogenetic and functional**
2 **diversity of regional host species pools matter**

3

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14

15

16 **Abstract**

17 Host specificity has a major influence on a parasite's ability to shift between human and
18 animal host species. Yet there is a dearth of quantitative approaches to explore variation in
19 host specificity across biogeographical scales, particularly in response to the varying
20 community compositions of potential hosts. We built a global dataset of intermediate host
21 associations for nine of the world's most widespread helminth parasites (all of which infect
22 humans). Using hierarchical models, we asked if realised parasite host specificity varied in
23 response to regional variation in the phylogenetic and functional diversities of potential host
24 species. Parasites were recorded in 4-10 zoogeographical regions, with some showing
25 considerable geographical variation in observed versus expected host specificity. Parasites

26 generally exhibited the lowest phylogenetic host specificity in regions with the greatest
27 variation in prospective host phylogenetic diversity, namely the Neotropical, Saharo-Arabian
28 and Australian regions. Globally, we uncovered notable variation in parasite host shifting
29 potential. Observed host assemblages for *Hydatigera taeniaeformis* and *Hymenolepis*
30 *diminuta* were less phylogenetically diverse than expected, suggesting limited potential to
31 spillover into unrelated hosts. Host assemblages for *Echinococcus granulosus*, *Mesocostoides*
32 *lineatus* and *Trichinella spiralis* were less functionally diverse than expected, suggesting
33 limited potential to shift across host ecological niches. By contrast, *Hydatigera taeniaeformis*
34 infected a higher functional diversity of hosts than expected, indicating strong potential to
35 shift across hosts with different ecological niches. We show that the realised phylogenetic
36 and functional diversities of infected hosts are determined by biogeographical gradients in
37 prospective host species pools. These findings emphasise the need to account for underlying
38 species diversity when assessing parasite host specificity. Our framework to identify variation
39 in realised host specificity is broadly applicable to other host-parasite systems and will
40 provide key insights into parasite invasion potential at regional and global scales.

41

42 **Keywords:** ecological fitting, environmental niche conservatism, host-parasite interactions,
43 host specificity, invasion potential, parasite global spread, phylogeography

44

45 **Introduction**

46 The spillover of parasites from one host species to another, and the sharing of parasites
47 among humans, domestic animals and wildlife hosts, are of central public and animal health
48 concern (Hassell et al. 2017, Hatcher et al. 2012). Understanding the underlying drivers of
49 parasite host specificity is crucial for disease risk prediction and mitigation (Sokolow et al.
50 2015, Wood et al. 2012), as well as for forecasting the establishment of novel host-parasite

51 associations following biotic invasions (Agosta and Klemens 2008). Yet, whether patterns of
52 host shifting (colonising a new host species by means other than co-speciation, resulting in
53 host range expansion) varies due to biogeographical variation in underlying species pools has
54 been only addressed in few studies (Krasnov et al. 2004), hampering the search for general
55 processes that govern multi-species host parasite interactions (Park et al. 2018, Poulin et al.
56 2011).

57 Specialisation of species, in terms of both resource use and biotic interactions, is a
58 crucial determinant of species distributions and community assembly across a range of scales
59 (Devictor et al. 2010). For parasites, some adaptation to a particular host environment is
60 required for within-host survival, reproduction and transmission maintenance, depicting a
61 parasite's fundamental niche as an end product of evolutionary adaptations to its host species.
62 Following contact with novel host species, parasite host shifting requires adherence to the
63 principles of 'ecological fitting' (Janzen 1985), which postulates that the sharing of key
64 characteristics with previous host species is necessary for successful infection (Brooks et al.
65 2006, Hoberg and Brooks 2008, Wells et al. 2015). The extent of a parasite's specialisation is
66 therefore a key determinant of invasion capacity and the likelihood of establishing novel
67 host-parasite associations (Agosta et al. 2010).

68 Besides host characteristics that allow parasites to switch hosts, host community
69 composition and contact patterns between different host species are key to host shifting
70 (Begon et al. 2002, Clark et al. 2017). At local scales, spatiotemporal variation in host species
71 presence and abundance can result in altered interspecific contact rates that ultimately drive
72 spatiotemporal gradients in a parasite's realised host range (Canard et al. 2014). This
73 heterogeneity in host composition will have important consequences for determining host
74 specificity for widespread parasites, particularly those that infect wildlife. At a global scale,
75 wildlife communities occur in distinct species communities depending on their

76 biogeographical history, the timing of speciation events and the distributions of habitat
77 biomes (Holt et al. 2013, Kraft et al. 2007, Wallace 1876). The emergence of parasites into
78 novel environments, particularly along invasion routes of globally distributed host species,
79 such as humans and commensal animals, involves contact with endemic species not
80 previously encountered as prospective hosts. Consequently, contemporary regional
81 opportunities for host-parasite species interactions likely set the stage for shaping a parasite's
82 realised niche.

83 It is reasonable to assume that the realised host specificity of parasites can vary across
84 regions. Yet, to our knowledge, few studies of parasite host specificity across
85 biogeographical scales account for variation in available hosts (Cooper et al. 2012, Doña et
86 al. 2017, Krasnov et al. 2004, Lootvoet et al. 2013, Poisot et al. 2017). Understanding how
87 host specificity relates to the composition of regional species pools can provide important
88 insights into the global invasion potential of parasites (Murray et al. 2015). A better
89 understanding of natural variation in host specificity could be used to quantify parasite
90 invasion potential or facilitate the identification of novel host shifts over distantly related host
91 species (by identifying relatively high phylogenetic or functional diversity of the regional
92 host spectra).

93 For helminth parasites that use intermediate host species in their life cycles, including
94 most of the focal tapeworms and nematode species of our study, the principles of ecological
95 fitting apply strongly to trophic relationships. Host shifting commonly occurs within similar
96 host feeding guilds (Hoberg and Brooks 2008), suggesting food web structure plays an
97 important role in facilitating helminth parasite invasions. Indeed, for many widespread
98 helminth parasites, host specificity appears less restricted at the intermediate host stage than
99 the definitive host stage, with non-adult intermediate stages able to infect various organs or
100 body cavities of a diversity of intermediate hosts (Morand et al. 2006). Though colonisation

101 of new bioregions requires ecological fitting across multiple trophic levels (due to the
102 necessity of both intermediate and definitive hosts, Malcicka et al. (2015)), host specificity at
103 the intermediate stage plays a key role in helminth parasite invasion potential. A prominent
104 example of the consequences of differing specificity strategies at the intermediate host level
105 is the comparison of two widespread tapeworm species of *Echinococcus*. Adults of *E.*
106 *granulosus* develop only in dogs (*Canis familiaris*) and a few other carnivores, but can utilise
107 a large range of herbivorous and omnivorous mammalian species as intermediate hosts.
108 Within its exotic range in Australia, the presence of dingos and dingo/dog hybrids that feed
109 on a large range of endemic wildlife, has enabled the establishment of stable transmission
110 cycles of *E. granulosus* through wild dogs and endemic wildlife (Jenkins 2006), illustrating
111 how host shifting into novel communities may be facilitated by particular regional conditions.
112 In contrast, *E. multilocularis* usually utilises foxes (*Vulpes vulpes*) as its definitive host
113 species and primarily infects voles/mice as intermediate hosts; although this congeneric
114 tapeworm also covers a large geographical range, its distribution is necessarily confined to
115 regions with a sufficient abundance of the major intermediate host species (i.e. voles) in
116 North America, Europe and northern Asia (Davidson et al. 2012). We propose that large scale
117 assessments of host-parasite interactions in relation to host compositional variation can detect
118 these patterns, providing a better understanding of the mechanisms driving parasite
119 distributions.

120 Here, we assess geographical variation in phylogenetic and functional host specificity
121 for nine of the most globally widespread mammalian helminth parasites (all of which infect
122 humans). By accounting for regional variation in the compositions of prospective
123 intermediate host species, we extend commonly used host specificity metrics to provide a
124 relatively unbiased, global-scale assessment of parasite host specificity and invasion
125 potential. We expect the phylogenetic and functional diversities of infected hosts to show

126 high regional variation for parasites whose transmission cycles are poorly maintained by
127 wildlife within their exotic range (such as *E. multilocularis*). Accordingly, we expect
128 different levels of parasite host specificity to be reflected by the particular host species
129 attributes that predict host association frequencies.

130

131 **Materials and methods**

132 *Mammalian helminth-host database*

133 We compiled a global database of mammalian host-parasite associations from the publicly
134 available Host-Parasite Database of the Natural History Museum (NHM), London (Gibson *et*
135 *al.*, 2005). Data extraction is described elsewhere, resulting in a database of 24,486 unique
136 combinations of host–parasite–country records for selected helminth taxa (Nematoda,
137 Cestoda, Trematoda), totalling 4,507 parasite species recorded from 1,366 mammalian host
138 species (Wells *et al.* 2018). Location names were standardised to country names of the
139 current world geopolitical map and assigned to one of 11 zoogeographical regions according
140 to Holt *et al.* (2013). We focussed on nine focal parasite species: *Calodium hepaticum*
141 (Nematoda), *Echinococcus granulosus* (Cestoda), *Echinococcus multilocularis* (Cestoda),
142 *Hydatigera taeniaeformis* (Cestoda), *Hymenolepis diminuta* (Cestoda), *Mesocestoides*
143 *lineatus* (Cestoda), *Taenia hydatigena* (Cestoda), *Trichinella spiralis* (Nematoda) and
144 *Versteria mustelae* (Cestoda). These species all infect humans, exhibit large mammalian host
145 ranges (each has been recorded in > 45 host species in our database), are globally distributed
146 and were sufficiently covered in our database for statistical inference.

147 To elucidate regional patterns in the composition of potential intermediate host
148 species, we gathered lists of all unique mammal species that have been sampled for parasites
149 (i.e. all host species recorded in the database) in each zoogeographical region. Unique lists of
150 potential hosts were generated for each parasite in each region where the parasite has been

151 recorded, and were constrained to those host species belonging to the same taxonomic orders
152 as the recorded host species (typically involving small mammals and ungulates). This was
153 done because we conservatively consider mammal species from the same orders to be the
154 most likely potential host species. For analysis (as outlined below), we excluded all species
155 belonging to the Carnivora from these lists to focus only on potential intermediate host
156 species (carnivores are typically definitive host species for the focal parasites). Note that this
157 selection comprises definitive hosts for *Hymenolepis diminuta*, which uses arthropods as
158 intermediate hosts. For each mammal species included in these parasite- and region-specific
159 selections (hereafter referred as mammalian species pools), associations with each of the
160 focal parasites were recorded as binary variables (presence-absence) for use as response
161 variables. We are aware that our dataset is erroneous in that it lacks recent records of host
162 parasite interactions (i.e. false zeros if true interactions are not recorded in the dataset and/or
163 novel species are missed out) and also may include accidental hosts in which parasites have
164 been recorded but cannot reproduce (i.e. false positives); while this limits inference on
165 important measures such as host breadth or transmission potential, we believe that our dataset
166 provides meaningful insights into the relative strength of phylogenetic and ecological signals
167 in host specificity, which were the focus of this study.

168

169 ***Mammalian host phylogeny and ecological trait data***

170 A central goal of this study was to assess whether variation in the phylogenetic and
171 ecological similarities of mammalian species predict patterns of parasite sharing across
172 regions. We proceeded by gathering ecological trait data from the PanTHERIA (Jones et al.
173 2009) and EltonTraits 1.0 (Wilman et al. 2014) databases to characterise all of the sampled
174 mammals using a range of traits likely to impact on their suitability as hosts for parasites with
175 different life histories. Selected traits were: body mass, which is a key feature of mammals in

176 terms of their metabolism and adaptation to environments; average longevity, litter size and
177 the average number of litters per year as demographic parameters that could be relevant for
178 enabling parasites to complete parts of their life cycles in a host; diet breadth (calculated as a
179 Shannon diversity index based on the proportional use of 10 diet categories as presented in
180 EltonTraits); range area, which we expect to affect the exposure to other mammalian host
181 species; average temperature and average precipitation within a host's distribution as an
182 indicator of climatic niche; latitudinal centroid of distribution as an indicator of the general
183 habitat and climate within which hosts are occurring across a gradient from tropical to polar
184 biotas; and habitat as multiple binary indicators of whether a species uses 1) forest, 2) open
185 vegetation, and/or 3) artificial/anthropogenic habitats. Information on specific habitat
186 utilisation was compiled from the International Union for the Conservation of Nature (IUCN)
187 database (IUCN, 2014). We did not include a larger set of ecological traits in our analysis to
188 avoid trait collinearity issues.

189 Sampling bias is likely to influence host-parasite occurrences in our database. We
190 queried the number of published references for each binomial wildlife species name from the
191 'Scopus' literature database (accessed 25/02/2017) as a measure of research effort (used as a
192 covariate in multiple regression models of host associations); we used this measure, since
193 more refined searches, such as the number of references linked only to parasites, included
194 large proportions of zeros and information on the true number of sampled individuals (which
195 should determine the chance that parasites are detected if prevalence is low) was not
196 available.

197 Phylogenetic relationships between sampled mammal species were estimated from a
198 recent mammalian supertree (Fritz et al. 2009). We used this tree to compute pairwise
199 phylogenetic distances based on a correlation matrix of phylogenetic branch lengths (Paradis
200 et al. 2004). We also quantified pairwise ecological distance between sampled mammal

201 species based on a generalised form of Gower's distance matrices (Gower 1971) using
 202 weighted variables based on all of the ecological trait variables described above, following
 203 methods in Pavoine et al. (2009). Phylogenetic and ecological distance matrices were scaled
 204 (dividing by the maximum for each distance matrix), so all distance measures ranged from
 205 zero to one. Data formatting and analyses were conducted in R version 3.4.3 (R Development
 206 Core Team 2017) and relied mainly on the packages *ape* (phylogenetic distance calculations)
 207 (Paradis et al. 2004), *ade4* (ecological distance calculations) (Dray and Dufour 2007) and
 208 *phytools* (phylogenetic tree plotting) (Revell 2011).

209

210 ***Functional and phylogenetic host specificity across biogeographical gradients***

211 To examine whether realised host specificities of focal parasite species varied in relation to
 212 the composition of prospective host species pools, we explored variation in ecological and
 213 phylogenetic distances among all infected pairs of host species (observed host diversity)
 214 versus those in the available mammalian species pools (expected host diversity) for each
 215 focal parasite in each region. For this, we used hierarchical linear regression analysis.

216 With $\mathcal{N}(\mu, \sigma^2)$ denoting normal distributions with mean μ and variance σ^2 , we write our
 217 models as

$$218 \quad dist \sim \mathcal{N}(\mu_{region} + \beta_{region}host, \sigma^2)$$

$$219 \quad \mu_{region} \sim \mathcal{N}(H_{\mu}, \sigma_{\mu}^2); \beta_{region} \sim \mathcal{N}(H_{\beta}, \sigma_{\beta}^2).$$

220 Here, μ_{region} denotes the region-specific average of either the functional or phylogenetic
 221 distances *dist* for mammalian species pools, whereas coefficient β_{region} is the region-specific
 222 estimate of pairwise differences (*dist*) between observed and expected host species (i.e.
 223 binary indicator variable $host = 1$ if mammal species is infected, 0 otherwise). H_{μ} and H_{β} are
 224 hyperpriors (i.e. global 'average' values) for the parameters μ and β ; all parameters were

225 estimated independently for phylogenetic (indexed as “*phyl*”) and functional (indexed as
226 “*funct*”) diversity (Supplementary Information, **Box S1**).

227 We fitted regressions and estimated β coefficients for each parasite in a Bayesian
228 framework with Markov Chain Monte Carlo (MCMC) sampling based on the Gibbs sampler
229 in the software JAGS version 4.3.0, operated via the R package *rjags* (Plummer 2016), which
230 conveniently allowed us to account for the hierarchical model structure (see Supplementary
231 Information, **Box S1**). Priors were specified with $H_\mu \sim \mathcal{N}(0, 100)$ and $\sigma \sim \text{dexp}(0.5)$. We ran
232 two chains of 100,000 iterations each for parameter adaptation, then sampled 5,000 posterior
233 parameter estimates. Chain mixing was inspected both visually and with the Gelman-Rubin
234 diagnostic (all values < 1.2). Given our hierarchical model structure, we interpreted effect
235 sizes of β_{region} as potential evidence that functional/phylogenetic distances between host
236 species differ from random draws of expected species from the respective mammalian species
237 pool; negative values of β_{region} indicate a higher functional/phylogenetic similarity between
238 observed host species than expected (i.e. smaller distances than expected), indicating higher
239 host specificity (Clark and Clegg 2017). Positive values of β_{region} indicate parasites infect
240 more distantly related host species than expected, indicating generalism. Estimates of μ_{region}
241 give information on the regional averages of observed – expected distances, whereas variance
242 terms σ_μ^2 and σ_β^2 indicate global variation in μ and β across regions where focal parasites
243 occur. We considered β effects as ‘significant’ if 95% credible intervals did not include zero.
244 We then used these β_{region} coefficients as response variables in linear models, including
245 parasite species and region as categorical covariates, to explore patterns of overall variation
246 in β_{region} .

247 We next gathered insights into the spread of parasites across regional host
248 communities by computing probabilistic estimates of the proportion of prospective host
249 species that a parasite infects (referred to herein as ‘host association rates’) within each

250 regional species pool (we did this separately for non-carnivoran and for carnivoran hosts, i.e.
251 species from the order Carnivora). Likely host association rates were generated from a
252 binomial distribution based on the number of observed host species and the number of
253 species in the mammalian species pools (Supplementary Information, **Box S2**). For these
254 estimates, we again used species-level ‘average’ hyperpriors and fitted the model in a
255 Bayesian framework to obtain posterior distributions. MCMC chain lengths and model
256 checking procedures were as above.

257

258 *Elucidating drivers of host associations with multiple regression*

259 To further explore intermediate host traits that may act as drivers of parasite infection, we
260 used hierarchical logistic regression to test which host attributes most likely predict host
261 association probability with any of the focal parasites. Association with the focal parasite was
262 included as a binary response (‘1’ if a species has been recorded as host species; ‘0’ if no
263 association has been recorded). Predictor variables included ecological trait variables and
264 numbers of published papers, which were log-transformed if featuring overdispersion (body
265 mass, range area, number of publications) and scaled (dividing centred values by one SD) to
266 facilitate comparison of effect sizes. To account for underlying phylogenetic relationships
267 between host species, we modelled variance-covariance relationships based on phylogenetic
268 distance matrices using a multivariate-normal error structure (i.e. a phylogenetic generalised
269 linear model; see Supplementary Information, **Box S3**). We also fitted these regression
270 models in a Bayesian framework using MCMC sampling. We chose this approach as
271 hierarchical models can combine dissimilar types of data (i.e. multiple numerical and
272 categorical covariates, together with phylogenetic distance matrices) in a consistent
273 probabilistic framework, and can accommodate for missing data through imputation. Specific
274 trait data, for example, are currently not available for a considerable diversity of mammalian

275 species; we imputed missing values of ecological trait covariates during MCMC updates,
276 randomly drawing values from priors according to the mean and variance of all observed trait
277 values (considering all information in the trait databases) from species in the same taxonomic
278 orders. Model fitting and assessment was conducted as specified above.

279

280 **Results**

281 The nine focal parasite species were recorded in 52 – 80 different mammalian host species
282 and across 4 – 10 different zoogeographical regions (**Table S1**). All parasite species have
283 been recorded infecting humans and, apart from *Hymenolepis diminuta* and *Versteria*
284 *mustelae*, were also recorded infecting domestic dogs (*Canis familiaris*). *Hymenolepis*
285 *diminuta*, which uses insects as intermediate hosts, was the only focal parasite species not
286 recorded infecting host species from the order Carnivora.

287 We found considerable evidence that host-parasite interactions vary across
288 zoogeographical regions. For all species, we detected significant variation (represented as
289 non-overlapping credible intervals) in the estimated host association rates of non-carnivoran
290 species pools between different regions (**Figure 1**). Host association rates of carnivoran hosts
291 also exhibited some regional variation, notably including relatively high host association rates
292 of up to 36% (95% CI: 25 – 52%) for *Mesocestoides lineatus* in the Neotropical region, as
293 well as host association rates of 35% in the Saharo-Arabian and 38% in the Neotropical
294 regions (both 95% CI: 24 – 51%) for *Trichinella spiralis*. Regional host association rates for
295 non-carnivoran and carnivoran host species were positively correlated for *Echinococcus*
296 *granulosus*, *Hydatigera taeniaeformis* and *Trichinella spiralis* (all Spearman rank
297 correlations $r > 0.7$, $p < 0.05$), respectively, indicating that increasing regional numbers of
298 definitive host species resulted also in increasing numbers of intermediate host species.

299 Across all regions, estimated host association rates were highest for *Hymenolepis diminuta*,
 300 with an overall average of 11% (95% CI: 5 – 21%) (**Figure 1**).

301

302 ***Regional variation in phylogenetic and functional host diversity***

303 Differences between observed and expected phylogenetic diversity of non-carnivoran host
 304 assemblages showed considerable variation across regions. Overall, the strongest evidence
 305 for phylogenetic host specificity was found for *Hydatigera taeniaeformis* and *Hymenolepis*
 306 *diminuta* (negative values for global hyperpriors $H_{\beta}(\text{phyl})$ of -0.08 with 95% CI of -0.12 – -
 307 0.03 and -0.10 with 95% CI of -0.14 – -0.06, respectively; suggesting these parasites infected
 308 hosts that were more closely related than expected) (**Figure 2**). In contrast, we found higher
 309 than expected phylogenetic host diversity (indicating broadly generalist parasites) for *E.*
 310 *granulosus* in the Oriental region and for *Trichinella spiralis* in the Nearctic, Neotropical and
 311 Australian regions (**Figure 2**). Overall, observed – expected regional phylogenetic host
 312 diversity estimates were higher (closer to zero, given that most effects are reported to be < 0)
 313 in the Saharo-Arabian, Neotropical and Australian regions than the global average (across all
 314 parasites, according to results from linear regression analysis), indicating that host specificity
 315 appears to be lowest in these regions. Notably, these regions comprised those with the highest
 316 variation in the phylogenetic diversity of regional mammalian species pools (**Figure 3**).

317 Comparisons of observed and expected functional host diversity indicated that the
 318 highest host specificities were attributed to *E. granulosus*, *M. lineatus*, *Taenia hydatigena* and
 319 *Trichinella spiralis* (all $H_{\beta}(\text{funct})$ estimates smaller than zero, suggesting these parasites
 320 infect hosts that are more functionally similar than expected). In contrast, low functional host
 321 specificity was recorded for *Hydatigera taeniaeformis* ($H_{\beta}(\text{funct})$ of 0.03 with 95% CI of 0.01
 322 – 0.06) (**Figure 2**). Observed – expected functional host diversity exhibited statistically
 323 significant regional variation for some species (i.e. *E. multilocularis*, *Hydatigera*

324 *taeniaeformis*, *Hymenolepis diminuta* and *Versteria mustelae*) (**Figure 2**), but no regional
325 trends were detectable when considering all parasites together (according to the linear
326 regression model). The overall functional diversity of regional mammalian species pools
327 exhibited particularly low variation in the Panamanian and Oceanian regions (**Figure 3**).
328

329 *Host attributes driving helminth parasite association probability*

330 We identified only a few host attributes that influenced parasite association probabilities
331 (**Figure 4**). The probability of a potential host to be associated with *E. granulosis* increased
332 with increasing body mass. Host association probability for *E. multilocularis* increased with
333 host longevity, but decreased with increasing average temperature within host ranges. For
334 *Taenia hydatigena*, association probability increased with increasing latitudinal centroid of
335 host species distributions. Large credible intervals for most parameters suggest that accurate
336 trait-based prediction of association frequency is limited using the current data and model.
337 Collectively, a much broader range of host attributes would have revealed ‘statistically
338 significant’ effects if underlying host phylogenetic relationships had been ignored (see
339 **Figure S1**). This suggests that, despite propensities for some parasites to infect a high
340 diversity of host species, host association probabilities are still strongly driven by host
341 phylogenetic relationships (**Figure 5**).
342

343 **Discussion**

344 Understanding drivers of parasite spillover is key to mitigating parasite transmission and the
345 health impacts of parasitic disease. Using a global database of helminth parasite interactions
346 with mammalian hosts, we show that realised phylogenetic and functional host specificities
347 differ between zoogeographical regions and across parasite species. Our study sheds valuable
348 light on the extent to which host selection and specificity vary depending on regional species

349 pools. We provide a framework to study host selection from databases of host-parasite
350 associations, offering quantitative insights into host shifting patterns for widespread parasites.
351 This information will provide useful new insights into how different parasite species may
352 spread across global scales and in response to distinct regional host species pools.

353

354 Our findings provide a greater understanding of host specificity for parasites of veterinary
355 and medical significance. The cestodes *Hydatigera taeniaeformis* and *Hymenolepis diminuta*,
356 for example, exhibited clear phylogenetic host specificity. In contrast, higher than expected
357 phylogenetic diversity of non-carnivoran hosts for the nematode *Trichinella spiralis* suggests
358 that host shifting by this parasite can involve distantly related species in some regions.

359 Overall, we found the lowest phylogenetic host specificity in regions with the greatest
360 variation in prospective host phylogenetic diversity, namely the Neotropical, Saharo-Arabian
361 and Australian regions (**Figure 3**). Due to the presence of taxonomically unique endemic
362 species, these regions contain pairs of closely, as well as distantly, related species.

363 Functional host specificity exhibited significant variation among regions for some
364 parasites (*Echinococcus multilocularis*, *Hydatigera taeniaeformis*, *Hymenolepis diminuta* and
365 *Versteria mustelae*), but no common geographical trends. We found lower than expected host
366 functional diversity for *E. granulosus*, *M. lineatus*, *Taenia hydatigena* and *Trichinella*
367 *spiralis*, indicating some degree of host specificity and suggesting a general tendency to
368 switch to novel hosts with similar ecological niches. In contrast, higher than expected
369 functional host diversity for *Hydatigera taeniaeformis* suggests that, for this cosmopolitan
370 tapeworm, the ecological niche of a prospective host species is not a strong determinant of
371 host shifting. This is in line with the broad diversity of intermediate hosts recorded previously
372 for this parasite (Lavikainen et al. 2016). Notably, given the positive correlation in host
373 association rates between non-carnivoran and carnivoran hosts observed for this tapeworm, a

374 plausible explanation for this pattern is that the diversity of carnivoran hosts (mainly felids)
375 with varying prey species in their diet facilitates host shifting to intermediate hosts across
376 different ecological niches. Alternatively, a large diversity of intermediate host species from
377 different ecological niches is also possible if the definitive host has access to a large diversity
378 of prey items, particularly if transmission involves only a single carnivore host species in
379 certain regions.

380

381 *Transmission cycles through novel host communities – feral or endemic species?*

382 Feral and invasive species are increasingly recognised as major agents for large-scale parasite
383 spread (Adlard et al. 2015, Blackburn and Ewen 2017, Hulme 2014, Wells et al. 2015). In our
384 study, domestic and commensal animal species, such as dogs, cats and commensal rats (genus
385 *Rattus*), serve as important host species and likely play major roles in spreading helminth
386 parasites worldwide. While it is difficult to identify the geographical origins of parasites and
387 their ancestral/original host species, the exploration of novel host communities in exotic
388 ranges allows us to ask whether transmission cycles are maintained by feral or endemic host
389 species. If endemic wildlife strongly contributed to increased phylogenetic diversity in
390 prospective host pools, parasites infecting a lower than expected host phylogenetic diversity
391 (i.e. *Hydatigera taeniaeformis*, *Hymenolepis diminuta* and *C. hepaticum*, in some regions)
392 may not be capable of regularly shifting to endemic wildlife species. Interestingly, we found
393 a lower than expected host phylogenetic diversity for *E. granulosus* in the Nearctic,
394 Palearctic, Panamanian and Afrotropical regions, but an opposite pattern in the Oriental
395 region (**Figure 2**). In this particular region, domestic dogs represent the only recorded
396 carnivoran host of *E. granulosus*, whereas a broad diversity of herbivorous/omnivorous
397 mammals are recorded as intermediate hosts (including small mammals such as the squirrel
398 *Ratufa indica*, ungulates such as *Bos taurus*, and the Asian elephant *Elephas maximus*).

399 Given the well-established transmission cycle of *E. granulosus*, which involves canine
400 definitive hosts consuming infected tissues of intermediate hosts, this example provides a
401 clear illustration that host shifting to distantly related intermediate host species is driven by
402 diet diversity of carnivoran host species (i.e. parasites will be unable to complete their
403 transmission if they infect intermediate hosts that are not consumed by an appropriate
404 definitive host). This is especially true for free-roaming domestic dogs and cats, whose prey
405 spectra likely increase with their ongoing encroachments into natural habitats, which is often
406 facilitated by human landscape conversion and environmental modifications (Baker et al.
407 2005, Doherty et al. 2016, Young et al. 2011). Likewise, domestic pet access to animals
408 sourced by humans, through hunting, the meat industry, agriculture or exotic pets, may
409 facilitate parasite transmission to a diversity of species if intermediate host tissue with vital
410 larval parasite stages are ingested and transmission is enabled (Jones et al. 2013, Salb et al.
411 2008). Contact and interaction opportunities between feral and endemic animals may
412 therefore play an important role in parasite spread at the human-domestic animal-wildlife
413 interface.

414

415 *Host attributes driving association risk*

416 Predicting parasite spread requires an understanding of host attributes that enable host
417 shifting (Han et al. 2016, Krasnov et al. 2010, Wells et al. 2015). Notably, if host shifting
418 among intermediate hosts is largely a consequence of sharing the same definitive host
419 predator, attributes that successfully predict infection risk can be linked to a suite of factors
420 that facilitate parasite survival and transmission from intermediate host species (i.e. through
421 ecological fitting), in addition to factors that determine whether these species are suitable
422 prey. We found that host traits predicted infection risk for only three of the nine focal
423 parasites species when accounting for host phylogeny. Positive correlations with body mass

424 (*E. granulosus*) and longevity (*E. multilocularis*) indicate some impact of host demographic
425 traits, whereas a negative correlation with average temperature within host ranges (*E.*
426 *multilocularis*) and a positive correlation with latitudinal centroid of host distributions
427 (*Taenia hydatigena*) suggest some geographical constraints. Host longevity has been
428 suggested as an important trait for helminth parasite infection, as sufficiently long lifespans
429 are needed for parasite within-host development and transmission (Morand and Harvey
430 2000). Surprisingly, features of habitat utilisation were not identified as predictors of
431 infection risks in our study. In previous work, we found that two commensal rat species
432 (*Rattus rattus* species complex and *R. norvegicus*) most intensively share helminth parasites
433 with wildlife species that are of least conservation concern (Wells *et al.*, 2015), which are
434 likely those species well adapted to anthropogenically modified landscapes. In another study,
435 we showed that the risk of being infested by the cosmopolitan cat flea (*Cenocephalides felis*),
436 which is arguably one of the most widespread mammalian ectoparasites, appears to be greater
437 for mammal species inhabiting anthropogenic environments (Clark *et al.* 2018). However,
438 whether such correlates are chiefly driven by ecological fitting that enables parasites to thrive
439 in different hosts, or, alternatively, by trophic interactions being concentrated within certain
440 habitats, is difficult to resolve using traits-based regression analyses. As most of our focal
441 parasites use dogs and other invasive carnivores as definitive hosts, the vast range of habitats
442 explored by these carnivores might explain the absence of stronger habitat effects for
443 predicting intermediate host infection risk. Further research into this topic is warranted. In
444 particular, unravelling drivers of infection patterns and host shifting for parasites with
445 different life histories, geographical distributions and transmission patterns could be an
446 interesting and fruitful research avenue.

447

448 *Scaling issues in studying specialisation and realised regional niches*

449 Our study is based on a large global database of host-parasite associations in different
450 regions/countries of the world. Although such data are useful for elucidating large-scale
451 macroecological patterns (Stephens et al. 2016, Wells et al. 2018), the necessary level of data
452 pooling and/or lack of more detailed data comes at the cost of neglecting fine-scale patterns
453 in species occurrences and interactions. Within zoogeographical regions, ranges of species do
454 not necessarily overlap. Therefore, species considered in regional species pools in our study
455 do not necessarily have sympatric occurrences in local communities. Moreover, landscape
456 structuring into different habitat types may further drive possible contacts and interactions
457 between host species. Gradients in habitats from urban to remote natural vegetation are strong
458 drivers of the structure of local host communities and parasite transmission pathways
459 (Liccioli et al. 2015, Wells et al. 2014). While our approach provides insights into regional
460 host assemblages, studies at a finer scale are necessary to determine realised host specificity
461 in local communities with truly sympatric species.

462

463 *Sampling bias and cryptic species*

464 The compilation of data from a large range of studies and references into quantitative
465 metaanalysis does not, unfortunately, allow rigorous evaluation of data accuracy. Nor does it
466 account for sampling bias the way that systematically conducted studies can, particularly
467 those with full records of sampling efforts and depositions of voucher specimens. Parasites
468 are likely to be overlooked in host species with low sampling intensity, especially if parasite
469 prevalence is low (Little 2004, Walther et al. 1995). Some records of host-parasite
470 associations may be accidental records ('false positives') of parasites that have been recorded
471 in a host species in which they cannot complete their life cycle. Moreover, references to
472 parasite scientific names may involve some level of misclassification and crypto-diversity (de
473 León and Nadler 2010); in the case of *Hydatigera taeniaeformis*, for example, it has been

474 suggested that different subspecies circulate in different hosts (Lavikainen et al. 2016).
475 Modern molecular tools may shed further light on different lineages and subspecies of the
476 examined parasite species. In the future, this may also refine our picture of host selection and
477 parasite spread amid the challenge to collect sufficiently large datasets and suitable
478 specimens for global comparative studies.

479

480 **Data deposition**

481 The data are available from the freely accessible databases cited in the manuscript.

482

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487 *Author contributions* – KW and NJC conceived the idea for this study. KW designed the
488 study, carried out the analysis and wrote the first draft. All authors interpreted results and
489 contributed to revisions.

490

491

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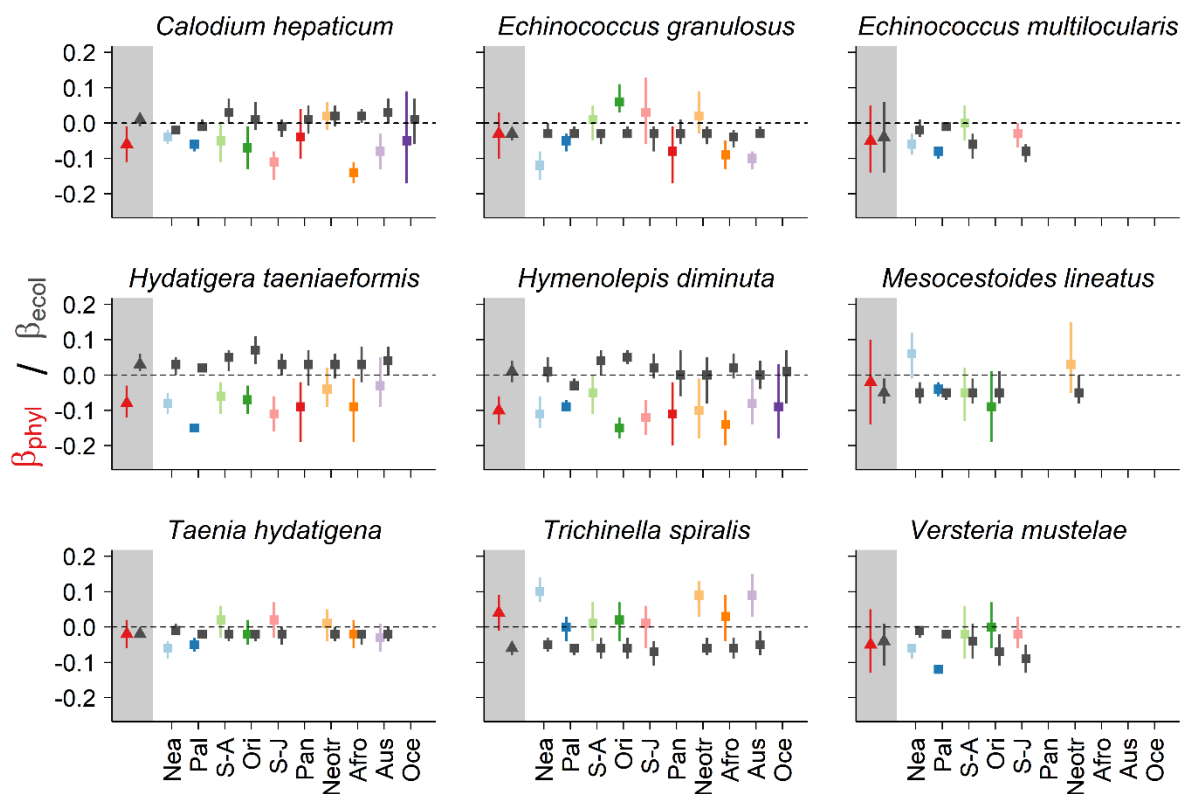
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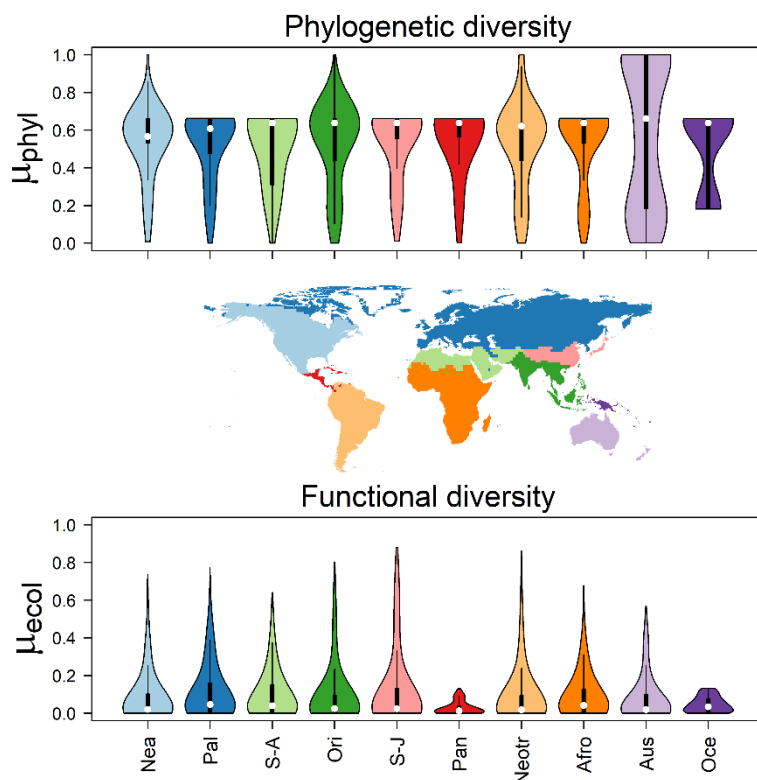
634 **Figure 1.** Relative host association rates of regional mammalian species pools by some of the
 635 most globally widespread helminth parasites. Regional host association rates represent the
 636 proportion of sampled mammalian species that are infected, estimated separately for non-
 637 carnivoran (various colours for different regions) and carnivoran hosts (black). Points are
 638 posterior modes (estimated using a MCMC sampling from an underlying binomial
 639 distribution), bars are 95% credible intervals. In the shaded sections, triangles represent
 640 global ‘averages’ (hyperprior) for each parasite (red: non-carnivoran hosts, black: order
 641 Carnivora). Zoogeographical regions are denoted as Nea: Nearctic, Pal: Palaearctic, S-A:
 642 Saharo-Arabian, Ori: Oriental, S-J: Sino-Japanese, Pan: Panamanian, Neotr: Neotropical,
 643 Afro: Afrotropical, Aus: Australian, Oce: Oceanian.

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653 **Figure 2.** Relative difference between observed and expected phylogenetic (various colours
 654 for different regions) and functional (black) diversity of intermediate (non-carnivoran) host
 655 species as estimated from regression coefficients. Values < 0 indicate pairs of infected hosts
 656 were more phylogenetically/functionally similar than expected based on random draws from
 657 regional mammalian species pools, indicating high host specificity. Values > 0 indicate pairs
 658 of infected host species were more distantly related than expected, suggesting host
 659 generalism. Boxes represent posterior modes, bars 95% credible intervals. Triangles are
 660 global ‘averages’ (hyperprior) for each parasite (red: host phylogenetic diversity, black: host
 661 functional diversity). Zoogeographical regions are denoted as Nea: Nearctic, Pal: Palaearctic,
 662 S-A: Saharo-Arabian, Ori: Oriental, S-J: Sino-Japanese, Pan: Panamanian, Neotr:
 663 Neotropical, Afro: Afrotropical, Aus: Australian, Oce: Oceanian.
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 667 **Figure 3.** Distribution of the phylogenetic (μ_{phyl}) and functional diversities (μ_{ecol}) of
 668 prospective mammalian intermediate host species assemblages (excluding Carnivora) for
 669 some of the most globally widespread helminth parasite species. Each violin plot shows the
 670 range of respective diversity measures calculated from pairwise phylogenetic and functional
 671 distances for all combination of sampled mammal species in different zoogeographical
 672 regions (Nea: Nearctic, Pal: Palaearctic, S-A: Saharo-Arabian, Ori: Oriental, S-J: Sino-

673 Japanese, Pan: Panamanian, Neotr: Neotropical, Afro: Afrotropical, Aus: Australian, Oce:
 674 Oceanian). Note that measures are restricted to species recorded in our host-parasite
 675 databases and do not fully represent true distribution of entire communities.

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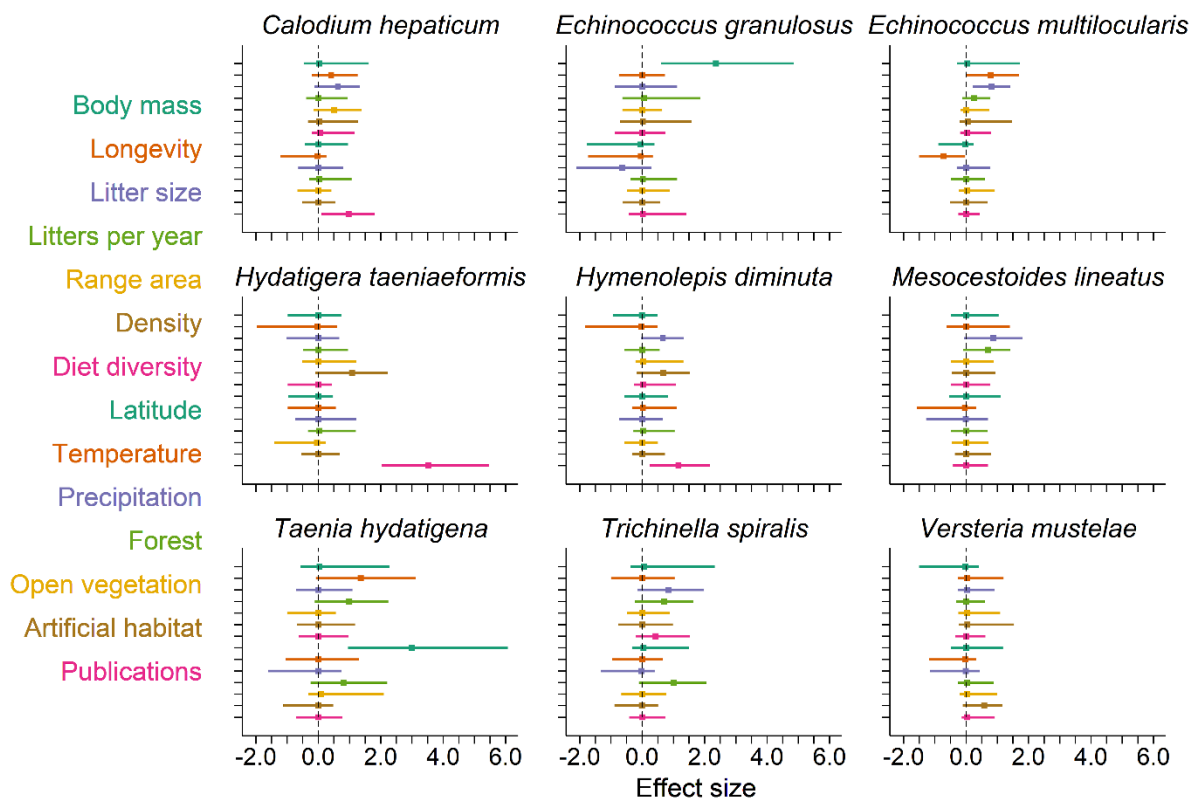
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683 **Figure 4.** Relative effect sizes of different covariates on the association probability of
 684 intermediate (non-carnivoran) mammalian host species with some of the most invasive and
 685 globally widespread helminth species. Note that carnivores were not included in the analysis
 686 to focus on species that most likely serve as intermediate hosts. Points are posterior modes,
 687 bars are 95% credible intervals.

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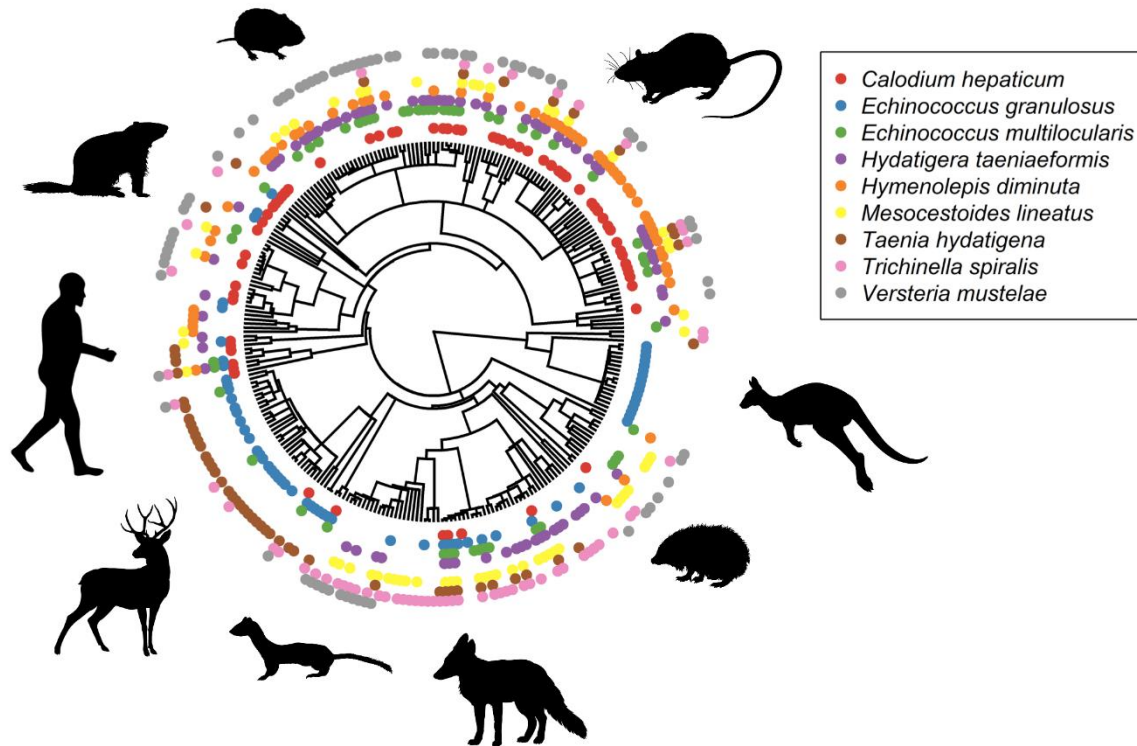
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Figure 5. Infection of different mammalian host species with globally widespread helminth species across a phylogeny of the 276 species that have been recorded to be infected with at least one of the focal parasites. The position of major host groups in the phylogenetic tree are indicated with silhouette images (clockwise from top: rats (Muridae), kangaroos (Potoroidae), hedgehogs (Erinaceidae), foxes (Canidae), martens (Mustelidae), deers (Cervidae), man (*Homo sapiens*), marmots (Sciuridae), voles (Cricetidae). Images were sourced from <http://www.supercoloring.com> under a creative commons license.