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1 **Title: Genetic and species-level biodiversity patterns are linked by**
2 **demography and ecological opportunity**

3
4 **Running title:** Geography of nuclear genetic diversity

5
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30

31 **Abstract:** The processes that give rise to species richness gradients are not well understood, but
32 may be linked to resource-based limits on the number of species a region can support. Ecological
33 limits placed on regional species richness would also limit population sizes, suggesting that these
34 processes could also generate genetic diversity gradients. If true, we might better understand how
35 broad-scale biodiversity patterns are formed by identifying the common causes of genetic
36 diversity and species richness. We develop a hypothetical framework based on the consequences
37 of regional variation in ecological limits to simultaneously explain spatial patterns of species
38 richness and neutral genetic diversity. Repurposing raw genotypic data spanning 38 mammal
39 species sampled across 801 sites in North America, we show that estimates of genome-wide
40 genetic diversity and species richness share spatial structure. Notably, species richness hotspots
41 tend to harbor lower levels of within-species genetic variation. A structural equation model
42 encompassing eco-evolutionary processes related to resource availability, habitat heterogeneity,
43 and human disturbance explained 78% of variation in genetic diversity and 74% of the variation
44 in species richness. These results suggest we can infer broad-scale patterns of species and genetic
45 diversity using two simple environmental measures of resource availability and ecological
46 opportunity.

47
48 **Keywords:** more individuals hypothesis, heterogeneity, Anthropocene, latitudinal diversity
49 gradient, carrying capacity, macroecology, macrogenetics

50 **Introduction**

51 Genetic diversity and species richness are the most fundamental levels of biodiversity because
52 they reflect within- and across-species contributions to ecosystem functioning (Oliver et al.
53 2015; Des Roches et al. 2021b). Genetic diversity underlies a population's capacity to adapt in
54 response to environmental change, and species richness enhances ecosystem resiliency to
55 perturbation. If we are to manage the current high rates of biodiversity loss, we need to better
56 understand how patterns of biodiversity are produced and how they interact across levels of
57 biological organization. Patterns of species richness are well-described, but because several
58 independent processes are capable of generating these patterns, their origins remain puzzling. We
59 know less about multi-species patterns of genetic diversity. However, there is good reason to
60 think that the processes forming patterns of species richness could simultaneously produce
61 spatial patterns in neutral genetic diversity (Vellend 2005; Evanno et al. 2009). This is because
62 spatial variation in neutral genetic diversity should reflect how local population-level
63 demographic and evolutionary processes interact with environments to produce species richness
64 gradients. If true, we may be able to infer processes underlying biodiversity patterns at both
65 genetic and species levels by attempting to understand their common causes. The accumulation
66 of open data now allows us to tackle these types of questions by repurposing and synthesizing
67 publicly archived raw data (e.g., Leigh et al. in press; Miraldo et al. 2016; Manel et al. 2020;
68 Schmidt et al. 2020a; Theodoridis et al. 2020; Schmidt and Garroway 2021). Here we produce a
69 continental map of spatial variation in neutral nuclear genetic diversity for North American
70 mammals, show that genetic diversity and species richness covary spatially and are negatively
71 correlated, and find empirical support suggesting that measures of resource availability and

72 heterogeneity predict both genetic diversity and species richness patterns through their effects on
73 demography.

74

75 We developed a conceptual framework to explain how genetic diversity and species richness
76 patterns could emerge from common causes. This framework extends predictions from well-
77 supported hypotheses for species richness patterns to the population genetic level. Hypotheses
78 for species richness gradients fall into three general categories related to evolutionary time,
79 evolutionary rates, and ecological limits (Mittelbach et al. 2007; Worm and Tittensor 2018;
80 Pontarp et al. 2019). We focus on ecological limits hypotheses—these posit that variation in
81 resource availability limits the number of species able to coexist in a particular area (Rabosky
82 and Hurlbert 2015). Here the speciation, extinction, and colonization dynamics of species are
83 analogous to the birth, death, and immigration dynamics that set carrying capacities at the
84 population level. Simulations suggest multiple hypotheses can produce species richness gradients
85 (Etienne et al. 2019), but the preponderance of theory suggests that ecological limits produce the
86 strongest and most stable gradients (Vellend 2005; Worm and Tittensor 2018; Etienne et al.
87 2019). There is also good empirical support for the likely importance of ecological limits in the
88 formation of species richness patterns (reviewed in Rabosky and Hurlbert 2015; Brodie 2019).
89 We thus considered ecological limits hypotheses as parsimonious starting expectations when
90 exploring the causes of biodiversity patterns (Etienne et al. 2019).

91

92 It is relatively straightforward to extend the consequences of ecological limits on community size
93 to the population genetic level. If environments limit the number of supportable species, they
94 must also limit the population sizes of species, and therefore affect the strength of genetic drift.

95 The first ecological limits hypothesis we consider is the more individuals hypothesis (Wright
96 1983). In terms of community composition, the more individuals hypothesis suggests that
97 resource availability imposes an upper limit on the number of individuals, and as a consequence,
98 the number of species an area can support (Currie 1991; Rabosky and Hurlbert 2015; Storch et
99 al. 2018). Diversity tends to increase with the number of individuals in an assemblage both in
100 terms of genetic diversity within populations and the number of species in a community (Kimura
101 1983; Hubbell 2001). Thus, the more individuals hypothesis predicts neutral genetic diversity
102 and species richness will be positively correlated and increase with resource availability (Fig. 1).

103 The second ecological limits hypothesis we consider pertains to environmental heterogeneity,
104 which includes variation in resources, habitat types, and habitat complexity (Stein et al. 2014).
105 Here we assume heterogeneity equates to niche availability. The idea of area-heterogeneity
106 trade-offs suggests that heterogeneous areas can support richer communities of more specialized
107 species, but these species should tend to have smaller population sizes because resources and
108 species are divided among niches (Kadmon and Allouche 2007; Allouche et al. 2012). Local
109 adaptation, and subsequently specialization, can also occur within and across species distributed
110 across heterogeneous environments. As increasingly specialized populations diverge, genetic
111 variation would be partitioned among locally adapted populations that may eventually no longer
112 interbreed. Compared to larger populations, these smaller populations would also more rapidly
113 lose genetic diversity due to genetic drift. If this were the case, we expect environmental
114 heterogeneity would be positively associated with species richness and negatively associated
115 with neutral genetic diversity (Fig. 1).

116 Contemporary rapid environmental change also affects biodiversity patterns, yet it is not
117 typically modelled in a way that makes it comparable to historical processes acting over long

118 periods. A major contemporary ecological limit on diversity is human land transformation.
119 Human activities such as urbanization reduce the amount of habitat available to wild populations
120 (McKinney 2006; Grimm et al. 2008) with consequences at genetic and species levels (Ceballos
121 et al. 2015; WWF 2018; Leigh et al. 2019; Schmidt et al. 2020a). Habitat loss, fragmentation,
122 and homogenization resulting from human land use alters resource and niche availability, thus
123 processes associated with ecological limits should play out in populations and communities of
124 urban wildlife. By reducing habitable area and resource heterogeneity, we predicted that the
125 effects of urbanization for mammals should also cause species richness and genetic diversity to
126 decrease in more heavily disturbed areas (Fig. 1).

127
128 The effects of resource availability and heterogeneity are not mutually exclusive, and in our
129 framework they can act in concert to produce biodiversity patterns. The links among our
130 hypotheses and their predictions are diagrammed in full in Figure 1. We jointly model both
131 hypotheses with a method that allows us to assess their relative importance for shaping genetic
132 diversity and species richness. Our predictions for the ways resource availability and
133 heterogeneity interact are consistent with previous work on species richness in North American
134 mammals (Kerr and Packer 1997), where heterogeneity becomes a more important determinant
135 of species richness as resource availability increases. If our model successfully captures known
136 relationships between species richness and environments, and genetic diversity behaves in the
137 ways we predict, we will have strong empirical evidence supporting the contention that
138 continental patterns of neutral genetic diversity and species richness are both are in part governed
139 by ecological limits.

140

141 Our specific objectives were threefold. Because biogeographic patterns of neutral nuclear genetic
142 diversity have not yet been mapped, we first produced a continental map of spatial patterns of
143 genetic diversity in North American mammals. To do this we repurposed publicly archived, raw,
144 neutral nuclear genetic data spanning 38 species and >34,000 individuals at 801 sample sites in
145 the United States and Canada. We then tested the degree to which patterns of genetic diversity
146 matched those of species richness. Having established shared patterns of spatial variation, we
147 then tested our proposed conceptual model based on ecological limits hypotheses where genetic
148 diversity and species richness are caused by common environmental factors (Fig. 1). We tested
149 our hypothetical model using structural equation modelling (SEM), a modelling framework that
150 fits hypothesis networks by accommodating multiple predictor and response variables. Our
151 approach (Fig. 2) allowed us to assess the relative importance of both hypotheses and the effects
152 of contemporary environmental change while accounting for species-level variation using
153 hierarchical models.

154

155 **Methods**

156 **Biodiversity data**

157 *Genetic diversity.* We used raw genotypic data compiled by Schmidt et al. (2020a,b). This data
158 set is comprised of repurposed raw microsatellite data from 34,841 individuals from 38
159 mammalian species sampled at 801 sites in the United States and Canada. With it we could
160 consistently calculate measures of gene diversity (Nei 1973) and population-specific F_{ST} across
161 sites (Weir and Goudet 2017). See Table 1 for a summary of the dataset. Microsatellite markers
162 estimate genome-wide diversity well (e.g., microsatellite and genome-wide diversity are
163 correlated at $R^2 \sim 0.83$; Mittell et al. 2015). They are commonly used in wildlife population

164 genetic studies because they are cost-effective and do not require a reference genome, which
165 allowed us to maximize sample size. Detailed methods for assembling this dataset can be found
166 in (Schmidt et al. 2020a). Briefly, we performed a systematic search for species names of native
167 North American mammals with keywords “microsat*”, “single tandem*”, “short tandem*”, and
168 “str” using the dataone R package, which interfaces with the DataONE platform to search online
169 open data repositories (Jones et al. 2017). We discarded search results that did not meet our
170 criteria for inclusion and removed results where study design may have influenced genetic
171 diversity. For example, we excluded non-neutral data and samples taken after a recent
172 bottleneck, translocations, managed or captive populations, or island populations. We
173 additionally removed populations with fewer than 5 individuals sampled. Gene diversity
174 estimates the richness and evenness of alleles in a population, and we used it here as our metric
175 for genetic diversity because it is minimally affected by sample size (Charlesworth and
176 Charlesworth 2010) (Fig. S1). Sample sites are treated as point locations.

177 *Species richness.* We downloaded range maps for terrestrial mammals native to North America
178 from the IUCN Red List database (IUCN 2019). We filtered these maps to retain ranges for
179 extant, native, resident, mainland species in R version 4.0.1 (R Core Team 2020). To generate a
180 map of species richness coincident with genetic sample sites, we estimated species richness by
181 summing the number of ranges overlapping each site.

182

183 **Maps and spatial variation partitioning**

184 *Genetic diversity and species richness maps.* Our first step was to map spatial patterns in genetic
185 diversity. We accomplished this using distance-based Moran’s eigenvector maps (MEMs) in the
186 package *adespatial* (Dray et al. 2017). MEMs detect spatial patterns in data using a matrix of

187 distances between sites—a neighbor matrix—whose eigenvalues are proportional to Moran’s I
188 index of spatial autocorrelation (Borcard and Legendre 2002; Borcard et al. 2004; Dray et al.
189 2006). MEMs are spatial eigenvectors that represent relationships between sites at all spatial
190 scales detectable by the sampling scheme. Multiple MEMs can be included in linear models to
191 identify spatial patterns in data because they are orthogonal. They are appropriate for use in
192 genetics because Moran’s I is a direct analog of Malécot’s estimator of spatial autocorrelation of
193 allele frequencies (Malécot 1955; Epperson 2005) which accurately summarizes neutral variation
194 in gene flow and allele frequencies (e.g., Sokal and Oden 1978; Epperson 2005). Distance-based
195 MEM analysis produces $n - 1$ MEMs (n being the number of sample sites), but only eigenvectors
196 corresponding to positive spatial autocorrelation are used. MEMs are ordered according to
197 spatial scale explained, with the first eigenvector explaining the broadest autocorrelation pattern.
198 We used linear regressions and the forward selection procedure described in (Blanchet et al.
199 2008) to select two sets of MEMs: one describing spatial patterns in genetic diversity and the
200 other describing species richness. Thirteen MEMs, ranging from broad to fine scales, explained
201 important spatial variation in gene diversity. Forty-three MEMs were important predictors of
202 species richness, and 8 of these patterns were shared by genetic diversity (significant MEMs are
203 listed in Fig. S3).

204 To restrict ourselves to broad spatial patterns, we focused on genetic and species MEMs with
205 Moran’s I values >0.25 . We fit individual linear regression models for species richness and
206 genetic diversity with corresponding broad-scale MEMs as covariates and plotted model
207 predicted values representing spatial patterns on maps of North America (Fig. 3). These MEMs
208 describe the broadest-scale spatial patterns at both levels of diversity. By using values of genetic
209 diversity and species richness described by these MEMs, we can visualize pure spatial variation

210 at the continental scale without local spatial patterns that may be due to environmental
211 idiosyncrasies, and without considering non-spatial variation in genetic diversity. We also
212 provided maps of raw genetic diversity and species richness values in Figure S2.

213
214 *Variation partitioning.* We next quantified the extent to which genetic diversity and species
215 richness covary spatially. Because MEMs for species richness and genetic diversity were
216 computed from the same set of coordinates, they were directly comparable. This allowed us to
217 identify shared spatial MEMs. We used linear regressions and variance partitioning to determine
218 what fraction of the total variation in species richness and genetic diversity could be attributed
219 to: (1) non-spatial variation, (2) non-shared spatial variation, and (3) shared spatial variation. We
220 partitioned variation as follows:

$$221 \quad y_{SR} \sim \alpha + \beta_{1S}(\text{MEM}_{1S}) + \beta_{2S}(\text{MEM}_{2S}) + \dots + \beta_{43S}(\text{MEM}_{43S}) + \epsilon$$

$$222 \quad y_{GD} \sim \alpha + \beta_{1G}(\text{MEM}_{1G}) + \beta_{2G}(\text{MEM}_{2G}) + \dots + \beta_{13G}(\text{MEM}_{13G}) + \epsilon$$

223 where α is the grand mean, and y_{SR} and y_{GD} are species richness and genetic diversity at sites.
224 MEM_S and MEM_G refer to the set of MEMs explaining spatial variation in species richness (43
225 MEMs) and genetic diversity (13 MEMs), respectively, and β s are their slopes. The coefficients
226 of variation (R^2) for these models give us the proportion of variation in each response variable
227 attributable to spatial variation. Subtracting these values from 1 gives the amount of non-spatial
228 variation.

229 To determine the amount of shared variation, we used the set of 8 MEMs shared between species
230 richness and genetic diversity (MEM_{SG}) as predictors in the regressions below:

$$231 \quad y_{SR} \sim \alpha + \beta_{1SG}(\text{MEM}_{1SG}) + \beta_{2SG}(\text{MEM}_{2SG}) + \dots + \beta_{8SG}(\text{MEM}_{8SG}) + \epsilon$$

232
$$y_{GD} \sim \alpha + \beta_{1SG}(\text{MEM}_{1SG}) + \beta_{2SG}(\text{MEM}_{2SG}) + \dots + \beta_{8SG}(\text{MEM}_{8SG}) + \epsilon$$

233 R² values from these models estimate the proportion of variation in genetic diversity and species
234 richness explained by shared spatial variation. Subtracting these values from the total spatial
235 variation in species richness and genetic diversity gives the proportion of non-shared spatial
236 variation.

237

238 **Structural equation modeling**

239 *Population size data.* The more individuals hypothesis is most applicable at broad spatial scales,
240 and when considering the total number of individuals that comprise a species (Storch et al.
241 2018). In place of census sizes for the species in our dataset, which are not consistently available,
242 we craft our hypothesis around species' long-term effective population sizes. The effective
243 population size is a concept defined in population genetics as the number of individuals in an
244 idealized population that experiences the same rate of genetic drift as the real population
245 (Charlesworth and Charlesworth 2010). Populations lose genetic diversity to drift at a rate
246 inversely proportional to the effective population size. Body size is routinely used as a proxy for
247 long-term effective population size at the species level (Frankham 1996; Corbett-Detig et al.
248 2015; Mackintosh et al. 2019; Buffalo 2021). Large bodied species that tend to have long
249 lifespans and produce few offspring generally have smaller effective population sizes than small,
250 fecund, short-lived species (Romiguier et al. 2014; Mackintosh et al. 2019). Thus body size
251 measured at the species level is an imperfect, but nevertheless useful substitution for census size.
252 We recorded adult body mass (g) for each species in our genetic dataset from the PanTHERIA
253 database (Jones et al. 2009) and log-transformed values before analysis. There were no obvious
254 outliers in these data.

255 *Environmental variables.* We used potential evapotranspiration as a surrogate for total ecosystem
256 resource availability (Currie 1991; Rabosky and Hurlbert 2015). Potential evapotranspiration is
257 an indicator of atmospheric energy availability and is one of the strongest environmental
258 correlates of species richness in North American mammals (Currie 1991; Krefl and Jetz 2007;
259 Fisher et al. 2011; Jiménez-Alfaro et al. 2016). As we predict, at the species level, that resource
260 availability across a range sets the long-term effective population size, we estimated mean range-
261 wide potential evapotranspiration (mm/yr) using annual data from 1970-2000 available via the
262 CGIAR Consortium for Spatial Information (Trabucco and Zomer 2019). For comparison, we
263 also measured mean range-wide actual evapotranspiration, an alternative measure of resource
264 availability, and present those results in the Supplementary Information.

265 We quantified heterogeneity and niche availability using a 250 m resolution map of land cover
266 types in North America (CEC et al. 2010). This map includes 19 land cover categories based on
267 satellite imagery collected in 2010 with multiple categories of forest, shrubland, grassland, polar
268 habitat types, wetland, cropland, barren land, built up land, and open water. Because the
269 heterogeneity hypothesis suggests species specialize on different resources within their range, we
270 quantified heterogeneity at sites rather than at the species level. We measured heterogeneity
271 using Simpson's diversity index. To assess scale dependence, we calculated Simpson's index
272 within four buffer zones around each site: 5000, 20000, 50000, and 100000 km². Lastly, we
273 quantified human disturbance at each site using human population density (CIESIN 2016)
274 measured within a 10 km buffer following Schmidt et al. (2020a).

275 *Analysis.* Structural equation modeling accommodates multiple dependent and independent
276 variables in a model network, and directional paths connecting variables represent causal

277 relationships. The strengths of direct paths are regression coefficients (Shipley 2016), and
278 indirect effects can be quantified by multiplying coefficients along paths of direct effects.
279 We constructed a graph of our conceptual model laid out in the introduction (Fig. 1), which we
280 then translated into a network of three linear models for body size, species richness, and genetic
281 diversity. In it, body size is predicted by resource availability, and species richness and genetic
282 diversity are each predicted by body size, heterogeneity, and human disturbance (Fig. 4a). We fit
283 structural equation models using piecewiseSEM in R (Lefcheck 2016; Lefcheck et al. 2019)
284 because this package accommodates complex model structures. We used a linear mixed-effects
285 model with a random intercept for species to account for species-level variation in genetic
286 diversity. PiecewiseSEM fits hierarchical models using the lme4 package (Bates et al. 2015).
287 Body size and species richness models were initially fit as linear regressions, but residuals from
288 both models were spatially autocorrelated at broad scales. We refit these regressions using
289 simultaneous autoregressive models in spatialreg (Bivand et al. 2013) and this successfully
290 removed spatial autocorrelation from the residuals. All variables were scaled and centered before
291 analysis to obtain standardized regression coefficients, allowing us to compare the strength of
292 relationships and the relative support for hypotheses across genetic and species levels.

293 Our model includes variables measured at the site level (genetic diversity, species richness,
294 heterogeneity, and human disturbance) and species level (body size, resource availability; Fig.
295 2). This hierarchical data structure introduces spurious correlations between variables sampled at
296 different levels that we know are not causal. For example, regressing human disturbance at sites
297 on species body size would estimate an artefactual experiment (the size of species researchers
298 choose to sample near cities)—not the effects of disturbance on body size. We can account for
299 these known non-causal relationships by allowing variables to have correlated errors (Lefcheck

300 2016). Correlated errors indicate that a relationship exists between variables, but allow the
301 direction of causality to be ambiguous: both could be caused by another factor not included in
302 the model (e.g., researcher species choice). We specified correlated errors between body size and
303 human population density, and body size and heterogeneity.

304 The conceptual model is evaluated by testing whether additional links are needed between
305 variables to make the proposed causal structure more consistent with the data. In piecewiseSEM,
306 missing links are tested using tests of directed separation (Shipley 2016), where the null
307 hypothesis is that two variables are independent conditional on other predictors in the model. A p
308 value for the model network is obtained by testing Fisher's C calculated from the p values
309 summed across directed separation tests (Lefcheck 2016; Shipley 2016). A model-wide $p < 0.05$
310 means the causal structure is not a good fit to the data and additional links are needed to resolve
311 dependencies. If $p > 0.05$, the model is considered acceptable because we fail to reject our causal
312 structure. This means that although we start with a focus on our conceptual model, the data can
313 suggest the addition or removal of links and our hypotheses can be updated for future testing
314 with new data.

315 We assessed model fit using R^2 values for each response variable in the model network. For
316 genetic diversity, we used marginal R^2 (R^2_m) which measures the total variation explained by
317 fixed effects, and conditional R^2 (R^2_c) which is the variation explained by both fixed and random
318 effects. For spatial body size and species richness regressions, we report Nagelkerke pseudo- R^2 .

319

320 **Effect of heterogeneity on population divergence**

321 After detecting a negative effect of heterogeneity on intraspecific genetic diversity in our
322 structural equation model, we performed a post hoc analysis to test whether environmental

323 heterogeneity also caused greater population differentiation within species. To test for
324 differentiation we calculated population-specific F_{ST} (Weir and Goudet 2017) as a measure of
325 genetic divergence using the hierfstat package (Goudet and Jombart 2015). Population-specific
326 F_{ST} can be interpreted as a relative estimate of the time since a population has diverged from a
327 common ancestor. This metric required at least 2 sampled populations in the original studies to
328 estimate, and due to this constraint 16 sites were excluded from this analysis. We controlled for
329 isolation-by-distance by including MEMs significantly related to F_{ST} to account for spatial
330 structure. We scaled and centered all variables, then used a linear mixed model controlling for
331 species differences by including it as a random effect.

332

333 **Results**

334 *Spatial patterns in genetic diversity and species richness*

335 There was no obvious relationship between latitude and nuclear genetic diversity (Fig. 3).
336 Similar to patterns of species richness, a longitudinal gradient in genetic diversity was the
337 dominant pattern for North American mammals—however, it appears regions with high species
338 richness have lower genetic diversity. We detected spatial patterns at genetic and species levels
339 of diversity. Sixty-five percent of the total variation in species richness and 24% of variation in
340 genetic diversity was spatially structured (Fig. 3). Variance partitioning suggested that 85% of
341 the total spatial variation in genetic diversity, and 32% of spatial variation in species richness
342 was accounted for by spatial patterns shared at both levels of diversity. This shared variation
343 implies that, to an extent, neutral genetic diversity and species richness are simultaneously
344 shaped by spatially structured environmental factors, and these shared processes account for
345 most of the spatial variation in genetic diversity.

346

347 *Joint environmental causes of genetic diversity and species richness*

348 We present results from the model using a 5000 km² heterogeneity buffer in the main text.

349 Results from wider heterogeneity buffers can be found in SI Tables S1-S4. Our conceptual

350 model, updated according to tests of directed separation, fit the data well (SEM $p = 0.33$, Fisher's

351 $C = 2.245$; Fig. 4, Table S1). Note that for structural equation models, $p > 0.05$ indicates that we

352 fail to reject our model. There was no residual spatial autocorrelation in body size and species

353 richness model residuals, and genetic diversity model residuals were spatially autocorrelated at

354 local scales (genetic diversity Moran's $I = 0.01$). These Moran's I values indicate very weak

355 spatial structure in the data, and so we decided not to integrate it into our model. Positive spatial

356 autocorrelation at such short distances is likely an artifact of irregular site locations and the

357 hierarchical nature of the data. A lack of strong spatial autocorrelation in the model residuals

358 suggests that the spatial structure of the diversity data was well captured by our model's

359 environmental covariates (Fig. S3). All predicted links in our conceptual model were supported

360 except that between body size and species richness (Fig. 4). Tests of directed separation

361 suggested additional direct links from resource availability to species richness, and genetic

362 diversity to species richness (Fig. 4). Effects of heterogeneity on genetic diversity were not

363 detectable at broader scales (Tables S2-S4). These relationships were consistent using actual

364 evapotranspiration as an alternative measure of resource availability (Table S5).

365 Resource availability, heterogeneity, and human disturbance, acting both directly and indirectly

366 through species population size, explained 20% of the variation in genetic diversity. The species-

367 level variation explained by the random effect brought the total variation in genetic diversity

368 explained by our model to 78%. The same model explained 74% of the variation in species

369 richness. Genetic diversity was strongly negatively related to body size. The direct effects of
370 resource heterogeneity on species richness and genetic diversity were of similar magnitude, and
371 directions of effects were as expected if processes associated with greater resource heterogeneity
372 reduce population sizes, lead to increased genetic drift, and facilitate local adaptation and
373 coexistence (Fig. 4, Table S1). However, because gene diversity is not a measure of divergence,
374 we additionally tested whether environmental heterogeneity predicted evolutionary divergence at
375 the population level. Heterogeneity was positively related to genetic divergence, but the effect
376 was not significant ($\beta = 0.06 \pm 0.04$ SE). Finally, human disturbance negatively affected both
377 species richness and genetic diversity, but its effects were stronger for genetic diversity (Fig. 4,
378 Table S1).

379

380 **Discussion**

381 We found striking continental spatial gradients in nuclear genetic diversity, and show that these
382 patterns are negatively correlated with patterns of species richness in North America (Simpson
383 1964) (Fig. 3). A considerable portion of the variation in genetic diversity and species richness
384 patterns could be explained by just three environmental factors: resource availability, resource
385 heterogeneity, and human disturbance. This is strong empirical evidence suggesting that genetic
386 diversity and species richness patterns emerge, in part, from the same environmental processes.

387

388 Both our maps and our structural equation model suggest that resource availability and
389 heterogeneity interact to produce biodiversity patterns at genetic and species levels. In North
390 America, the threshold where environmental heterogeneity presumably becomes a more
391 important determinant of species richness than resource availability lies roughly along the US-

392 Canada border where potential evapotranspiration reaches ~1000 mm/yr (Kerr and Packer 1997).
393 Near this threshold is also where we see longitudinal patterns of genetic diversity emerge.
394 Although the negative correlation between spatial patterns of genetic diversity and species
395 richness is most apparent in species richness hotspots (particularly in the southwest), structural
396 equation modeling incorporating both hypotheses gives us a more nuanced view of the
397 connections between these patterns. Indeed, effects related to resource availability and
398 heterogeneity were of similar magnitude (Fig. 4). Population size and genetic diversity increased
399 with resource availability, and though the link between species' long-term effective population
400 sizes and species richness was unsupported, species richness also increased with resource
401 availability. Moreover, we detected a positive relationship between genetic diversity and species
402 richness as predicted if population and community size increase with resource availability. It
403 may be that effective population size, measured using species body size, is too coarse an
404 indicator of census population size to detect an effect on species richness at sites—if so, site-
405 level measures of genetic diversity could be a better indicator of local population sizes.
406
407 Our results suggest that once a minimum energy threshold is reached, populations can afford to
408 specialize in heterogeneous environments while maintaining viable population sizes. In this way,
409 the interplay between ecological limits and ecological opportunity simultaneously produces
410 biogeographic patterns in genetic diversity and species richness. This interpretation of our results
411 assumes that an environmentally set equilibrium between speciation, immigration and extinction
412 has been reached. There is good evidence for this in North American mammals, where
413 diversification rates have slowed as diversity increased (Alroy 2009; Brodie 2019). However, the
414 specific ways environments shape nuclear genetic- and species-level diversity will likely differ

415 across taxa and regions depending on whether or not they have reached equilibrium (e.g.,
416 Schmidt et al. 2021). Though we measure contemporary genetic diversity, historical variation in
417 resource availability and heterogeneity likely contribute to the patterns we detect because they
418 reflect whether populations have experienced large contractions in the recent past (Hewitt 2000).
419 However, in the past when communities may not have been at equilibrium, it seems likely that
420 other processes could have been the predominant drivers of biodiversity patterns. Indeed,
421 hypotheses about species richness patterns have likely been a topic of debate for so long because
422 several processes operating with different importance across the timeline of diversification are
423 capable of producing gradients (Etienne et al. 2019). It has been suggested that time for
424 speciation should be most detectable more immediately following broad-scale environmental
425 change, and when all regions are colonized, habitats that provide more opportunities for
426 speciation should over time become the most diverse (Pontarp and Wiens 2017). As diversity
427 increases, diversification rates slow as regions approach equilibrium (Brodie 2019). It follows
428 that the relative importance of evolutionary time and diversification rates as contributors to
429 biodiversity patterns varies with time with patterns ultimately affected by variation in ecological
430 limits (Rabosky and Hurlbert 2015; Pontarp and Wiens 2017; Storch et al. 2018).

431

432 Contemporary environmental change is our chance to explore pre-equilibrium processes. Cities
433 are the newest and most rapidly expanding biome, and it is clear that they have already
434 profoundly affected biodiversity patterns (Palumbi 2001; WWF 2018; Schmidt et al. 2020a). At
435 this early stage of colonization it is unlikely that urban communities have reached equilibrium,
436 suggesting processes related to evolutionary time and diversification will predominate until more
437 niches are occupied. Indeed, there is some evidence that following an initial extinction debt after

438 rapid urbanization, older cities support higher species richness (Aronson et al. 2014). Human
439 disturbance had a negative effect on genetic diversity in our model, and also reduces gene flow
440 in mammals (Schmidt et al. 2020a). This suggests that there is potential for population
441 divergence and local adaptation if new urban niches are exploited and spatially varying selection
442 is sufficiently strong in cities. The extent to which urban populations adapt to local
443 environmental conditions is an ongoing and active field of study, and no consensus has been
444 reached (Lambert et al. 2021). Equilibrium levels of genetic diversity and species richness in
445 urban communities thus seem likely to strongly depend on resource availability and
446 heterogeneity both within and across cities, but these aspects of urban environments are not yet
447 well defined or understood (Norton et al. 2016; Des Roches et al. 2021a).

448
449 Notably, the negative correlation we find between spatial patterns of species richness and nuclear
450 genetic diversity runs opposite the relatively consistent positive correlations found between
451 species richness and mitochondrial genetic diversity gradients (Martin and McKay 2004; Adams
452 and Hadly 2012; Miraldo et al. 2016; Manel et al. 2020; Theodoridis et al. 2020). Mitochondrial
453 DNA has several idiosyncrasies associated with the specific biology of mitochondria that
454 distinguish it from genetic diversity measured with neutral nuclear DNA (Schmidt and Garroway
455 2021). The most commonly used mitochondrial markers are the protein-coding genes
456 *cytochrome oxidase I* and *cytochrome b*, which very likely do not evolve under neutrality
457 (Galtier et al. 2009). Unlike neutral nuclear DNA, mitochondrial genetic diversity is not
458 consistently related to life history, ecological traits, or census and effective population sizes
459 (Bazin et al. 2006; Nabholz et al. 2008; James and Eyre-Walker 2020). Mitochondrial genetic
460 diversity is thus a very different quantity than the neutral nuclear diversity estimates we use here,

461 and its lack of relationship with population size makes it unsuited for testing hypotheses based
462 on ecological limits. Using genetic diversity metrics estimated from neutral nuclear DNA allows
463 us to more directly link environments to species richness through demography, population size,
464 and by extension, species life history traits which partly set the effective population size.
465
466 Ecosystem sustainability, given environmental perturbations occurring more frequently due to
467 human causes, depends on the resiliency of landscapes, communities, and populations (Oliver et
468 al. 2015). Our framework and the results presented herein suggest that we can understand
469 continental patterns of species richness and genetic diversity using two simple measures of
470 resource availability and heterogeneity. This is potentially informative for conservation practices
471 aiming to conserve both of these levels of biodiversity at once. Maps of neutral nuclear genetic
472 diversity can identify regions where long-term effective population sizes may have been
473 historically small, indicating areas where low levels of neutral genetic diversity are not
474 necessarily of immediate conservation concern (e.g., Yates et al. 2019). However, population
475 declines due to recent human disturbance in areas with historically low genetic diversity may
476 warrant specific attention. Furthermore, designing protected area networks based on species
477 richness to maintain beta diversity, or variation between sites (Bush et al. 2016; Socolar et al.
478 2016), will likely also capture differentiated populations with complementary genetic
479 compositions. The connections between environments, species richness, and genetic diversity we
480 find here suggest we should be able to make informed decisions for the joint conservation of
481 species and genetic diversity with knowledge of few environmental parameters.

482

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494

495 **Data availability:** Synthesized genetic data is available from the Dryad Data Repository
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497 available from open online sources (see Methods).

498

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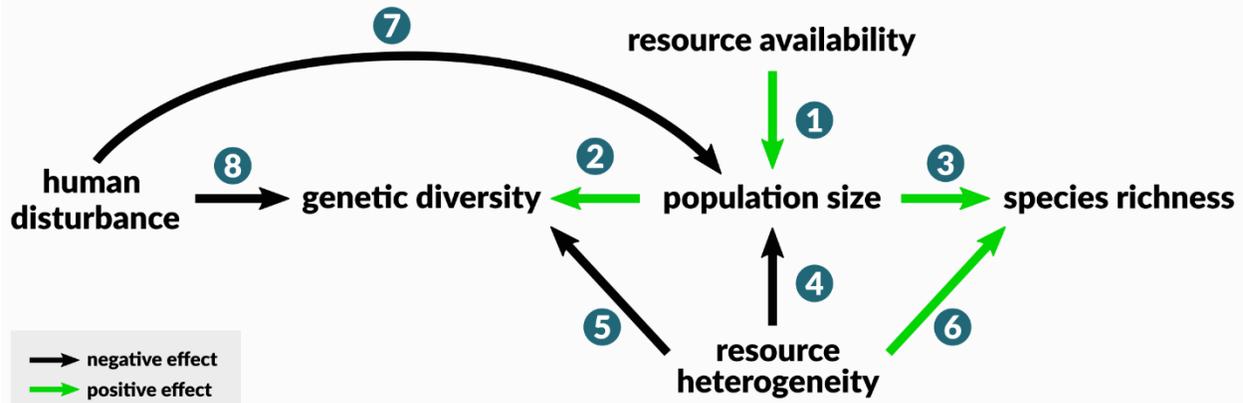
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701

702 **Table 1.** Data summary. Summary of aggregated raw genetic data: mean gene diversity, mean number of loci, median number of
703 individuals at sites per species. Species mass (kg); species richness = mean species richness at sites; energy = mean potential
704 evapotranspiration across species' ranges (mm/yr), heterogeneity = mean land cover diversity (Simpson's Index) within a 5,000 km²
705 zone around a site; human population = mean human population density across sites. Ranges of values are given in parentheses for
706 species with multiple sample sites.

Species (# sites)	Gene diversity	# loci	# Individuals	Mass	Species richness	Energy	Heterogeneity	Human population
<i>Alces alces</i> (2)	0.47 (0.43–0.51)	10	44.5 (40–49)	481	34.5 (34–35)	694.5	0.81 (0.78–0.84)	134.79 (1.45–268.14)
<i>Antilocapra americana</i> (1)	0.67	19	175	46.9	63	1615.39	0.73	3.42
<i>Bison bison</i> (8)	0.47 (0.43–0.51)	29	26.5 (7–31)	620	47.62 (32–69)	745.94	0.68 (0.4–0.82)	1.3 (0.52–3.42)
<i>Canis latrans</i> (41)	0.77 (0.69–0.82)	10	7 (5–10)	12	48.39 (40–55)	1039.97	0.7 (0.27–0.85)	134.92 (1.54–1463.37)
<i>Canis lupus</i> (1)	0.66	12	62	35	44	642.5	0.78	5.85
<i>Glaucomys volans</i> (8)	0.75 (0.65–0.81)	7	18.5 (6–120)	0.07	49.12 (47–51)	1287.09	0.68 (0.58–0.8)	7.31 (1.04–33.59)
<i>Lasionycteris noctivagans</i> (1)	0.83	18	87	0.01	53	1252.72	0.71	2.4
<i>Lasiurus cinereus</i> (1)	0.88	19	132	0.03	53	1126.83	0.71	2.4
<i>Leopardus pardalis</i> (2)	0.47 (0.36–0.58)	10	35 (28–42)	11.9	51 (49–53)	2287.6	0.77 (0.76–0.77)	27.12 (18.73–35.51)
<i>Lepus americanus</i> (39)	0.66 (0.48–0.76)	8	15 (7–100)	1.57	50.44 (2–73)	750.2	0.65 (0.27–0.81)	79.95 (0.69–2711.29)
<i>Lynx canadensis</i> (33)	0.72 (0.46–0.75)	14.15 (14–15)	26 (13–328)	9.77	43.82 (6–50)	655.47	0.73 (0.61–0.81)	4.59 (1.04–56.48)
<i>Lynx rufus</i> (65)	0.73 (0.56–0.79)	14.37 (9–17)	27 (7–141)	6.39	55.6 (33–81)	1459.73	0.62 (0.19–0.83)	189.69 (1.04–3540.4)
<i>Martes americana</i> (29)	0.63 (0.54–0.67)	12	22 (11–47)	0.88	45.86 (42–50)	709.47	0.73 (0.65–0.79)	1.21 (0.69–2.27)
<i>Mephitis mephitis</i> (1)	0.81	9	345	2.4	53	1230.39	0.73	34.19
<i>Microdipodops megacephalus</i> (3)	0.78 (0.73–0.82)	11	62 (49–69)	0.01	64.33 (59–70)	1780.52	0.45 (0.37–0.56)	1.04 (1.04–1.04)
<i>Microdipodops pallidus</i> (2)	0.73 (0.73–0.73)	10	52.5 (42–63)	0.01	59 (58–60)	2045.67	0.25 (0.24–0.27)	1.04 (1.04–1.04)
<i>Myotis lucifugus</i> (65)	0.83 (0.72–0.9)	9.2 (8–11)	33 (11–167)	0.01	44.45 (32–66)	971.21	0.75 (0.21–0.86)	25.96 (0–493.88)
<i>Myotis septentrionalis</i> (15)	0.87 (0.85–0.88)	5	54 (34–110)	0.01	42.13 (41–43)	952.73	0.82 (0.74–0.85)	16.05 (1.04–123.03)
<i>Odocoileus hemionus</i> (67)	0.62 (0.2–0.72)	10.55 (10–18)	29 (7–262)	83.8	57.72 (2–87)	1356.11	0.61 (0.08–0.84)	36.97 (0.83–1213.54)
<i>Odocoileus virginianus</i> (64)	0.81 (0.76–0.84)	14	32.5 (10–79)	75	48.95 (46–52)	1243.86	0.55 (0.32–0.74)	57.42 (6.13–351.21)
<i>Oreamnos americanus</i> (1)	0.52	22	102	71.3	37	743.39	0.79	2.06
<i>Otospermophilus beecheyi</i> (3)	0.75 (0.72–0.78)	11	61 (40–104)	0.6	64.33 (57–69)	1634.31	0.6 (0.54–0.71)	6.18 (3.08–9.03)
<i>Ovis canadensis</i> (16)	0.61 (0.48–0.67)	40.12 (16–210)	42.5 (10–276)	74.6	49.5 (44–63)	1553.5	0.38 (0.15–0.73)	1.27 (1.04–3.42)
<i>Pekania pennanti</i> (34)	0.62 (0.52–0.66)	16	20.5 (7–48)	3.75	45.56 (3–51)	808.85	0.65 (0.25–0.8)	130.82 (0–2620)

<i>Peromyscus leucopus</i> (36)	0.82 (0.75–0.87)	13.19 (10–18)	20 (5–38)	0.02	44.83 (12–53)	1475.67	0.63 (0.3–0.83)	2412.04 (4.86–10000)
<i>Peromyscus maniculatus</i> (10)	0.77 (0.75–0.8)	10.9 (10–11)	12.5 (6–31)	0.02	48.3 (47–51)	1139.04	0.75 (0.62–0.83)	9.44 (1.04–62.41)
<i>Procyon lotor</i> (1)	0.84	10	330	6.37	51	1330.93	0.69	68.91
<i>Puma concolor</i> (13)	0.48 (0.33–0.58)	33.62 (10–46)	51 (21–739)	53.9	61.77 (50–82)	1561.58	0.64 (0.43–0.85)	104.17 (1.04–691.74)
<i>Rangifer tarandus</i> (82)	0.77 (0.45–0.87)	16.96 (14–21)	24 (5–283)	108	40.26 (5–63)	546.54	0.65 (0.28–0.83)	1.11 (0.69–5.11)
<i>Sylvilagus transitionalis</i> (3)	0.42 (0.32–0.47)	10	48 (6–103)	0.81	50.33 (50–51)	1070.02	0.75 (0.7–0.8)	161.12 (43.25–244.49)
<i>Tamiasciurus douglasii</i> (14)	0.65 (0.58–0.72)	9	10.5 (7–24)	0.22	65 (54–70)	1237.95	0.6 (0.53–0.82)	7.76 (1.04–93)
<i>Tamiasciurus hudsonicus</i> (12)	0.66 (0.48–0.77)	9	11 (5–48)	0.2	62.58 (54–68)	804.72	0.61 (0.49–0.73)	1.71 (1.04–5.6)
<i>Taxidea taxus</i> (12)	0.73 (0.43–0.82)	17.33 (12–20)	34.5 (19–649)	7.84	49.25 (39–56)	1403.56	0.59 (0.25–0.81)	44.68 (1.04–297.98)
<i>Ursus americanus</i> (43)	0.72 (0.32–0.82)	15 (8–20)	18 (5–2444)	111	51.35 (0–86)	791.39	0.7 (0.23–0.84)	50.31 (0.52–1065.89)
<i>Ursus arctos</i> (19)	0.67 (0.51–0.77)	9.89 (8–20)	48 (14–729)	196	36.68 (1–68)	568.29	0.6 (0.22–0.75)	1.25 (1.04–5.11)
<i>Ursus maritimus</i> (35)	0.69 (0.56–0.8)	15.09 (8–24)	31 (6–1050)	375	9.17 (2–33)	369.94	0.55 (0.27–0.76)	0.82 (0–1.04)
<i>Vulpes lagopus</i> (3)	0.72 (0.68–0.78)	9	28 (8–42)	3.6	25 (22–27)	455.51	0.73 (0.72–0.75)	1.04 (1.04–1.04)
<i>Vulpes vulpes</i> (16)	0.65 (0.53–0.74)	11.44 (8–13)	30 (9–116)	4.84	44.81 (24–54)	836.89	0.71 (0.39–0.83)	882.65 (1.04–3667.27)

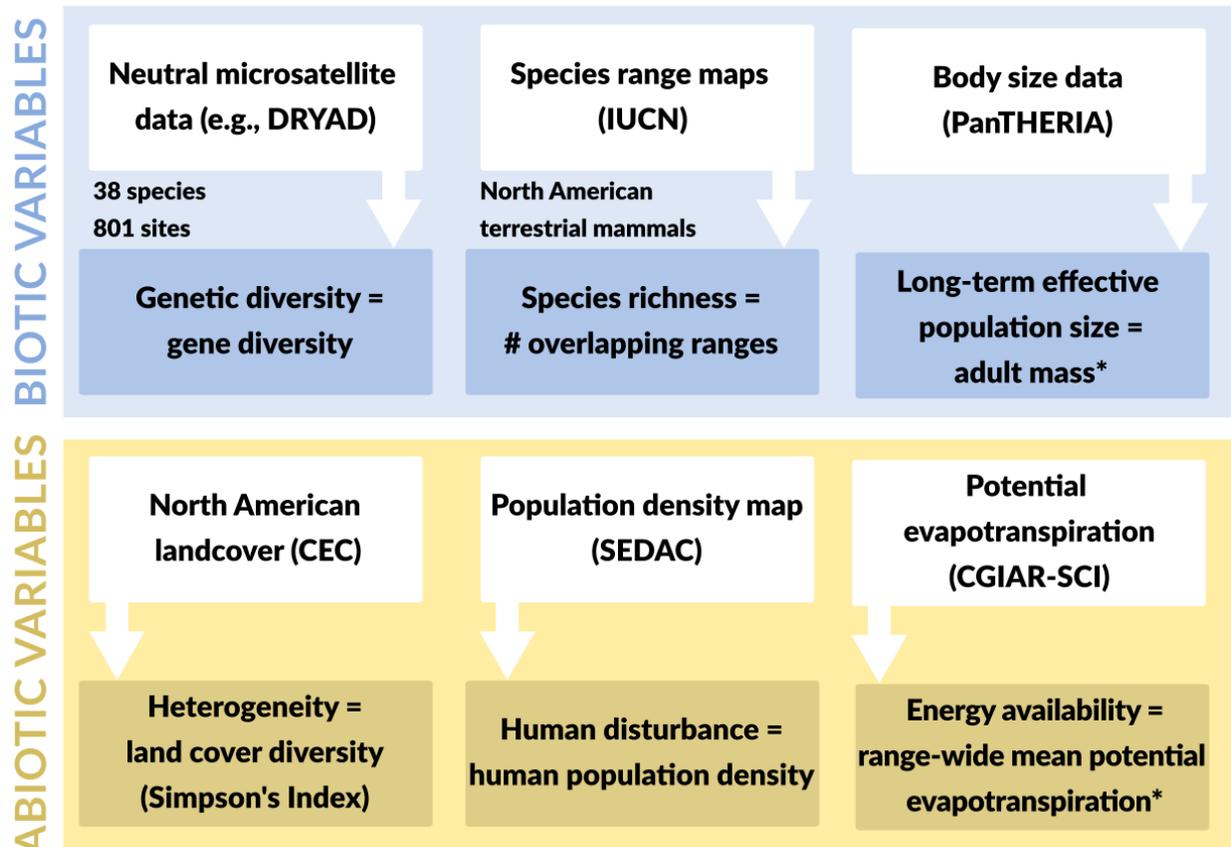


708

709 **Fig. 1.** Framework integrating genetic diversity into ecological limits hypotheses. We focus on
710 two major ecological limits pathways which stem from resource availability (the more
711 individuals hypothesis) and resource heterogeneity. Under the more individuals hypothesis,
712 resource availability across a species range positively affects species' long-term effective
713 population sizes (1). Nuclear genetic diversity increases with the effective population size (2). If
714 population size is regulated by resource availability, it will be positively associated with
715 community size and thus species richness (3). In heterogeneous environments, populations and
716 species specialize to different niches but have smaller population sizes (4). Specialization
717 reduces gene flow (5) and enhances species' ability to coexist (6). Human land transformation
718 reduces wildlife habitat (7) and gene flow among populations (8).

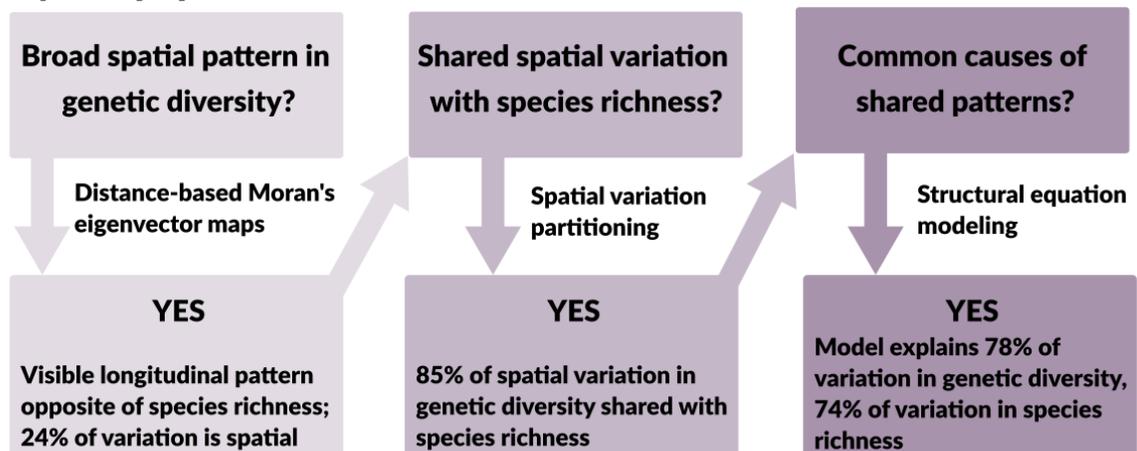
719

Data synthesis



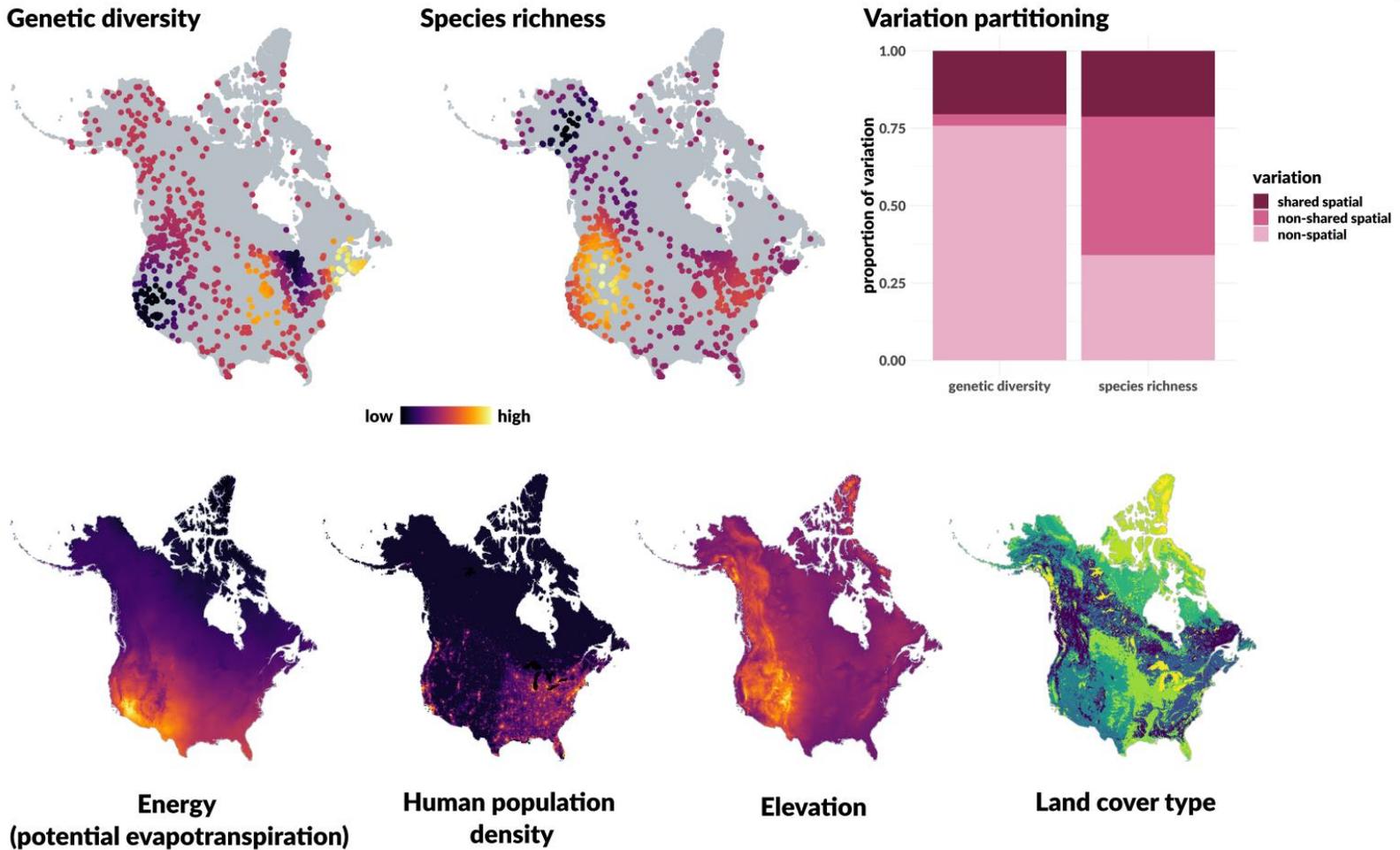
*Units = species

Analysis pipeline



720

721 **Fig. 2.** Methodological workflow detailing data sources and our series of analyses. For structural
722 equation models, variables were either measured at each of 801 sample sites for which genetic
723 diversity data was available, or at the species level ($n = 38$ species).



724

725 **Fig. 3.** Spatial patterns of biodiversity and environmental factors. (*Top row*) Locations of 801 North American mammal populations
 726 for which raw microsatellite data was available in public repositories. Point color indicates predicted values of genetic diversity and
 727 species richness based on spatial patterns detected in the data. The variation partitioning plot shows the proportion of variation in
 728 genetic diversity and species richness which can be explained by spatial factors. Spatial variation is further broken down into shared

729 and non-shared spatial variation. (*Bottom row*) Major environmental features of North America. Note land cover is categorical and
730 colors represent different types. Elevation is shown for reference, but was not included in our models.
731

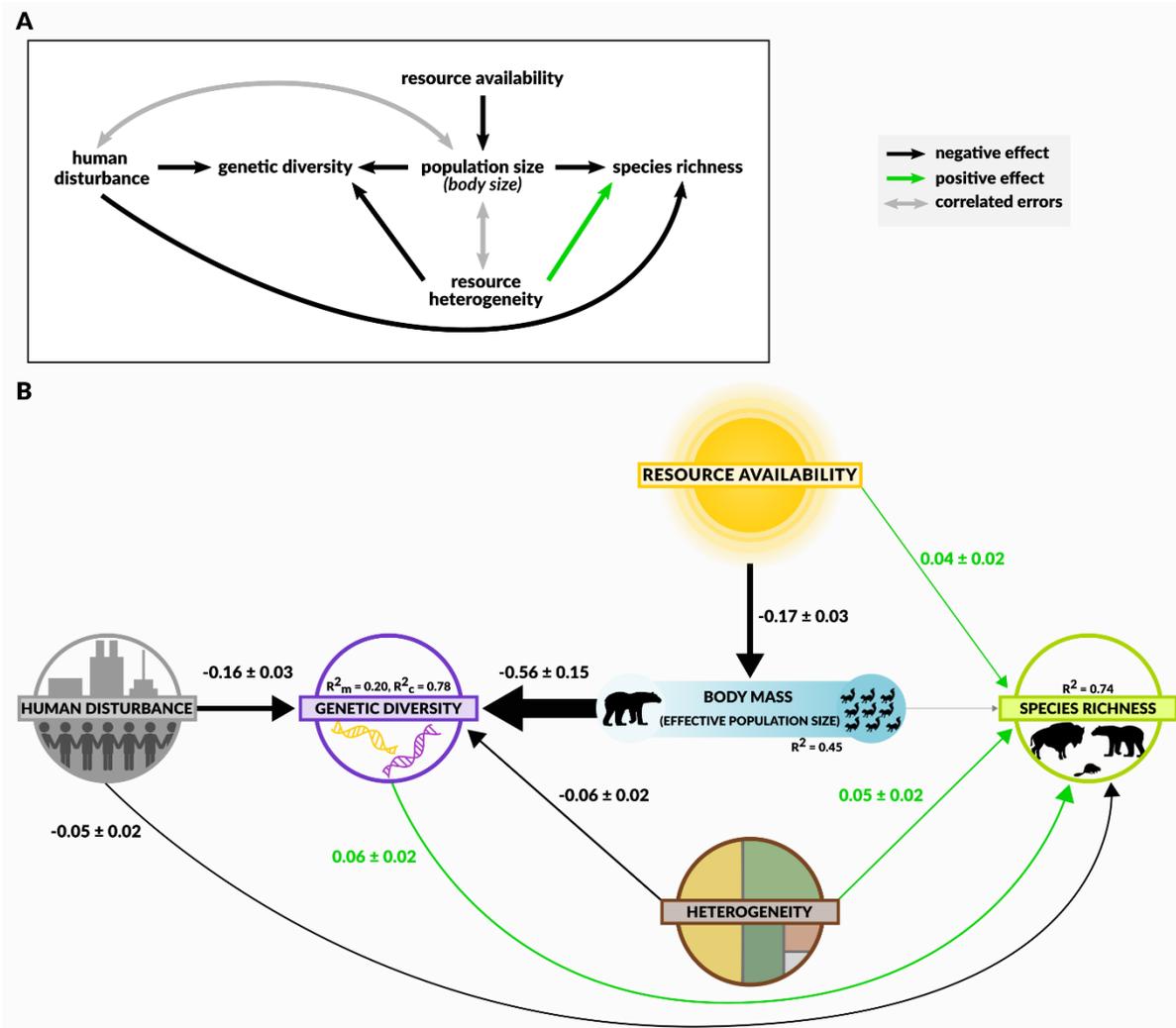


Fig. 4. Structural equation models. (a) Our conceptual hypothesis network, modified from Figure 1 to accommodate variables measured at species and site levels. Single-headed arrows represent unidirectional relationships between variables. Grey double-headed arrows indicate variables with correlated errors that were excluded from model evaluation (see Methods). (b) Structural equation model results. Green and black lines are positive and negative relationships, respectively, and the grey line is an unsupported link. Line widths reflect partial regression coefficients, which are listed for each path with standard errors. R^2 values are the amount of variation explained for each response variable. Genetic diversity was fit with a random effect for species: R^2_m is the variation explained by fixed effects only, and R^2_c is the variation explained by fixed and random effects.

Supplementary Information for: Genetic and species-level biodiversity patterns are linked by demography and ecological opportunity

Includes:

Figures S1-S3

Tables S1-S5

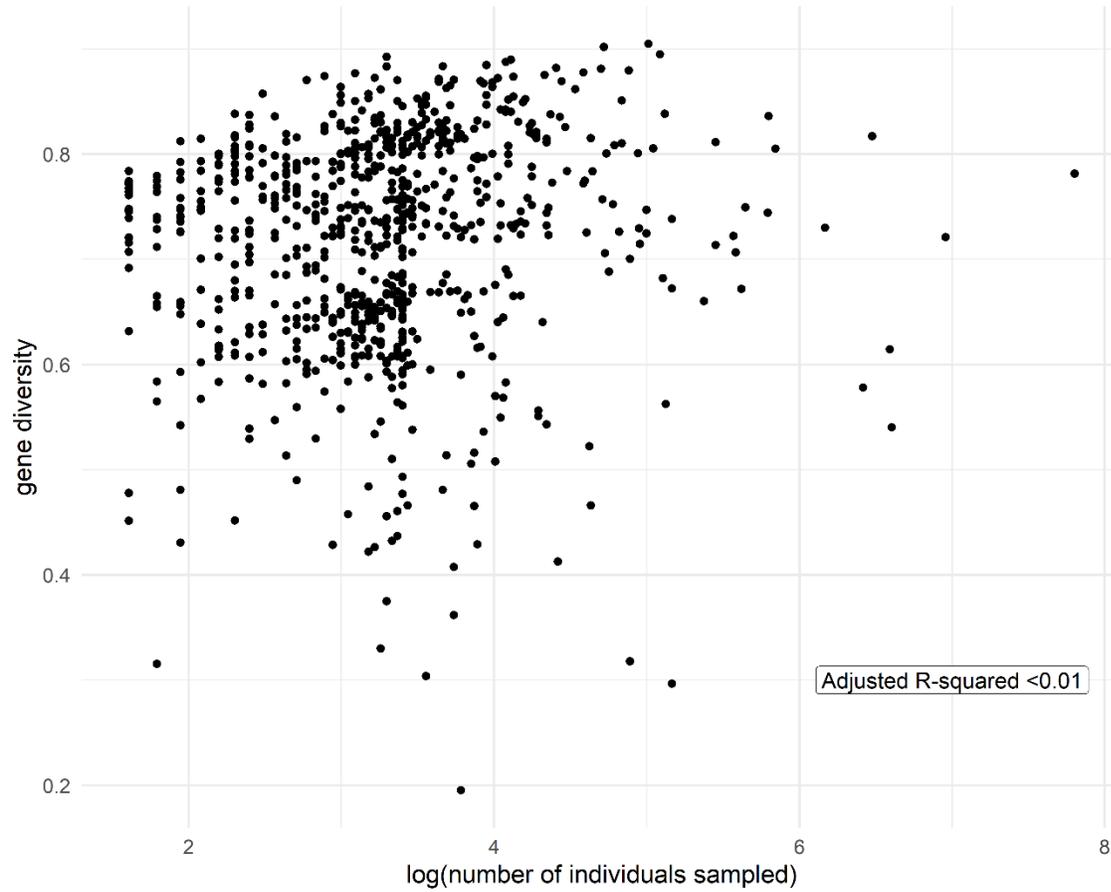
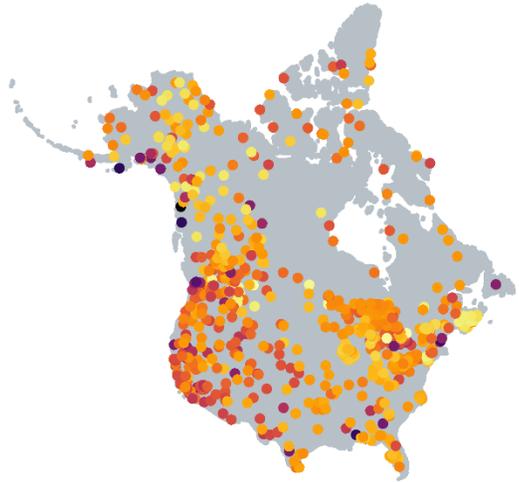


Figure S1. Plot of gene diversity vs. sample size. Gene diversity as a metric of genetic diversity depends on allele frequencies and is minimally affected by sample size. Larger populations have more rare alleles, which contribute little to gene diversity.

Genetic diversity (raw data)



Species richness (raw data)

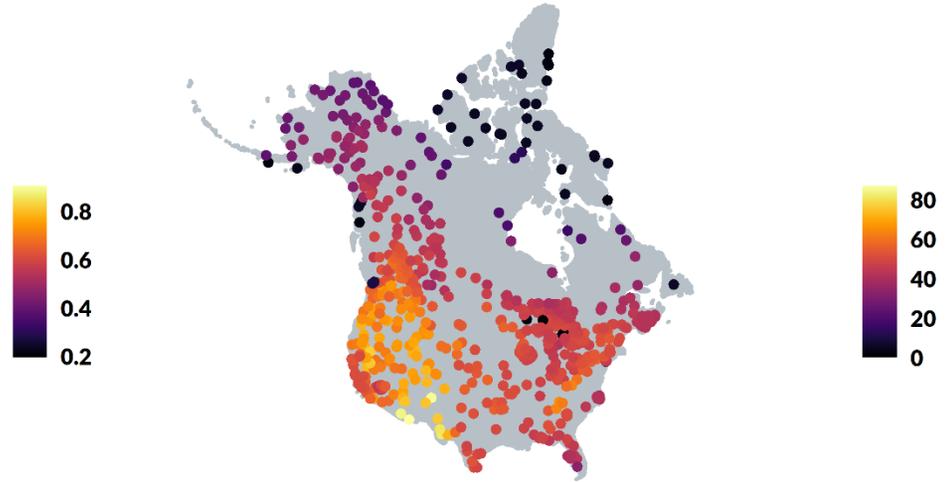


Figure S2. Maps of raw genetic diversity (gene diversity) and species richness data for each site. Clear gradients are visible in species richness but not genetic diversity. This is because most (65%) variation in species richness was spatial, in contrast to genetic diversity where comparatively less (24%) variation was spatially structured (Fig. 3).

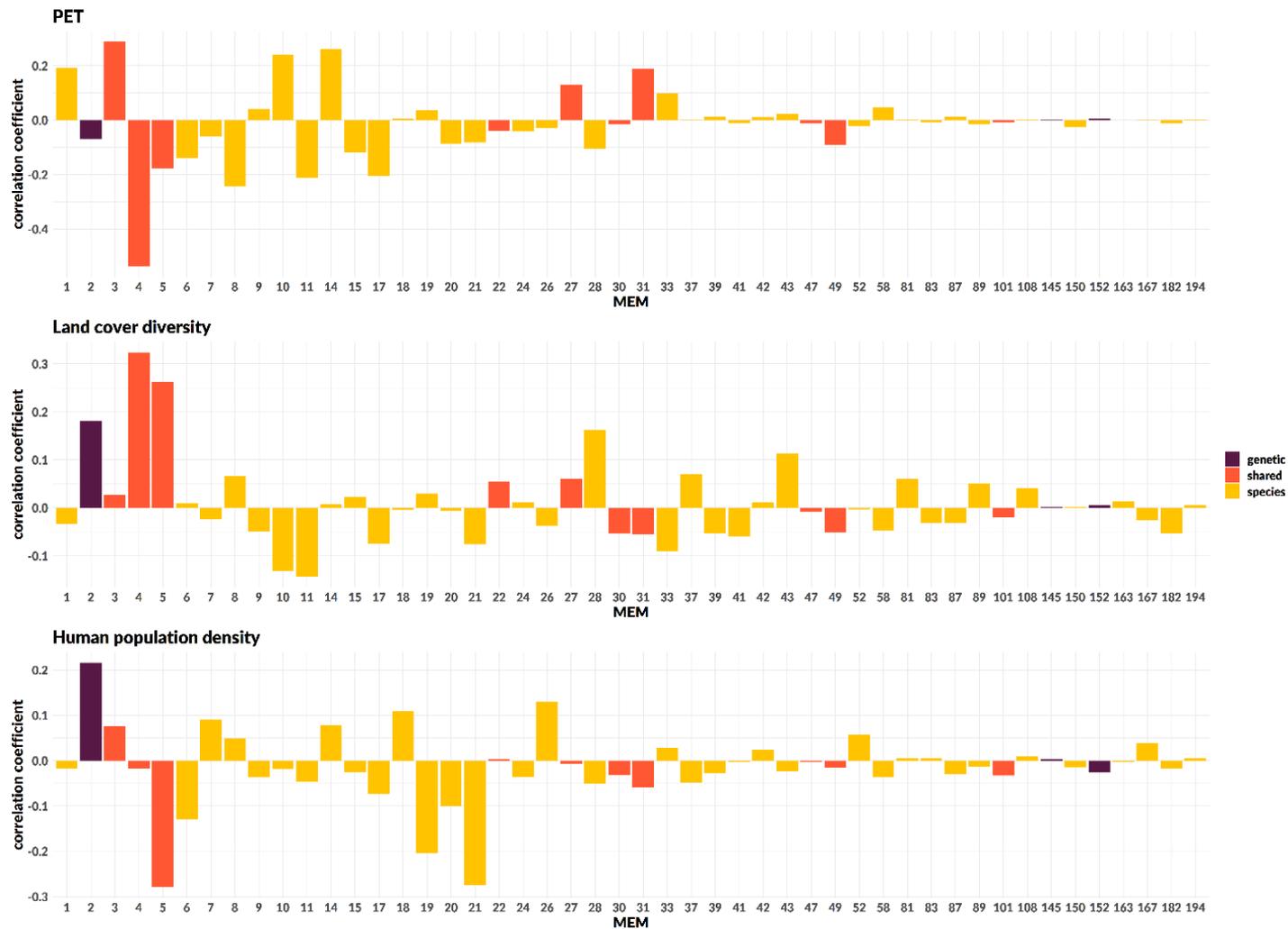


Figure S3. Correlation coefficients for spatial patterns (MEMs) and environmental variables measured at the site level: potential evapotranspiration (PET), land cover diversity, and human population density. MEMs describe spatial patterns in genetic diversity, species richness, or both (shared spatial patterns). MEMs are ordered from broad (MEM1) to fine scale (MEM194) patterns. Strong correlations indicate that environmental variables included in structural equation models account for broad scale spatial patterns present in genetic diversity and species richness.

1 **Table S1.** Path coefficients and standard errors for structural equation model presented in main
2 text (Fisher's $C = 2.25$, $p = 0.33$, 2 degrees of freedom). Heterogeneity is measured within 5000
3 km^2 of a site.

Response	Predictor	Estimate \pm SE
genetic diversity	human population density	-0.16 \pm 0.03
genetic diversity	body size	-0.56 \pm 0.15
genetic diversity	heterogeneity	-0.06 \pm 0.02
body size	PET	-0.17 \pm 0.03
species richness	body size	0.02 \pm 0.02
species richness	heterogeneity	0.05 \pm 0.02
species richness	human population density	-0.05 \pm 0.02
species richness	PET	0.04 \pm 0.02
species richness	genetic diversity	0.06 \pm 0.02
Correlated errors		Partial correlation coefficient
body size	human population density	0.10*
body size	heterogeneity	-0.02

4

5 **Table S2.** Path coefficients and standard errors for structural equation model; heterogeneity is
 6 measured within 20000 km² of a site (Fisher's C = 2.09, $p = 0.35$, 2 degrees of freedom).

Response	Predictor	Estimate ± SE
genetic diversity	human population density	-0.16 ± 0.03
genetic diversity	body size	-0.57 ± 0.15
genetic diversity	heterogeneity	-0.04 ± 0.03
body size	PET	-0.17 ± 0.03
species richness	body size	0.02 ± 0.02
species richness	heterogeneity	0.06 ± 0.02
species richness	human population density	-0.05 ± 0.02
species richness	PET	0.05 ± 0.02
species richness	genetic diversity	0.06 ± 0.02
Correlated errors		Partial correlation coefficient
body size	human population density	0.10*
body size	heterogeneity	-0.03

7

8 **Table S3.** Path coefficients and standard errors for structural equation model; heterogeneity is
9 measured within 50000 km² of a site (Fisher's C = 1.78, $p = 0.41$, 2 degrees of freedom).

Response	Predictor	Estimate ± SE
genetic diversity	human population density	-0.17 ± 0.03
genetic diversity	body size	-0.57 ± 0.15
genetic diversity	heterogeneity	0.00 ± 0.03
body size	PET	-0.17 ± 0.03
species richness	body size	0.02 ± 0.02
species richness	heterogeneity	0.06 ± 0.02
species richness	human population density	-0.06 ± 0.02
species richness	PET	0.05 ± 0.02
species richness	genetic diversity	0.06 ± 0.02
Correlated errors		Partial correlation coefficient
body size	human population density	0.10*
body size	heterogeneity	-0.03

10

11

12 **Table S4.** Path coefficients and standard errors for structural equation model; heterogeneity is
 13 measured within 100000 km² of a site (Fisher's C = 1.54, *p* = 0.46, 2 degrees of freedom).

Response	Predictor	Estimate ± SE
genetic diversity	human population density	-0.18 ± 0.03
genetic diversity	body size	-0.56 ± 0.15
genetic diversity	heterogeneity	0.04 ± 0.03
body size	PET	-0.17 ± 0.03
species richness	body size	0.02 ± 0.02
species richness	heterogeneity	0.05 ± 0.02
species richness	human population density	-0.05 ± 0.02
species richness	PET	0.04 ± 0.02
species richness	genetic diversity	0.06 ± 0.02
Correlated errors		Partial correlation coefficient
body size	human population density	0.10*
body size	heterogeneity	-0.03

14

15

16 **Table S5.** Path coefficients and standard errors for structural equation model using actual
 17 evapotranspiration (AET) as a measure of resource availability. Heterogeneity is measured
 18 within 5000 km² of a site (Fisher's C = 0.53, *p* = 0.77, 2 degrees of freedom). Genetic diversity
 19 $R^2_m = 0.20$; $R^2_c = 0.78$; body size $R^2 = 0.48$; species richness $R^2 = 0.74$.

Response	Predictor	Estimate ± SE
genetic diversity	human population density	-0.16 ± 0.03
genetic diversity	body size	-0.56 ± 0.15
genetic diversity	heterogeneity	-0.06 ± 0.02
body size	AET	-0.33 ± 0.03
species richness	body size	0.03 ± 0.02
species richness	heterogeneity	0.04 ± 0.02
species richness	human population density	-0.05 ± 0.02
species richness	AET	0.05 ± 0.02
species richness	genetic diversity	0.05 ± 0.02
Correlated errors		Partial correlation coefficient
body size	human population density	0.09*
body size	heterogeneity	-0.01

20

21