1 **Title: Population demography maintains biogeographic boundaries**

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34

35 **Abstract**

36 Global biodiversity is organized into biogeographic regions that comprise distinct biotas. The
37 contemporary factors maintaining differences in species composition between regions are poorly
38 understood. Given evidence that populations with sufficient genetic variation can adapt to fill new
39 habitats, it is surprising that more homogenization of species assemblages across regions has not
40 occurred. Theory suggests that expansion across biogeographic regions could be limited by reduced
41 adaptive capacity due to demographic variation along environmental gradients, but this possibility has
42 not been empirically explored. Using three independently curated data sets describing continental
43 patterns of mammalian demography and population genetics, we show that populations near
44 biogeographic boundaries have lower effective population sizes and genetic diversity, and are more
45 genetically differentiated. These patterns are consistent with reduced adaptive capacity in areas where
46 one biogeographic region transitions into the next. That these patterns are replicated across mammals
47 suggest they are stable and generalizable in their contribution to long-term limits on biodiversity
48 homogenization. Understanding the contemporary processes that maintain compositional differences
49 among regional biotas is crucial for our understanding of the current and future organization of global
50 biodiversity.

51

52

53 **Introduction**

54 Naturalists and biodiversity scientists have long been fascinated by the dramatic faunal and floral

55 transitions we observe among regions (von Humboldt 1807; Sclater 1858; Wallace 1876; Udvardy 1975;

56 Kreft and Jetz 2010; Holt et al. 2013). The factors that differentiate these geographically distinctive

57 species assemblages—*biogeographic regions*—are key to understanding the current organization of

58 biodiversity. The origins of biodiversity patterns are often viewed as the result of macroevolutionary

59 regional speciation-extinction and colonization dynamics occurring across millions of years (Holt et al.

60 2013; Lomolino et al. 2016). While these processes underlie the evolution of distinct biotas, they do not

61 explain the processes that sustain regional variation and limit homogenization. The biological constraints

62 that sustain biogeographic regions should result from population-level processes that limit species'

63 abilities to expand into new ecozones. However, the extent to which population-level demographic and

64 genetic processes might scale up to shape continental biotas has yet to be empirically tested.

65 Biogeographic regions are defined from species distributional data, and boundaries between regions are

66 areas with notable increases in species turnover coinciding with a relatively high number of species'

67 range limits. Transitions between biogeographic regions are typically characterized by the meeting of

68 distinct biomes or ecozones, and the overlap of various habitats form a patchy environmental mosaic

69 (Ferro and Morrone 2014). We might expect that populations with sufficient genetic variation would be

70 capable of colonizing and adapting to adjacent habitats, eventually causing regional species assemblages

71 to merge. However, species assemblages remain clustered forming distinctive biogeographic regions.

72 Theory on the evolution of species ranges suggests that changes in the demography and genetic

73 diversity of populations associated with heterogeneous and changing environments could limit the

74 efficiency with which populations adapt to neighboring environments with different conditions, thereby

75 limiting expansion (Eckert et al. 2008; Connallon and Sgrò 2018; Polechová 2018). Patterns of decreasing

76 population density and effective population size, and increasing genetic differentiation consistently

77   emerge in simulations of population demographics across environmental gradients (Polechová and

78   Barton 2015; Polechová 2018; Bridle et al. 2019). Contemporary effective population size is an estimate

79   of the rate at which a population loses genetic diversity due to genetic drift, and it is inversely

80   proportional to the efficiency with which selection can act on beneficial genetic variants (Charlesworth

81   and Charlesworth 2010; Ellegren and Galtier 2016). Thus, range expansion across biogeographic

82   transition zones could be restricted because of limits on the efficiency of local adaptation, due to the

83   increased strength of drift relative to selection, and the steepness of the environmental gradient

84   (Polechová 2018). Both biotic and abiotic factors contribute to the steepness of environmental gradients

85   (Case and Taper 2000; Goldberg and Lande 2007; Polechová and Barton 2015). However, in the absence

86   of clines in effective population size, adaptation and spread along environmental gradients remains

87   theoretically possible (Kirkpatrick and Barton 1997; Polechová 2018).

88   We therefore predict that transitions between biogeographic regions should be characterized by multi-

89   species gradients in the density and genetic characteristics of populations. Assuming underlying

90   environmental gradients are associated with biogeographic transitions, we predicted that effective

91   population size, genetic diversity, and population density would decrease nearer to transition zones, and

92   that genetic differentiation would increase. There are also steep environmental gradients associated

93   with moving from inland to coastal habitats. Thus, if the logic underlying our predictions for

94   biogeographic transitions holds, we should also expect to see the same pattern with increasing

95   proximity to coastal biogeographic boundaries. We tested these predictions for North and South

96   American mammals due to the wealth of demographic, biogeographic, and genetic data available from

97   these regions. Our analyses took advantage of three independently curated open-source genetic and

98   demographic data sets (Lawrence et al. 2018, 2019; Santini et al. 2018a, 2019; Schmidt et al. 2020a,

99   2020b) and previously described delineations of biogeographic regions (Holt et al. 2013). If our models

100   successfully capture our predicted population-level gradients across these independent data sets, we

101   will have strong empirical evidence supporting the general importance of contemporary population-

102   level processes for preventing wholesale homogenization of communities across biogeographic regions.

103

104   **Methods**

105   **Data sources**

106   *Genetic diversity.* We used data from the MacroPopGen database for our estimates of site-level genetic

107   diversity (Lawrence et al. 2018, 2019). MacroPopGen aggregates data summaries from the literature for

108   vertebrates in the Americas and includes georeferenced, site-level data for 147 mammal species

109   sampled at 1874 sites across North and South America (Fig. S1). We used the raw site-level estimates of

110   genetic diversity provided on sheet 2 of the MacroPopGen database (Lawrence et al. 2018), rather than

111   the re-grouped populations based on genetic differentiation described in their main data set (see next

112   section for reasoning). We selected gene diversity (the average probability that two alleles chosen at

113   random from a sample site are different) as our metric of genetic diversity because it is not strongly

114   influenced by sample size (Charlesworth and Charlesworth 2010), which varies widely in this data set

115   (range: 2 – 1563 individuals per sampling location; mean 48 individuals ± 93 SD). This value is reported

116   as H_e (expected heterozygosity) in MacroPopGen but we note the term *gene diversity* is used when

117   treating this value as the probability of selecting two different alleles from non-random mating

118   populations (Nei 1973). This and all other population genetic data sets used here are based on

119   microsatellite loci, for which diversity is well correlated with genome-wide diversity (correlated at R^2

120   ~0.83; Mittell et al. 2015)

121   *Effective population size and genetic differentiation.* To assess spatial variation in local contemporary

122   effective population size and genetic differentiation, we used a multispecies microsatellite data set

123   compiled by Schmidt et al. (2020a, 2020b) which includes data for 38 mammal species sampled across

124   801 sites in Canada and the United States (Fig. S1). These data differ from MacroPopGen because they

125   are aggregated raw genotypes instead of compiled literature summaries, which allows users to calculate

126   population genetic metrics that are less routinely presented in the literature. From these data we

127   estimated contemporary effective population size (Do et al. 2014) and population-specific F_{ST} (Weir and

128   Goudet 2017).

129   We estimated the effective population size of the parental generation using the linkage disequilibrium

130   method implemented in the NeEstimator software (Do et al. 2014). Effective population size is reliably

131   measured using linkage disequilibrium (Waples and Do 2010), however, estimates of infinity are

132   returned if populations are very large or if sampling error overwhelms the signal of genetic drift. Sites

133   were excluded from analyses in these cases. We were able to estimate effective population size for 629

134   sites in 37 species.

135   We calculated population-specific F_{ST} (Weir and Goudet 2017) using the raw genotypic data in Schmidt

136   et al. (2020a, 2020b). Population-specific F_{ST} estimates the extent of co-ancestry across all sites in each

137   species sample—not pairs of sites—and returns a relative, site-level estimate of how far each site has

138   diverged from the common ancestor of populations sampled at all sites. The MacroPopGen data set

139   contains F_{ST} estimates for more populations than the Schmidt et al. data set, but these estimates are

140   summaries of pairwise estimates of F_{ST} for genetic populations defined using a universal threshold that

141   was not suited to our analyses. MacroPopGen F_{ST} estimates are estimated with the extension of pairwise

142   F_{ST} for multiallelic markers like microsatellites (G_{ST}; Nei 1973), and thus depend on the genetic diversity

143   in the sampled populations. Estimates do not vary between 0 and 1, but have a maximum value of $1-H_s$

144   (Charlesworth 1998; Hedrick 1999) where H_s is the mean heterozygosity of subpopulations. This means a

145   universal threshold is incompatible with our analyses because the genetic definition of a population and

146   our interpretation of F_{ST} will vary for each species. For this reason, we use the raw site-level data instead

147   of regrouped populations based on an F_{ST} threshold, and recalculate a population-specific F_{ST} metric.

148   Computing population-specific F_{ST} requires at least two sample sites, so we were unable to measure

149   differentiation when the original genotype data were sampled at a single site. Population-specific F_{ST} was

150   estimable for 785 sites in 31 species.

151   *Population density.* TetraDENSITY (Santini et al. 2018a, 2019) is a global database of >18,000 population

152   density estimates (individuals/km^2) for terrestrial vertebrates. From this data set, we used density

153   estimates for 246 mammal species at 1058 sites in North and South America (Fig. S1). Given the nature

154   of this aggregated data set, species sampled at the same coordinate location sometimes had multiple

155   density estimates for different reasons, including long-term temporal studies with density estimates

156   across years, multiple methods used to estimate density, or estimates given for multiple localities within

157   sampling areas. These types of studies made up a minority (25%) of the overall data set, and most of the

158   data (88%) had a maximum of 2 density estimates for species per site. Records for different species

159   collected by different research groups were unevenly temporally sampled, making it impractical to

160   incorporate time into our models. As variation in population density due to temporal change or

161   methodology was not our focus here, we took the average density for species sampled at the same sites.

162   Moreover, sampling method was found to explain little of the variation in population density at broad

163   spatial and taxonomic scales in the TetraDENSITY data set (Santini et al. 2018b).

164   We checked the data to ensure there were no island sites, where frequent gene flow with continental

165   populations would be unlikely. This was only the case for TetraDENSITY, and in total we excluded 5 sites

166   that were in the Galapagos, the Caribbean, and Hawaii. We retained the Arctic Archipelago, which is

167   continuous habitat for Arctic species such as polar bears, which were the most consistently sampled

168   species in this region, due to the presence of sea ice.

169 *Biogeographic regions.* We focused on the biogeographic regions of continental North and South

170 America. We used biogeographic regions previously defined by Holt et al. (2013). Holt et al. produced

171 both phylogenetically-based and distribution-based biogeographic regions by clustering mammal species

172 assemblages (defined as the set of species co-occurring within a grid cell). We used the distribution-

173 based maps produced for mammals (see Fig. S6C in Holt et al. 2013), which were generated following

174 procedures similar to those of Kreft and Jetz (2010). We used distribution-based maps because the

175 biogeographic boundaries generated with this approach reflect areas of relatively high overlap in the

176 range limits of multiple species, whereas using the phylogenetic approach, boundaries would reflect

177 regional transitions at higher taxonomic levels (genus, family, etc.). The distribution-based maps are

178 generated from the clustering of βsim (turnover) values among mammal assemblages, and are robust to

179 changes in data quality and completeness (Holt et al. 2013). In this data set North and South America

180 are comprised of eight biogeographic regions (Fig. S2).

181 The transition between biogeographic regions are areas where there is a detectable increase in species

182 turnover. Thus, boundary lines between regions are better thought of as the statistical mean point of a

183 transition from one region to the next, rather than a hard boundary containing entire species' ranges.

184 Sampling locations for species may therefore cross biogeographic region boundaries. The transitional

185 environments we are interested in occur on both sides of the lines we use as regional delineations. Thus

186 we did not restrict our sample to species fully bounded within biogeographic regions as we were

187 interested in characteristic demographic processes across regional transitions. We note that in our data,

188 most species were sampled in a single region (70% of species for genetic diversity, 65% for effective

189 population size, 61% for population differentiation, and 80% of species for population density; Fig. S5).

190 We calculated the geodesic distance (km) to the nearest biogeographic boundary using the dist2Line

191 function in the geosphere package v1.5.0 (Hijmans 2019). Geodesic distance is an accurate measure of

192   the shortest distance between two points along a curved surface. We computed geodesic distances

193   using the default WGS84 ellipsoid.

194   **Statistical Analysis**

195   We tested whether distance to the nearest biogeographic boundary was correlated with effective

196   population size, genetic diversity, genetic differentiation, and population density using four Bayesian

197   generalized linear mixed models (GLMM) in the brms package (Bürkner 2019). We ran 4 GLMMs, each

198   with distance to biogeographic boundary as the independent variable, and one of the density or genetic

199   measures as response variables. These data have a hierarchical structure, with sample sites nested

200   within species. We incorporated this structure in our random effect terms. Random intercepts for

201   species account for variation in species' means for each response variable, and random slopes allow the

202   effect of distance to vary across species within the model. Here, species were treated as random

203   samples from a common distribution, so that we can interpret coefficient estimates as the general effect

204   of distance to boundary across all species. If the posterior distribution of the general effect of distance

205   falls entirely above or below zero, this indicates that species have similar positive or negative responses

206   to distance. In contrast, a posterior distribution that overlaps zero may indicate that many species have

207   no detectable response to distance (species-specific coefficient estimates are zero), or that different

208   species have strong positive and negative relationships with distance, generalizing to no overall effect.

209   To visualize results and distinguish between these possibilities, we extracted and plotted species-specific

210   coefficients from the fitted GLMMs. We ran all models with 4 chains with minimum 2000 iterations and

211   weakly informative normal priors on beta parameters with a mean of zero and standard deviation of 1.

212   We used default priors for other model parameters.

213   Because the nearest biogeographic region boundaries could be either interior region borders or

214   coastlines, we tested whether boundary type affected our results. We classified the nearest boundary

215   for each site as either coastal or interior (Figs. S3, S4). We then re-fit the models described above

216   including a fixed effect for boundary type with an interaction term allowing the effect of distance to vary

217   with boundary type. We included random slope terms for all fixed effects and interactions. Results from

218   models containing boundary type as an interaction term are presented in Table S1.

219   We tested model residuals for spatial autocorrelation with Moran tests (package spdep; Bivand et al.

220   2013). The population density model was the only model without significant spatial autocorrelation. We

221   re-ran models for effective population size, genetic diversity, and genetic differentiation using

222   simultaneous autoregressive (SAR) lag models implemented in brms to address spatial autocorrelation.

223   SAR lag models incorporate a spatial weights matrix to account for autocorrelation in the response

224   variable by estimating the strength of spatial dependencies among sites as an additional model

225   parameter.

226

227   **Results**

228   Our analyses included gene diversity estimates (Lawrence et al. 2019) from 147 mammal species

229   sampled at 1874 sites across North and South America after filtering, that had a mean of 0.65 ± 0.14 SD

230   (range: 0.04 – 0.94; Figs. 1, S6; Table S2). We used estimates of effective population size (Schmidt et al.

231   2020b) for 37 mammal species at 629 sites (median 66.00; 1.00 – 199578.00 individuals per population;

232   Figs. 1, S6; Table S2). For population differentiation (Schmidt et al. 2020b) we estimated population-

233   specific F_{ST} for 31 species sampled from 785 sites across North America (mean 0.06 ± 0.08 SD; range: -

234   0.05 – 0.72; Figs. 1, S63; Table S2). Finally, for population density (Santini et al. 2018a), we included 246

235   mammal species from 1058 sites (median 9.93; range 0.001 – 11900 individuals/km^2; Figs. 1, S6; Table

236   S2).

237   Genetic diversity, effective population size, genetic differentiation, and population density were all

238   correlated with a sample site's distance from the nearest biogeographic boundary in our hierarchical

239   regression models (Fig 2; Table 1). In general, as distance from biogeographic boundaries increased,

240   effective population size and genetic diversity also increased, while genetic differentiation and

241   population density decreased (Fig. 2). In other words, genetic differentiation and population density

242   were higher near biogeographic boundaries, while effective population size and genetic diversity were

243   lower. Species-specific effects underlying the overall effects (shown in Fig. 2, Figs. S7-S9) trended in the

244   same directions, with no patterns that would suggest moderating effects of species traits or

245   phylogenetic relationships (Figs. S7-S9). Outlier species with strong effects were not consistent across

246   genetic or demographic metrics (Fig. 2). We found no evidence for an interaction between the effect of

247   distance and the type of biogeographic boundary (i.e., whether the nearest boundary was coastal or

248   interior) for genetic variables (Table S1), however there was an interactive effect for population density

249   (estimate = 0.12; 0.01 – 0.23 95% CI; Table S1, Fig. S10). The negative relationship between the nearest

250   distance to biogeographic boundary and population density was primarily associated with coastlines,

251   not interior boundaries (Fig. S10). In addition, the population density effect was not correlated with

252   effects for genetic variables (Figs. S11, S12). Population density does not appear to be generally related

253   to biogeographic region boundaries.

254

255   **Discussion**

256   We show that contemporary population demographics, reflected in neutral nuclear genetic diversity and

257   differentiation, vary consistently among species depending on a population's proximity to biogeographic

258   boundaries, whether internal or coastal. Genetic diversity, contemporary effective population size, and

259   genetic differentiation each varied in ways that suggest that populations located closer to transitions

260   between biogeographic regions may be less capable of adapting to the different environmental

261   conditions in and beyond those transitional boundary environments (Fig. 2). Stronger genetic drift and

262   reduced adaptive capacity near biogeographic region transitions thus appear to be an important factor

263   in maintaining distinctive species assemblages between biogeographic regions.

264   The spatial organization of global biodiversity results from complex, interacting processes (e.g.,

265   historical, evolutionary, ecological) acting over time to shape the biogeographic patterns we observe

266   today (Pianka 1966; Brown 2014; Schemske and Mittelbach 2017; Lawrence and Fraser 2020). In

267   mammals, biogeographic boundaries are related to tectonic plate movements, and these boundaries are

268   associated with deeper divergences in the phylogenetic compositional similarity of mammal

269   assemblages across regions (Ficetola et al. 2017, 2021). Climatic and physical barriers such as mountains

270   have also influenced dispersal and population demography over long periods to shape regional species

271   assemblages (Ficetola et al. 2021). These historical and contemporary factors have created

272   biogeographic patterns that are, as our results suggest, in part maintained by local microevolutionary

273   processes limiting population adaptation and therefore spread. Differences in the composition of

274   species assemblages among biogeographic regions thus appear to be maintained by evolutionary limits

275   as predicted by theory (Eckert et al. 2008; Polechová 2018). These evolutionary limits are potentially

276   imposed by environmental factors that our results suggest limit population size and promote

277   differentiation in a consistent manner across hundreds of species at continental extents.

278   We used globally defined biogeographic regions for mammals and focused on North and South America

279   (Holt et al. 2013). These regions describe general patterns of species turnover, and so are not expected

280   to capture genetic and demographic patterns across all species. While we identified general genetic and

281   demographic patterns associated with sample location, some species did not align with general trends

282   (Fig. 2). For example, wolverines (*Gulo gulo*) and caribou (*Rangifer tarandus*) had higher genetic diversity

283   and effective population sizes, respectively, nearer transition zones, and American red squirrel

284   (*Tamiasciurus hudsonicus*) populations tended to be more differentiated towards region interiors. These

285   species highlight that there are clearly important species-specific factors that disrupt general patterns in

286   population size and genetic diversity across biogeographic regions (Fig. 2). Patterns of genetic diversity

287   and population demography across species ranges may differ based on demographic history (e.g., timing

288   and location of bottlenecks), thus outliers are expected and should depend on individual species and

289   population histories. Outlier species (labeled in Fig. 2) were sampled in one or two biogeographic

290   regions, suggesting that these large effect sizes were not consistently associated with species that had

291   previously expanded their range across biogeographic boundaries. Our goal was to describe general

292   patterns in population demography and genetics across the Americas in relation to biogeographic

293   regions, but future investigations at continental or more local scales (e.g., Morrone 2014) would permit

294   a more focused examination of the environmental or geographic features involved in generating these

295   patterns, albeit with fewer species.

296   We hypothesized that genetic diversity, effective population size, and population density should all

297   decrease near biogeographic boundaries. However, we found that population density tended to be

298   higher nearer boundaries, though the effect was small relative to genetic metrics, and species-level

299   coefficient estimates were spread across positive and negative values (Fig. 2). Furthermore, the

300   interaction term in our models suggested this effect was driven primarily by distance to the coast (Figs.

301   2, S10; Table S1). This suggests that processes unrelated to biogeographic transition zones underlie this

302   relationship. That patterns of genetic diversity, effective population size, and population differentiation

303   were unaffected by whether boundaries were coastal or interior suggests that environmental

304   heterogeneity and associated effects on population size and gene flow could explain the general

305   patterns we find across biogeographic regions.

306   Transitional areas between biogeographic regions are often considered conservation priorities because

307   of their high biodiversity (Smith et al. 2001; Spector 2002; Kark et al. 2007). Environmental transition

308 zones and ecotones more generally are sometimes thought of as speciation pumps, where

309 environmental variation and barriers to gene flow create interesting evolutionary arenas with high

310 potential for isolation, differentiation, and speciation (Schilthuizen 2000; Doebeli and Dieckmann 2003).

311 One idea in conservation biogeography is that locally adapted populations occupying transition zones

312 may be better equipped to withstand environmental change because they are already adapted to new

313 environments that differ from regional cores (Smith et al. 2001; Spector 2002; Whittaker et al. 2005).

314 From this perspective, transitional areas between biogeographic regions would be of high conservation

315 value due to their combination of high species richness, phylogenetic diversity, and populations of

316 genetic significance. However, our findings suggest that prioritizing the regional conservation of

317 transition zones over more central locations may run counter to policies intending to maximize genetic

318 diversity and species' long-term evolutionary potential (Hoban et al. 2020). There will be trade-offs

319 when conserving regions for biodiversity at genetic and species levels. Indeed, spatial correlations

320 between species richness and genetic diversity in general are not straightforward (Kahilainen et al. 2014;

321 Laroche et al. 2015) and these two levels of biodiversity tend to be negatively correlated in

322 heterogeneous environments (Schmidt et al. 2022).

323 Through their effects on local population demography, environmental factors appear to set general

324 evolutionary limits that contribute to biogeographic patterns at continental scales. Consistent with

325 existing theory (Polechová and Barton 2015; Polechová 2018; Bridle et al. 2019), our results suggest that

326 population demography interacts with environmental transitions in ways that limit population

327 expansion across environmental gradients. Our macrogenetic (Blanchet et al. 2017; Leigh et al. 2021)

328 work adds a bottom-up perspective (i.e., starting at the population-level) to the exploration of

329 biogeographic region formation that has to date been lacking. Population-level microevolutionary

330 processes appear to shape contemporary biodiversity patterns associated with biogeographic regions.

331 **Acknowledgements**

344   **Author contributions**

345   All authors contributed significantly to question development and study design. CS curated data and

346   performed the analyses with input from CJG and JPL. CS and CJG wrote the first draft of the manuscript

347   and all authors contributed substantially to revisions.

348   **Data accessibility**

349   All data is already in the public domain and sources are cited in the references. Data and code to

350   reproduce analyses are available on FigShare

351   (https://figshare.com/articles/dataset/Data_from_Population_demography_maintains_biogeographic_

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485

486   **Table 1.** Model summaries for the effect of distance to the nearest biogeographic boundary on genetic
487   and demographic parameters. Effect sizes are given with 95% credible intervals (CI). Rho (ρ) is the
488   coefficient of spatial autocorrelation (for simultaneous autoregressive models only), also presented with
489   95% credible intervals. Standard deviations (σ) with 95% CIs are given for species random effect
490   intercepts and slopes**.**

variable *(# sites, # species)*	distance to boundary	ρ	$\sigma_{intercept}$	σ_{slope}
effective population size *(629, 37)*	0.14 (-0.01 – 0.30)	0.16 (0.06 – 0.25)	0.42 (0.27 – 0.61)	0.25 (0.10 – 0.44)
genetic diversity *(1874, 147)*	0.18 (0.10 – 0.26)	0.17 (0.13 – 0.21)	0.93 (0.81 – 1.06)	0.25 (0.17 – 0.34)
genetic differentiation *(785, 31)*	-0.23 (-0.45 – -0.02)	0.14 (0.06 – 0.22)	0.49 (0.36 – 0.67)	0.45 (0.29 – 0.69)
population density *(1058, 246)*	-0.07 (-0.13 – -0.01)	–	0.88 (0.8 – 0.97)	0.18 (0.12 – 0.25)

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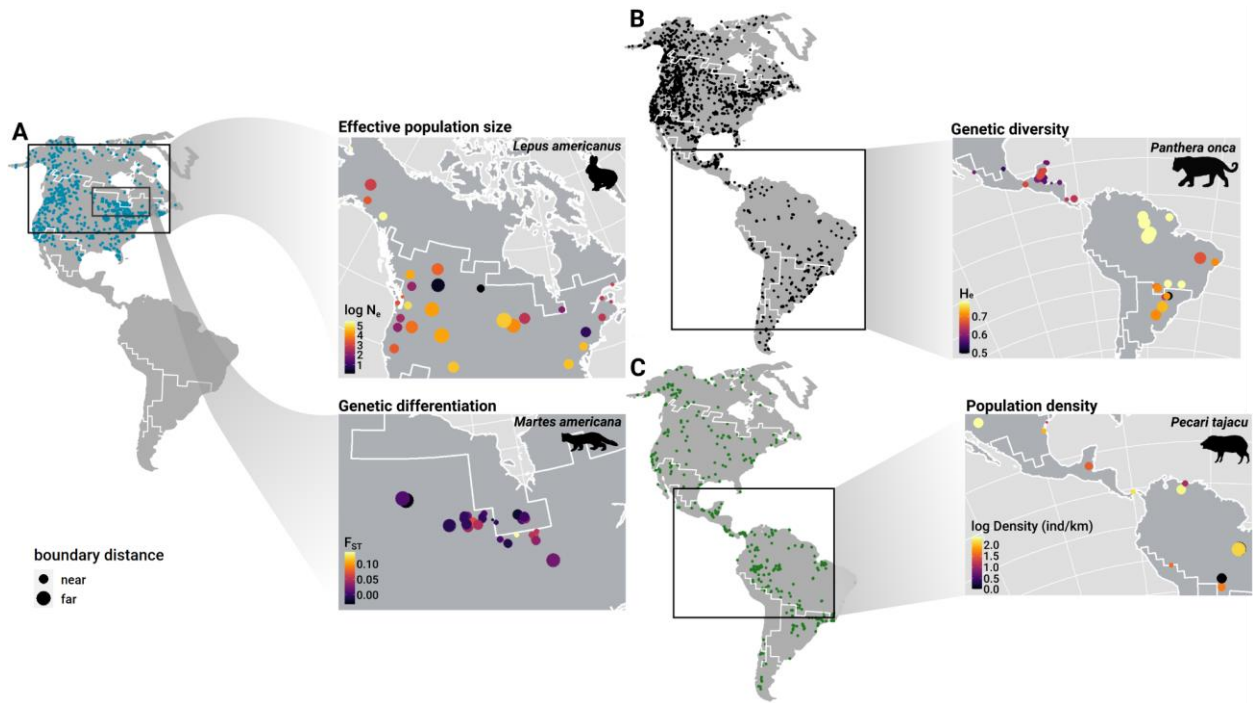
Figure 1. Continental maps show the locations of sites used in this study (A: effective population size and genetic differentiation (F_{ST}) estimates from Schmidt et al. data compiled from raw genotypes; B: MacroPopGen genetic diversity (H_e) estimates; C: TetraDENSITY population density records). One species was sampled at each site. Inset maps show site level values of genetic and demographic variables for select species. The size of points denotes site distance from the nearest biogeographic region boundary.

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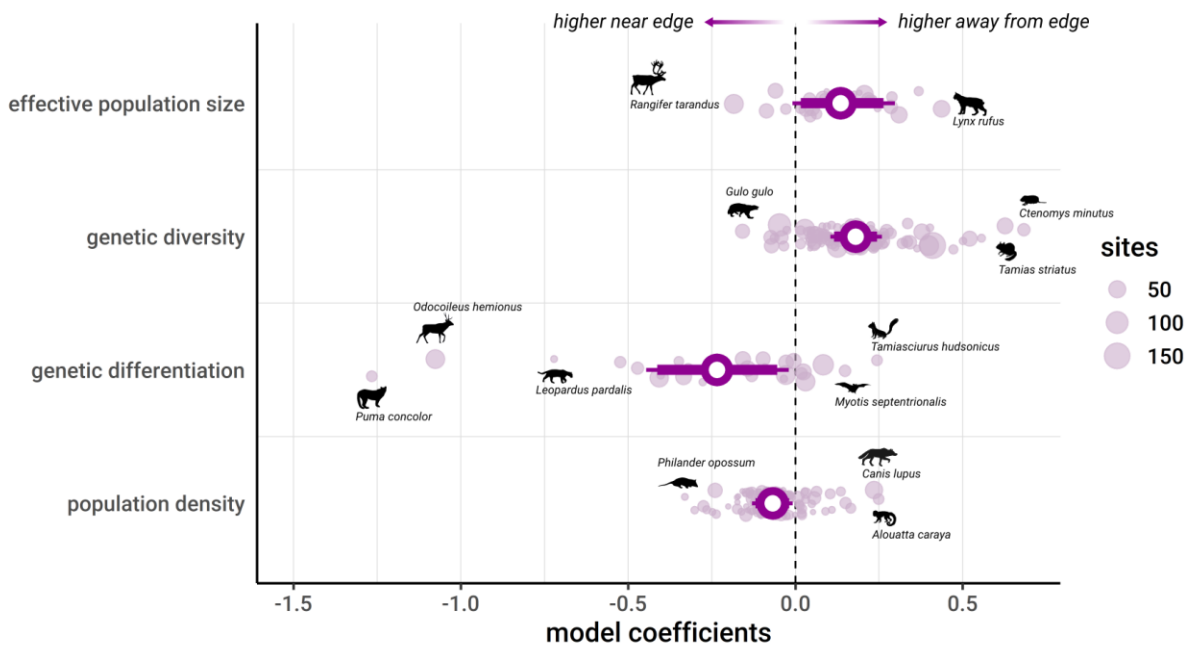
Figure 2. Model coefficients for the effect of distance from biogeographic boundary on population biodiversity variables. Open circles are global coefficient estimates; narrow and thick bars represent 95% and 90% credible intervals respectively. Pale points are the species-specific coefficient estimates that underlie the global estimate, and their diameter denotes the number of sample sites included for that species. Effective population size and genetic diversity increase moving away from region boundaries while genetic differentiation and population density are higher closer to boundaries. Select species at the tails of the distributions of species-specific effects are shown.

508

509 **Supplementary information for: Population demography maintains biogeographic boundaries**

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511 Colin J. Garroway

512

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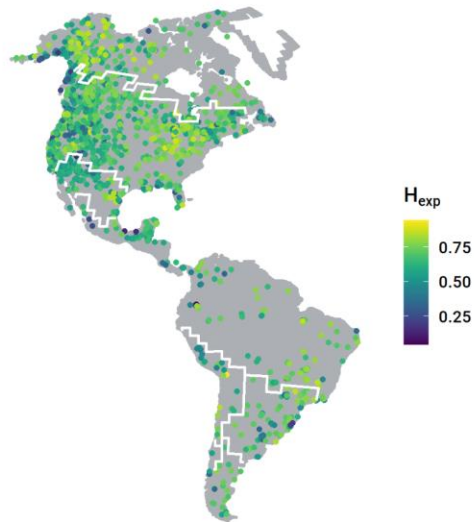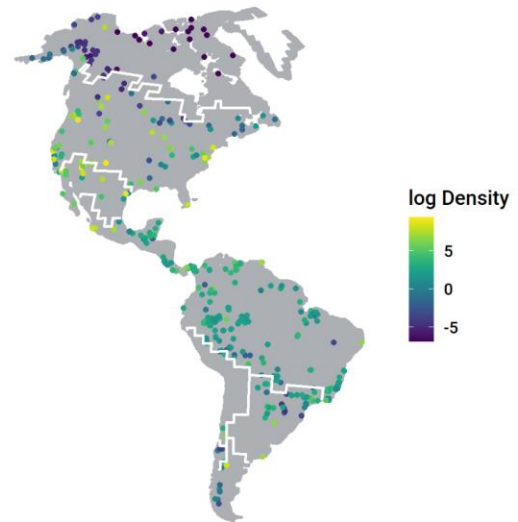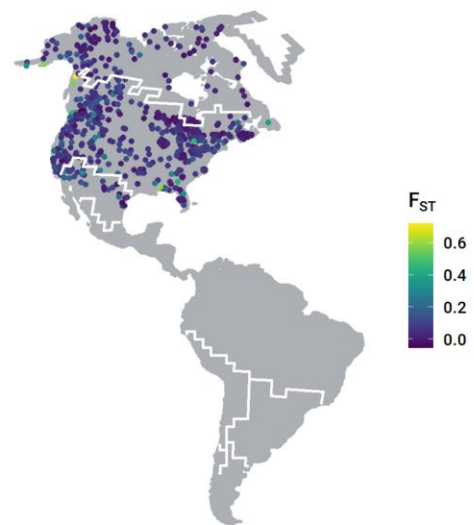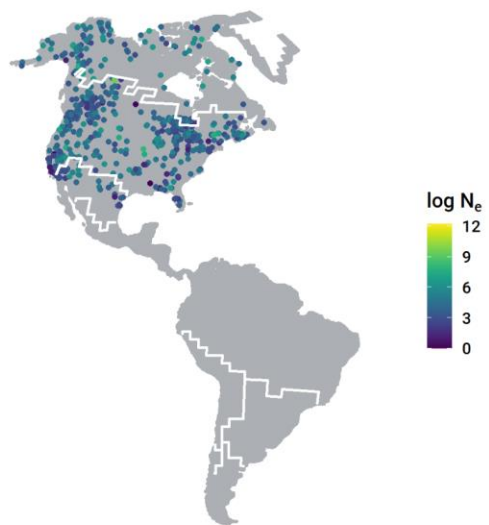
Figure S1. Maps of raw values for population-level biodiversity variables.
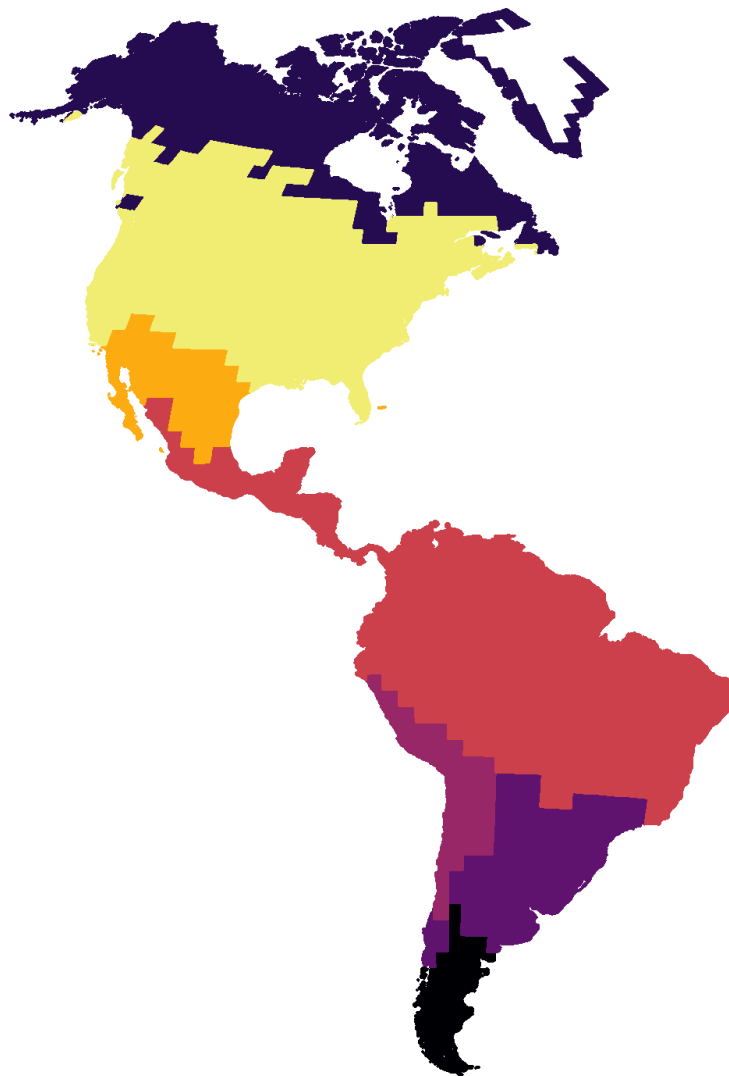
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535   **Figure S2.** Biogeographic regions of mammals in North and South America (from Holt et al. 2013)

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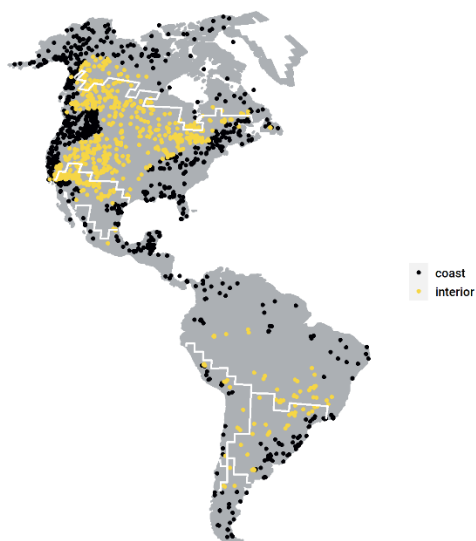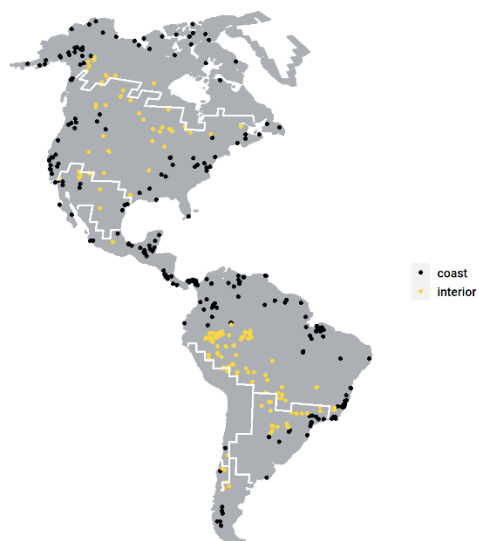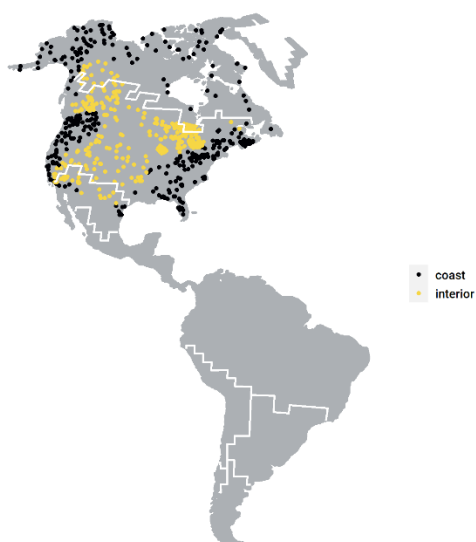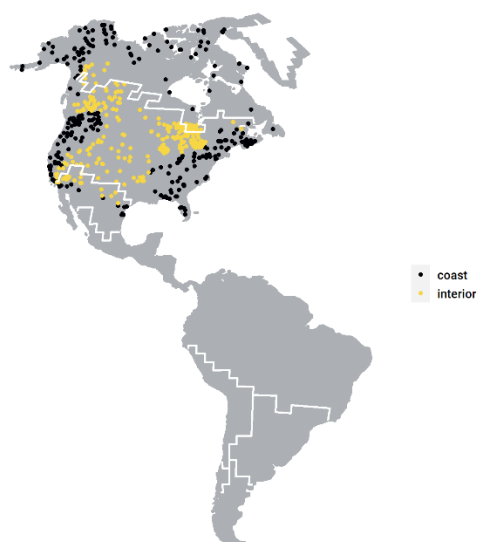
Figure S3. Maps showing whether sample site was nearer to a coastline (black) or interior biogeographic boundary (yellow).
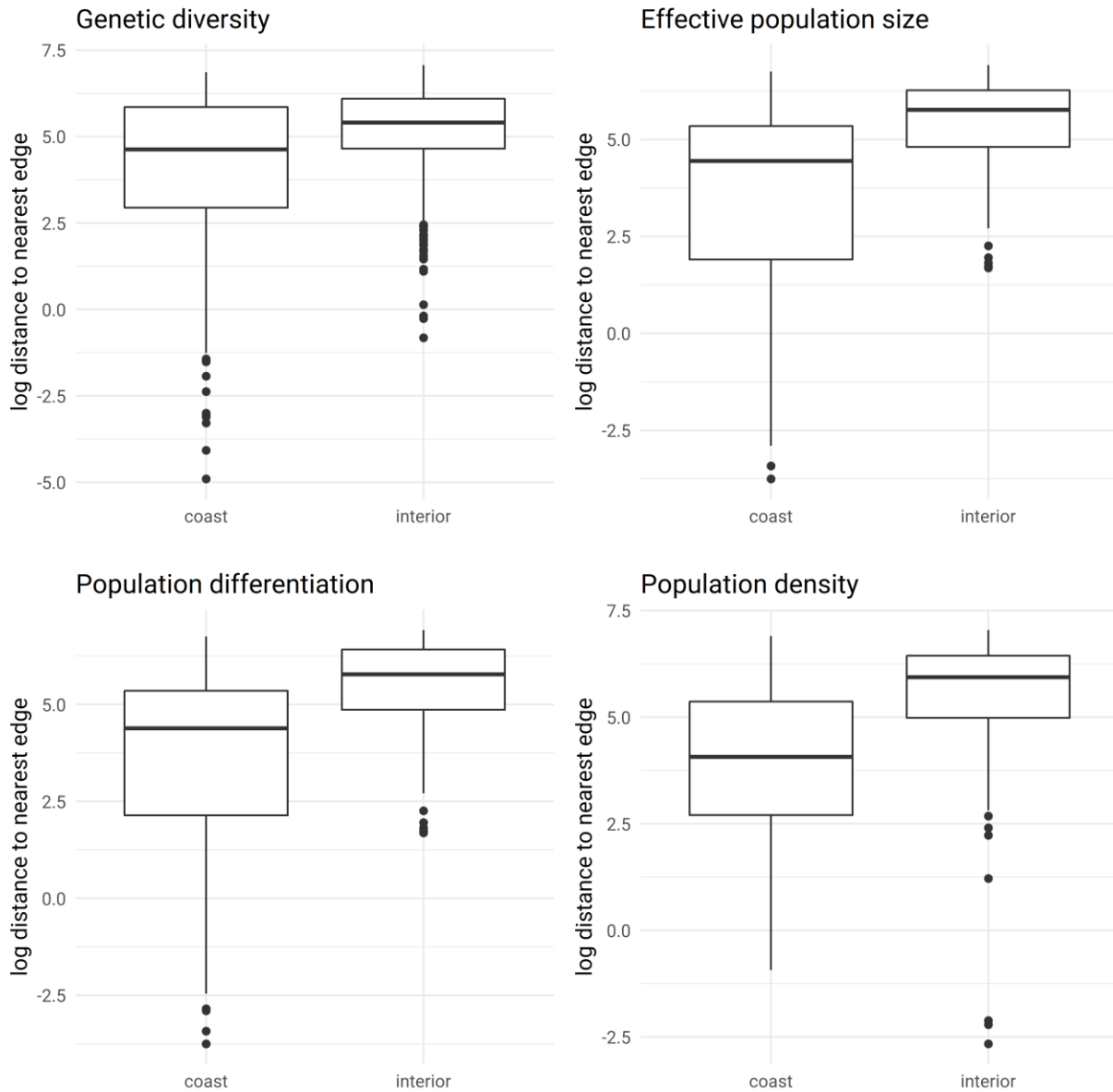
Figure S4. Boxplots comparing distributions in distance to edge values for coastal versus internal biogeographic region boundaries. There were no strong differences in distance across different boundary types.
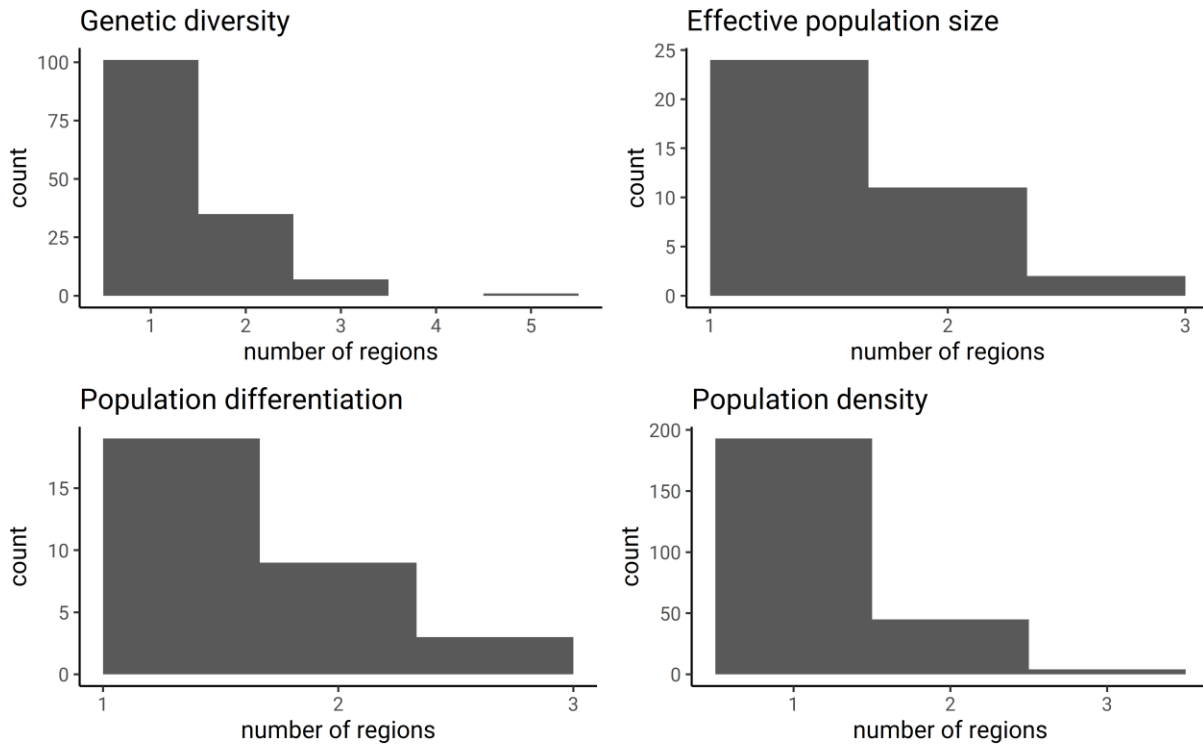
Figure S5. Histograms showing the counts of species with sample sites located in one or multiple regions. Most species were sampled in a single region for all variables (70% of species for genetic diversity, 65% for effective population size, 61% for population differentiation, and 80% of species for population density).
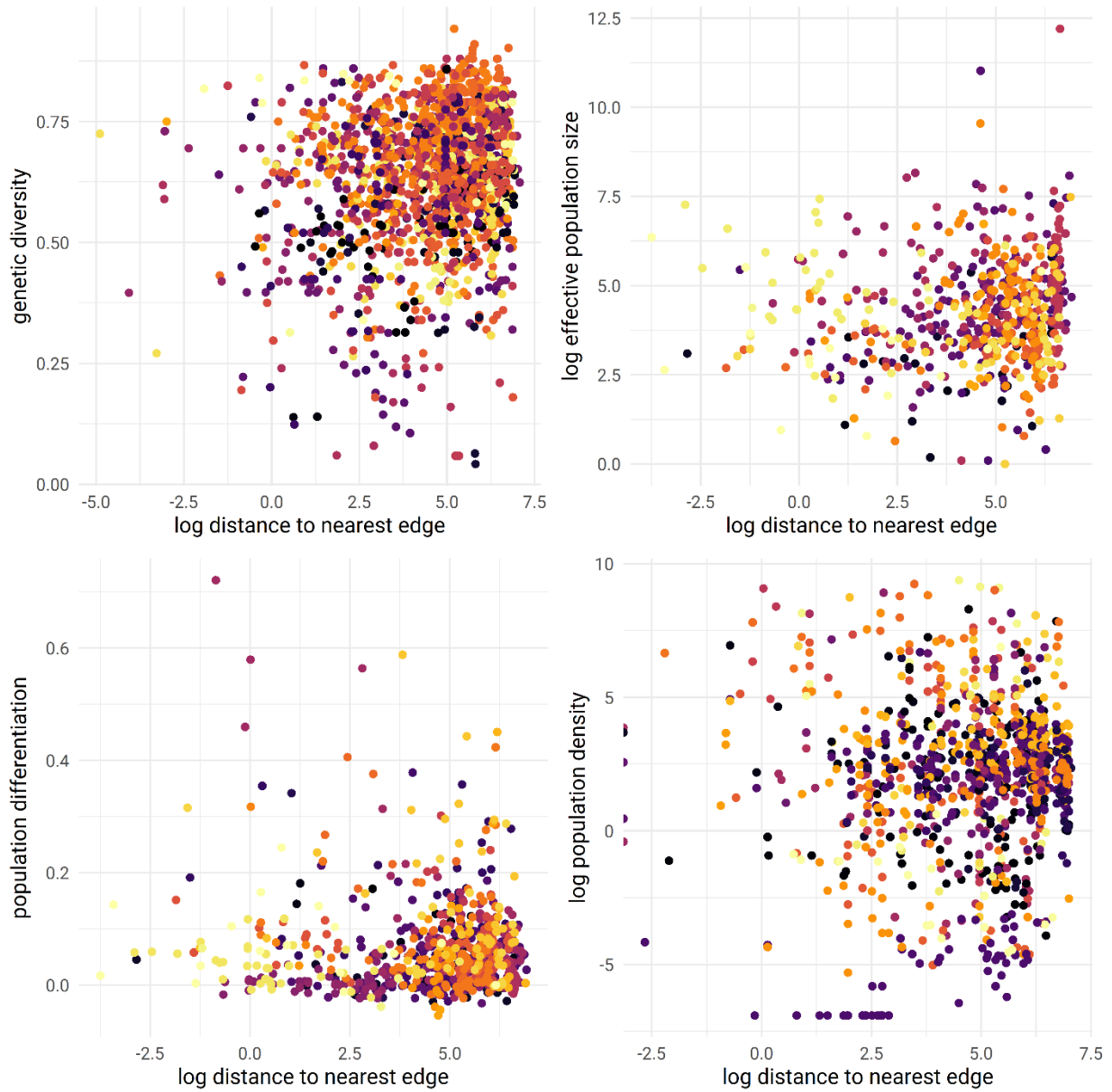
Figure S6. Scatterplots of raw data. Distance to edge (km), effective population size (individuals), and population density (individuals/km^2) are log transformed. Points are colored by species.
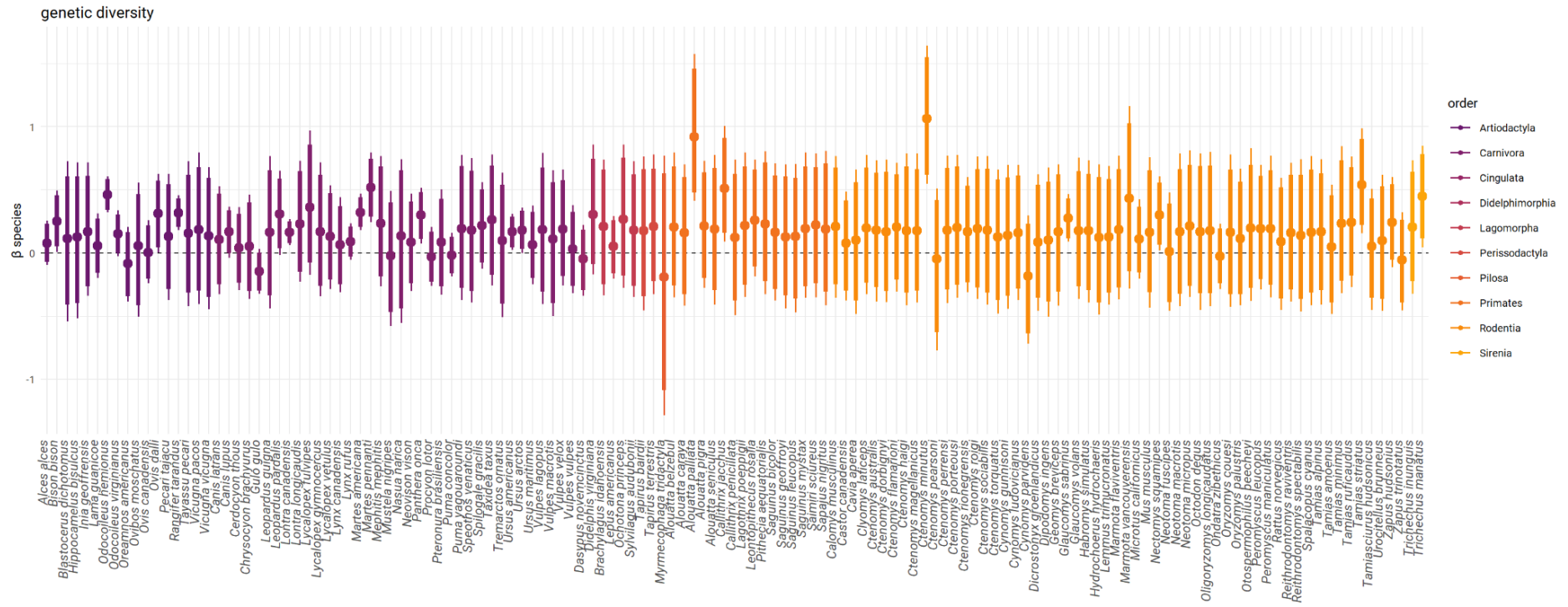
Figure S7. Species-level effects of distance to nearest biogeographic boundary on genetic diversity. Thin and thick bars are 95% and 90% credible intervals, respectively.
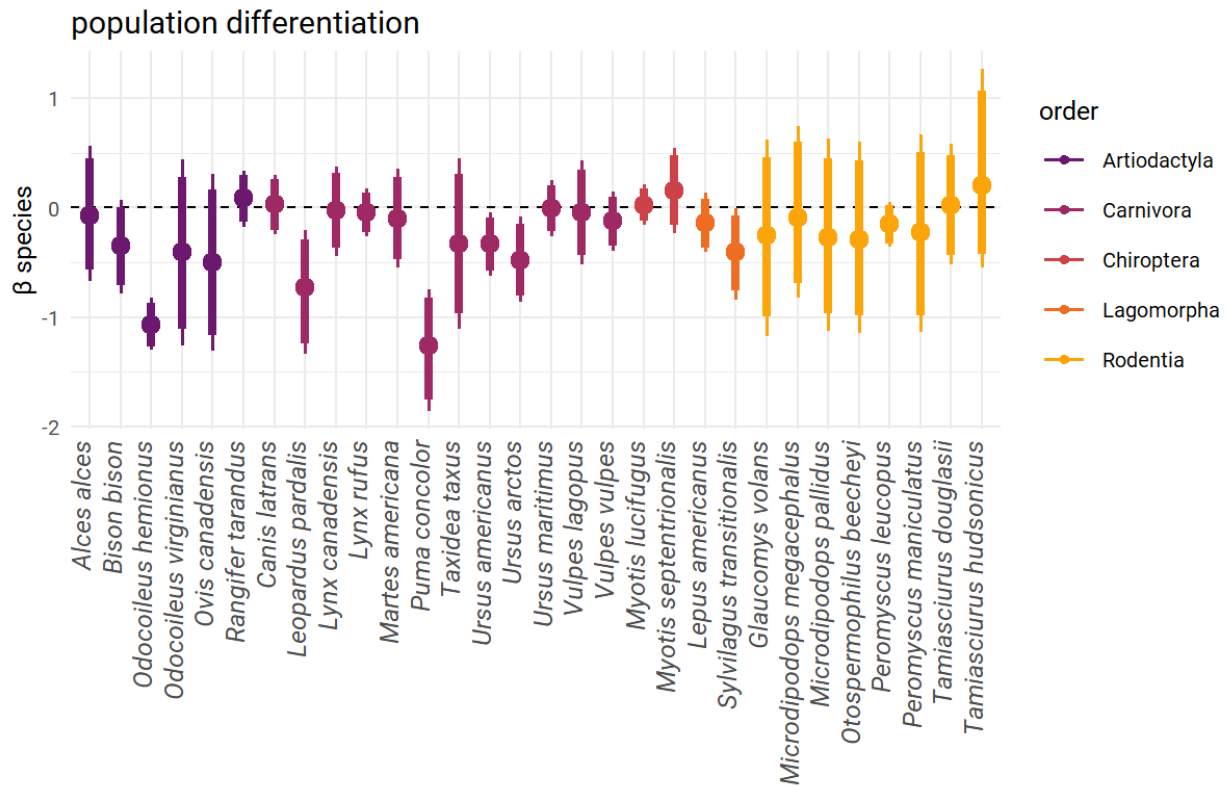
Figure S8. Species-level effects of distance to nearest biogeographic boundary on genetic differentiation. Thin and thick bars are 95% and 90% credible intervals, respectively.

Figure S9. Species-level effects of distance to nearest biogeographic boundary on population density. Thin and thick bars are 95% and 90% credible intervals, respectively.
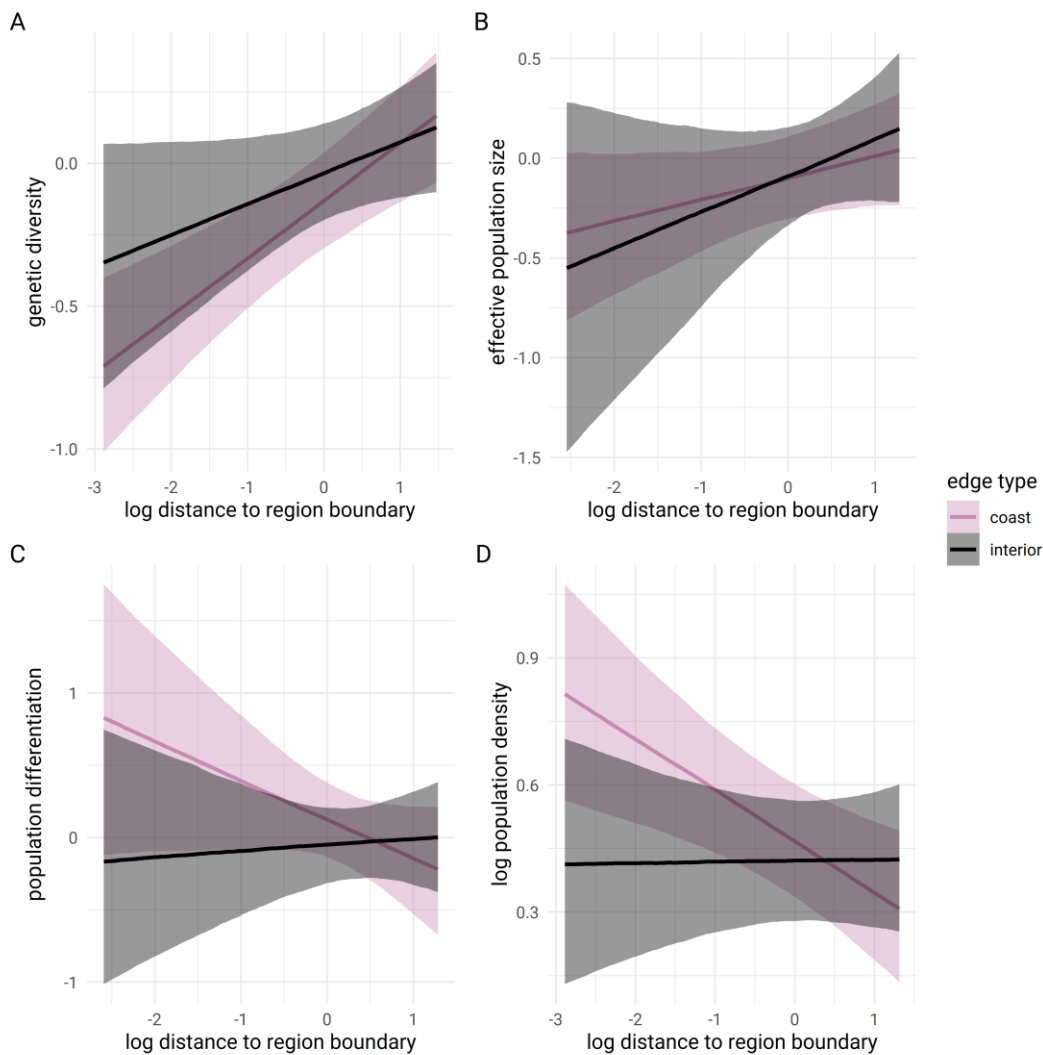
Figure S10. Interaction effect of the type of biogeographic boundary (coastal or interior) on the relationship between the distance to nearest boundary and mammal population genetics and demography. Note all variables were scaled and centered in our models to make effects comparable, and these transformed values are presented here. Effects were only significantly different for population density (d), where increasing population density nearer to boundaries appears to be driven by coastlines.

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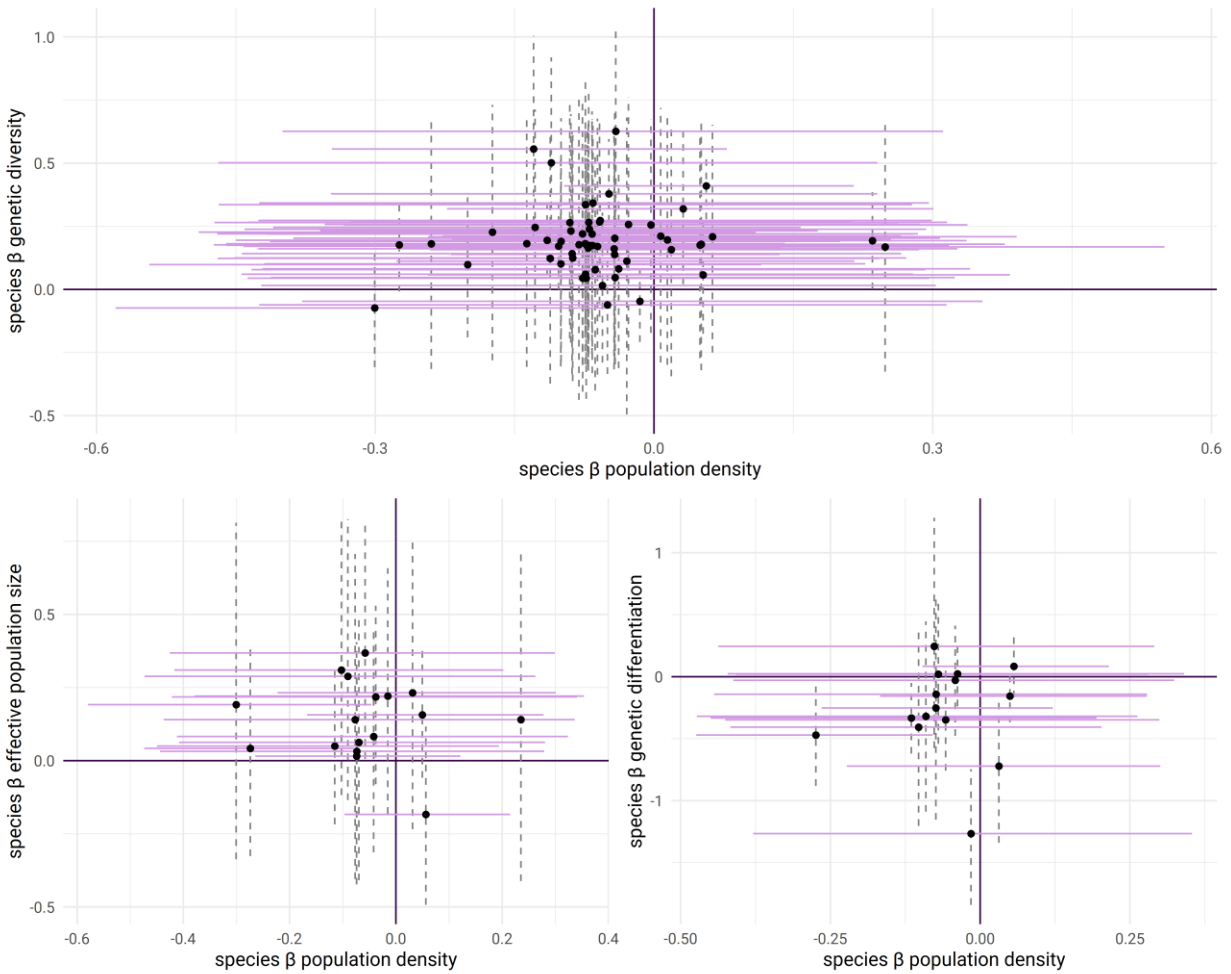
Figure S11. Relationships between species' distance to region edge effect sizes (β) for population density vs. genetic diversity, effective population size, and genetic differentiation for matching species across datasets. Points are species-specific coefficient estimates, purple lines represent 95% credible intervals for population density coefficient estimates, dashed grey lines are 95% credible intervals for the coefficient of the genetic variable on the y axis. Dark lines highlight β = 0 for both axes. Effect sizes for population density are unrelated to effect sizes for genetic variables.

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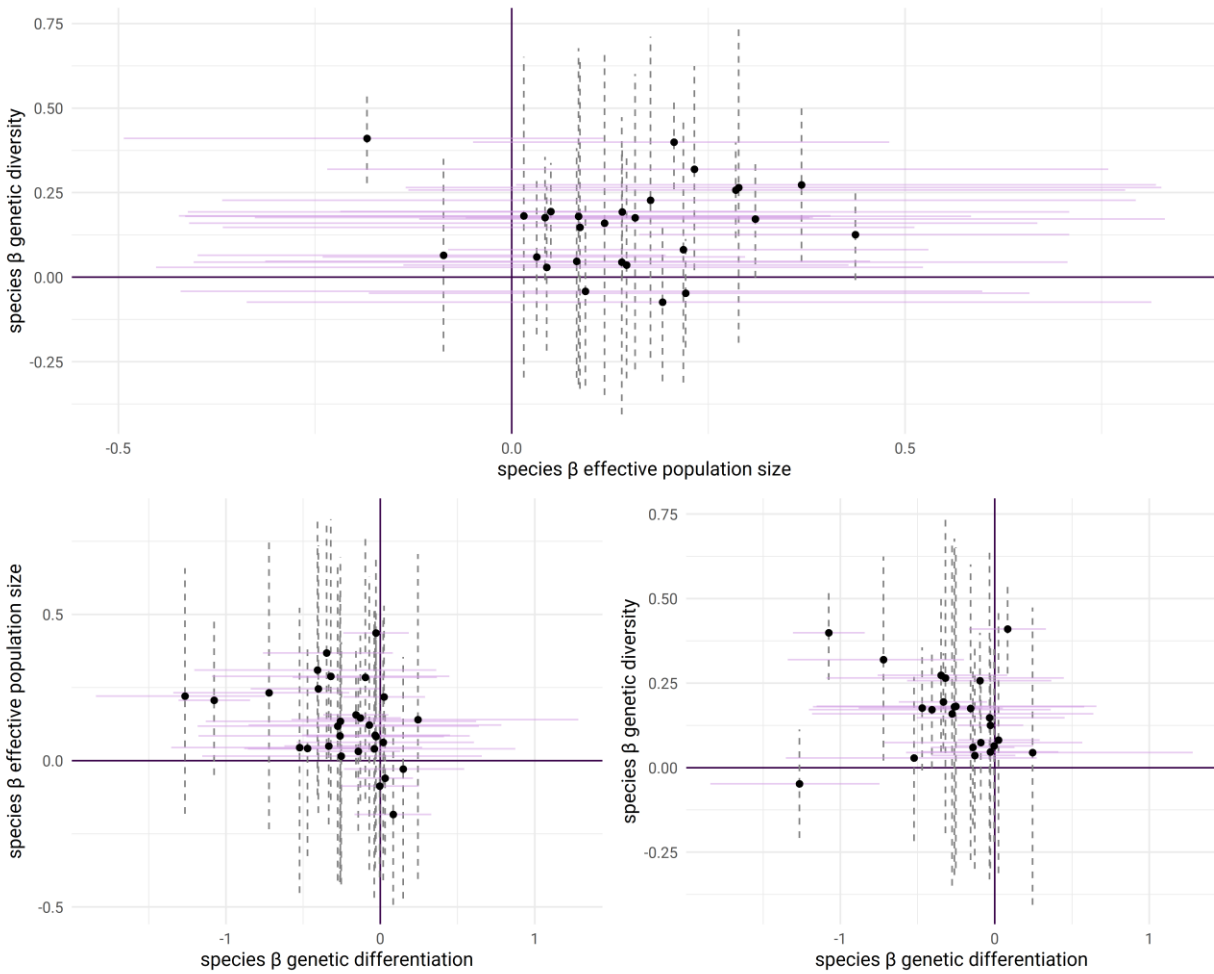
Figure S12. Relationships between species' distance to region edge effect sizes (β) for genetic diversity, effective population size, and genetic differentiation for matching species across datasets. Points are species-specific coefficient estimates, purple lines are 95% credible intervals for x-axis variables, and dashed grey lines are 95% credible intervals for y-axis variables. Dark lines highlight β = 0 for both axes. *Top*: Coefficient estimates for effective population size and genetic diversity are weakly positively related. *Bottom*: Coefficient estimates for effective population size and genetic diversity are weakly negatively related to coefficients for genetic differentiation.

Table S1. Effect sizes and 95% credible intervals of models accounting for boundary type (coastal vs interior). There was no interaction between boundary type and distance (boundary type*distance) for any genetic variable and a weak effect for population density, indicating that the effect of distance only depended on boundary type for population density. The effect of distance on population density was more strongly associated with coastlines (see Fig. S8).

variable	boundary type * distance	distance to boundary	boundary type: interior
effective population size	0.08 (-0.23 – 0.38)	0.11 (-0.03 – 0.26)	0.01 (-0.23 – 0.38)
genetic diversity	-0.09 (-0.24 – 0.05)	0.20 (0.10 – 0.29)	0.10 (0.01 – 0.18)
genetic differentiation	0.32 (-0.11 – 0.71)	-0.27 (-0.60 – 0.06)	-0.17 (-0.46 – 0.10)
population density	0.12 (0.01 – 0.23)	-0.12 (-0.20 – -0.04)	-0.05 (-0.18 – 0.08)

33 **Table S2.** List of species included in analyses and the number of sites per species in each dataset. We
34 used gene diversity estimates from MacroPopGen (Lawrence et al. 2019). Numbers of sites are given
35 separately for effective population size (N_e) and population differentiation (F_{ST}) data from Schmidt et al.
36 (Schmidt et al. 2020). Population density estimates are from the TetraDENSITY database (Santini et al.
37 2018).

Order	Species	MacroPopGen	Schmidt et al. (N_e)	Schmidt et al. (F_{ST})	TetraDENSITY
Artiodactyla	*Blastocerus dichotomus*	1	0	0	3
Artiodactyla	*Tayassu pecari*	5	0	0	5
Artiodactyla	*Vicugna pacos*	5	0	0	0
Artiodactyla	*Oreamnos americanus*	24	1	0	0
Artiodactyla	*Ovis canadensis*	75	16	14	0
Artiodactyla	*Ovibos moschatus*	3	0	0	11
Artiodactyla	*Hippocamelus bisulcus*	1	0	0	9
Artiodactyla	*Mazama americana*	0	0	0	1
Artiodactyla	*Catagonus wagneri*	0	0	0	1
Artiodactyla	*Mazama gouazoupira*	0	0	0	1
Artiodactyla	*Ozotoceros bezoarticus*	0	0	0	2
Artiodactyla	*Inia geoffrensis*	2	0	0	0
Artiodactyla	*Sus scrofa*	0	0	0	7
Artiodactyla	*Pecari tajacu*	3	0	0	13
Artiodactyla	*Lama guanicoe*	24	0	0	1
Artiodactyla	*Vicugna vicugna*	16	0	0	0
Artiodactyla	*Alces alces/Alces americanus*	40	0	2	39
Artiodactyla	*Cervus elaphus*	0	0	0	3
Artiodactyla	*Rangifer tarandus*	151	68	82	22
Artiodactyla	*Odocoileus hemionus*	74	54	66	0
Artiodactyla	*Odocoileus virginianus*	67	43	64	9
Artiodactyla	*Antilocapra americana*	0	1	0	0
Artiodactyla	*Bison bison*	23	7	8	1
Artiodactyla	*Ovis dalli*	24	0	0	3
Carnivora	*Puma yagouaroundi*	1	0	0	0
Carnivora	*Eira barbara*	0	0	0	1
Carnivora	*Ursus maritimus*	14	31	35	0
Carnivora	*Mephitis mephitis*	5	1	0	0
Carnivora	*Spilogale gracilis*	8	0	0	0
Carnivora	*Taxidea taxus*	6	11	11	1
Carnivora	*Leopardus pardalis*	11	2	2	11
Carnivora	*Nasua narica*	2	0	0	1
Carnivora	*Lycalopex fulvipes*	2	0	0	0
Carnivora	*Lycalopex gymnocercus*	2	0	0	0
Carnivora	*Neogale vison*	3	0	0	0
Carnivora	*Gulo gulo*	29	0	0	0
Carnivora	*Vulpes lagopus*	1	2	3	0
Carnivora	*Lynx canadensis*	11	30	33	1

Carnivora	*Lynx rufus*	77	48	65	0
Carnivora	*Leopardus guigna*	1	0	0	0
Carnivora	*Chrysocyon brachyurus*	19	0	0	0
Carnivora	*Lycalopex vetulus*	11	0	0	0
Carnivora	*Speothos venaticus*	2	0	0	1
Carnivora	*Lontra longicaudis*	4	0	0	0
Carnivora	*Lontra canadensis*	44	0	0	0
Carnivora	*Pekania pennanti*	35	32	34	0
Carnivora	*Pekania pennanti*	35	32	34	0
Carnivora	*Mustela nigripes*	3	0	0	0
Carnivora	*Canis lupus*	36	1	0	52
Carnivora	*Canis latrans*	6	24	41	1
Carnivora	*Cerdocyon thous*	9	0	0	1
Carnivora	*Vulpes vulpes*	5	16	16	0
Carnivora	*Vulpes macrotis*	8	0	0	0
Carnivora	*Vulpes velox*	17	0	0	0
Carnivora	*Tremarctos ornatus*	3	0	0	0
Carnivora	*Ursus americanus*	46	35	41	4
Carnivora	*Ursus arctos*	37	19	18	14
Carnivora	*Nasua nasua*	0	0	0	3
Carnivora	*Procyon lotor*	27	1	0	3
Carnivora	*Martes americana*	45	25	29	0
Carnivora	*Pteronura brasiliensis*	4	0	0	0
Carnivora	*Panthera onca*	41	0	0	8
Carnivora	*Puma concolor*	107	13	12	2
Chiroptera	*Aeorestes cinereus*	0	1	0	0
Chiroptera	*Myotis septentrionalis*	0	11	15	0
Chiroptera	*Lasionycteris noctivagans*	0	1	0	0
Chiroptera	*Myotis lucifugus*	0	34	65	0
Cingulata	*Euphractus sexcinctus*	0	0	0	1
Cingulata	*Priodontes maximus*	0	0	0	1
Cingulata	*Chaetophractus villosus*	0	0	0	1
Cingulata	*Dasypus novemcinctus*	7	0	0	1
Didelphimorphia	*Marmosops fuscatus*	0	0	0	1
Didelphimorphia	*Thylamys elegans*	0	0	0	1
Didelphimorphia	*Monodelphis brevicaudata*	0	0	0	1
Didelphimorphia	*Tlacuatzin canescens*	0	0	0	1
Didelphimorphia	*Marmosa paraguayana*	7	0	0	0
Didelphimorphia	*Marmosa demerarae*	0	0	0	1
Didelphimorphia	*Metachirus nudicaudatus*	0	0	0	1
Didelphimorphia	*Caluromys philander*	0	0	0	1
Didelphimorphia	*Didelphis aurita*	0	0	0	1
Didelphimorphia	*Marmosa robinsoni*	0	0	0	1
Didelphimorphia	*Didelphis virginiana*	11	0	0	2

Didelphimorphia	*Didelphis marsupialis*	0	0	0	3
Didelphimorphia	*Philander opossum*	0	0	0	2
Eulipotyphla	*Sorex cinereus*	0	0	0	1
Eulipotyphla	*Sorex arcticus*	0	0	0	1
Eulipotyphla	*Blarina brevicauda*	0	0	0	1
Lagomorpha	*Ochotona collaris*	0	0	0	1
Lagomorpha	*Sylvilagus audubonii*	2	0	0	0
Lagomorpha	*Brachylagus idahoensis*	4	0	0	0
Lagomorpha	*Lepus americanus*	42	30	39	1
Lagomorpha	*Sylvilagus aquaticus*	0	0	0	1
Lagomorpha	*Sylvilagus transitionalis*	0	2	3	0
Lagomorpha	*Ochotona princeps*	10	0	0	2
Lagomorpha	*Lepus europaeus*	0	0	0	1
Lagomorpha	*Oryctolagus cuniculus*	0	0	0	1
Lagomorpha	*Sylvilagus floridanus*	0	0	0	2
Perissodactyla	*Tapirus pinchaque*	0	0	0	1
Perissodactyla	*Tapirus bairdii*	2	0	0	4
Perissodactyla	*Tapirus terrestris*	1	0	0	2
Pilosa	*Tamandua tetradactyla*	0	0	0	1
Pilosa	*Myrmecophaga tridactyla*	2	0	0	2
Pilosa	*Cyclopes didactylus*	0	0	0	1
Pilosa	*Tamandua mexicana*	0	0	0	1
Pilosa	*Bradypus variegatus*	0	0	0	1
Primates	*Sapajus libidinosus*	0	0	0	9
Primates	*Ateles chamek*	0	0	0	18
Primates	*Alouatta sara*	0	0	0	3
Primates	*Callicebus dubius*	0	0	0	3
Primates	*Callithrix flaviceps*	0	0	0	4
Primates	*Cheracebus purinus*	0	0	0	7
Primates	*Sapajus xanthosternos*	0	0	0	1
Primates	*Plecturocebus brunneus*	0	0	0	1
Primates	*Alouatta pigra*	2	0	0	16
Primates	*Alouatta guariba*	0	0	0	14
Primates	*Callicebus ornatus*	0	0	0	1
Primates	*Alouatta macconnelli*	0	0	0	5
Primates	*Chiropotes albinasus*	0	0	0	1
Primates	*Plecturocebus cupreus*	0	0	0	20
Primates	*Cheracebus lugens*	0	0	0	1
Primates	*Mico intermedius*	0	0	0	1
Primates	*Saimiri boliviensis*	0	0	0	23
Primates	*Chiropotes utahickae*	0	0	0	5
Primates	*Pithecia aequatorialis*	1	0	0	0
Primates	*Plecturocebus discolor*	1	0	0	4
Primates	*Saguinus leucopus*	2	0	0	2

Primates	*Saguinus midas*	0	0	0	3
Primates	*Leontopithecus rosalia*	5	0	0	7
Primates	*Alouatta palliata*	4	0	0	14
Primates	*Alouatta belzebul*	4	0	0	8
Primates	*Aotus azarai*	0	0	0	4
Primates	*Cheracebus torquatus*	0	0	0	3
Primates	*Brachyteles arachnoides*	0	0	0	2
Primates	*Cacajao calvus*	0	0	0	7
Primates	*Pithecia irrorata*	0	0	0	10
Primates	*Brachyteles hypoxanthus*	0	0	0	4
Primates	*Saguinus niger*	0	0	0	4
Primates	*Aotus nancymaae*	0	0	0	10
Primates	*Cebus olivaceus*	0	0	0	4
Primates	*Saguinus bicolor*	4	0	0	0
Primates	*Aotus lemurinus*	0	0	0	1
Primates	*Pithecia pithecia*	0	0	0	3
Primates	*Saguinus geoffroyi*	3	0	0	21
Primates	*Callithrix geoffroyi*	0	0	0	7
Primates	*Aotus nigriceps*	0	0	0	7
Primates	*Aotus vociferans*	0	0	0	8
Primates	*Leontopithecus chrysomelas*	0	0	0	2
Primates	*Callithrix aurita*	0	0	0	3
Primates	*Callithrix penicillata*	1	0	0	5
Primates	*Leontopithecus chrysopygus*	0	0	0	5
Primates	*Pithecia monachus*	0	0	0	17
Primates	*Chiropotes chiropotes*	0	0	0	1
Primates	*Callicebus personatus*	0	0	0	7
Primates	*Cacajao melanocephalus*	0	0	0	2
Primates	*Saimiri oerstedii*	0	0	0	2
Primates	*Lagothrix lugens*	0	0	0	2
Primates	*Lagothrix poeppigii*	1	0	0	6
Primates	*Lagothrix cana*	0	0	0	10
Primates	*Saguinus labiatus*	0	0	0	3
Primates	*Callicebus nigrifrons*	0	0	0	3
Primates	*Callithrix kuhlii*	0	0	0	1
Primates	*Sapajus nigritus*	1	0	0	18
Primates	*Sapajus nigritus*	1	0	0	18
Primates	*Saguinus melanoleucus*	0	0	0	3
Primates	*Mico argentatus*	0	0	0	3
Primates	*Callithrix jacchus*	3	0	0	1
Primates	*Leontocebus fuscicollis*	0	0	0	38
Primates	*Saguinus mystax*	1	0	0	19
Primates	*Saguinus oedipus*	0	0	0	1
Primates	*Saguinus imperator*	0	0	0	7

Primates	*Cebuella pygmaea*	4	0	0	9
Primates	*Callimico goeldii*	0	0	0	2
Primates	*Alouatta caraya*	3	0	0	12
Primates	*Alouatta seniculus*	1	0	0	30
Primates	*Ateles belzebuth*	0	0	0	4
Primates	*Ateles geoffroyi*	0	0	0	10
Primates	*Ateles paniscus*	0	0	0	3
Primates	*Cebus albifrons*	0	0	0	32
Primates	*Sapajus apella*	0	0	0	47
Primates	*Cebus capucinus*	0	0	0	5
Primates	*Lagothrix lagotricha*	0	0	0	5
Primates	*Saimiri sciureus*	2	0	0	19
Primates	*Plecturocebus moloch*	1	0	0	0
Primates	*Chiropotes satanas*	0	0	0	7
Primates	*Pithecia albicans*	0	0	0	6
Primates	*Leontopithecus caissara*	2	0	0	1
Primates	*Saguinus nigricollis*	0	0	0	2
Primates	*Saguinus pileatus*	0	0	0	1
Primates	*Callicebus lucifer*	0	0	0	2
Primates	*Callicebus melanochir*	0	0	0	3
Primates	*Callicebus pallescens*	0	0	0	1
Primates	*Callicebus regulus*	0	0	0	4
Rodentia	*Tamiasciurus hudsonicus*	3	4	12	1
Rodentia	*Thomomys bottae*	0	0	0	2
Rodentia	*Dipodomys ordii*	0	0	0	2
Rodentia	*Peromyscus leucopus*	35	32	36	3
Rodentia	*Peromyscus maniculatus*	16	10	9	8
Rodentia	*Ondatra zibethicus*	31	0	0	0
Rodentia	*Bolomys urichi*	0	0	0	1
Rodentia	*Microtus californicus*	23	0	0	1
Rodentia	*Mus musculus*	15	0	0	0
Rodentia	*Rattus norvegicus*	20	0	0	0
Rodentia	*Hydrochoerus hydrochaeris*	2	0	0	2
Rodentia	*Octodon degus*	1	0	0	2
Rodentia	*Proechimys guairae*	0	0	0	2
Rodentia	*Dipodomys ingens*	5	0	0	0
Rodentia	*Neotoma mexicana*	0	0	0	2
Rodentia	*Neotoma micropus*	1	0	0	1
Rodentia	*Neotoma fuscipes*	4	0	0	0
Rodentia	*Dipodomys spectabilis*	0	0	0	1
Rodentia	*Dipodomys nelsoni*	0	0	0	1
Rodentia	*Microdipodops megacephalus*	0	3	3	0
Rodentia	*Cuniculus paca*	0	0	0	4
Rodentia	*Abrocoma bennettii*	0	0	0	2

Rodentia	*Microtus miurus*	0	0	0	2
Rodentia	*Tamias cinereicollis*	0	0	0	1
Rodentia	*Tamias ruficaudus*	29	0	0	0
Rodentia	*Tamias townsendii*	0	0	0	1
Rodentia	*Tamias umbrinus*	0	0	0	1
Rodentia	*Proechimys semispinosus*	0	0	0	5
Rodentia	*Proechimys guyannensis*	0	0	0	1
Rodentia	*Reithrodontomys raviventris*	2	0	0	0
Rodentia	*Sigmodon alstoni*	0	0	0	1
Rodentia	*Sciurus deppei*	0	0	0	1
Rodentia	*Oligoryzomys longicaudatus*	1	0	0	1
Rodentia	*Tamiasciurus douglasii*	0	11	14	1
Rodentia	*Peromyscus crinitus*	0	0	0	2
Rodentia	*Chaetodipus baileyi*	0	0	0	1
Rodentia	*Chaetodipus nelsoni*	0	0	0	1
Rodentia	*Handleyomys melanotis*	0	0	0	1
Rodentia	*Dasyprocta azarae*	0	0	0	1
Rodentia	*Zygodontomys brevicauda*	0	0	0	1
Rodentia	*Oryzomys couesi*	4	0	0	1
Rodentia	*Zapus hudsonius*	12	0	0	0
Rodentia	*Ctenomys australis*	3	0	0	0
Rodentia	*Ctenomys magellanicus*	2	0	0	0
Rodentia	*Clyomys laticeps*	1	0	0	0
Rodentia	*Neacomys tenuipes*	0	0	0	1
Rodentia	*Oecomys concolor*	0	0	0	1
Rodentia	*Syntheosciurus granatensis*	0	0	0	5
Rodentia	*Neotomodon alstoni*	0	0	0	1
Rodentia	*Peromyscus keeni*	0	0	0	1
Rodentia	*Geomys bursarius*	0	0	0	1
Rodentia	*Dipodomys deserti*	0	0	0	1
Rodentia	*Abrothrix longipilis*	0	0	0	3
Rodentia	*Abrothrix olivaceus*	0	0	0	3
Rodentia	*Nectomys squamipes*	15	0	0	0
Rodentia	*Reithrodontomys spectabilis*	4	0	0	0
Rodentia	*Reithrodontomys chrysopsis*	0	0	0	1
Rodentia	*Peromyscus perfulvus*	0	0	0	1
Rodentia	*Heteromys pictus*	0	0	0	1
Rodentia	*Microdipodops pallidus*	0	2	2	0
Rodentia	*Geomys breviceps*	4	0	0	1
Rodentia	*Ctenomys porteousi*	8	0	0	0
Rodentia	*Heteromys anomalus*	0	0	0	1
Rodentia	*Chinchilla lanigera*	0	0	0	1
Rodentia	*Dasyprocta punctata*	0	0	0	2
Rodentia	*Otospermophilus beecheyi*	3	3	3	0

Rodentia	*Neotoma macrotis*	1	0	0	0
Rodentia	*Thomomys talpoides*	0	0	0	2
Rodentia	*Oryzomys palustris*	3	0	0	1
Rodentia	*Osgoodomys banderanus*	0	0	0	1
Rodentia	*Perognathus flavus*	0	0	0	2
Rodentia	*Cavia aperea*	1	0	0	0
Rodentia	*Urocitellus richardsonii*	0	0	0	2
Rodentia	*Perognathus inornatus*	0	0	0	1
Rodentia	*Perognathus parvus*	0	0	0	1
Rodentia	*Chaetodipus penicillatus*	0	0	0	2
Rodentia	*Onychomys torridus*	0	0	0	1
Rodentia	*Perognathus fasciatus*	0	0	0	1
Rodentia	*Neotoma bryanti*	0	0	0	1
Rodentia	*Habromys simulatus*	2	0	0	0
Rodentia	*Dasyprocta leporina*	0	0	0	3
Rodentia	*Neotoma albigula*	0	0	0	2
Rodentia	*Neotoma floridana*	0	0	0	1
Rodentia	*Peromyscus eremicus*	0	0	0	2
Rodentia	*Peromyscus gossypinus*	0	0	0	1
Rodentia	*Peromyscus melanotis*	0	0	0	1
Rodentia	*Sigmodon hispidus*	0	0	0	2
Rodentia	*Peromyscus californicus*	0	0	0	3
Rodentia	*Trinomys iheringi*	0	0	0	1
Rodentia	*Myoprocta pratti*	0	0	0	1
Rodentia	*Ctenomys sociabilis*	1	0	0	0
Rodentia	*Reithrodontomys megalotis*	0	0	0	2
Rodentia	*Tamias minimus*	4	0	0	1
Rodentia	*Xerospermophilus spilosoma*	0	0	0	1
Rodentia	*Tamias striatus*	41	0	0	1
Rodentia	*Cynomys gunnisoni*	3	0	0	0
Rodentia	*Cynomys ludovicianus*	20	0	0	0
Rodentia	*Glaucomys sabrinus*	19	0	0	1
Rodentia	*Myodes gapperi*	0	0	0	2
Rodentia	*Oecomys bicolor*	0	0	0	1
Rodentia	*Tamias alpinus*	2	0	0	0
Rodentia	*Thomomys mazama*	0	0	0	1
Rodentia	*Castor canadensis*	9	0	0	0
Rodentia	*Hesperosciurus griseus*	0	0	0	3
Rodentia	*Urocitellus brunneus*	25	0	0	0
Rodentia	*Myodes rutilus*	0	0	0	1
Rodentia	*Ctenomys talarum*	0	0	0	1
Rodentia	*Calomys musculinus*	2	0	0	0
Rodentia	*Reithrodontomys fulvescens*	0	0	0	1
Rodentia	*Neotoma lepida*	0	0	0	1

Rodentia	*Phyllotis darwini*	0	0	0	2
Rodentia	*Phenacomys intermedius*	0	0	0	1
Rodentia	*Peromyscus boylii*	0	0	0	1
Rodentia	*Peromyscus aztecus*	0	0	0	1
Rodentia	*Peromyscus polionotus*	2	0	0	0
Rodentia	*Ctenomys haigi*	1	0	0	0
Rodentia	*Spalacopus cyanus*	1	0	0	0
Rodentia	*Ctenomys dorbignyi*	4	0	0	0
Rodentia	*Ctenomys roigi*	2	0	0	0
Rodentia	*Ctenomys sp.*	14	0	0	0
Rodentia	*Tamias amoenus*	8	0	0	1
Rodentia	*Glaucomys volans*	2	4	8	0
Rodentia	*Geomys attwateri*	0	0	0	1
Rodentia	*Callospermophilus lateralis*	0	0	0	1
Rodentia	*Lemmus trimucronatus*	4	0	0	0
Rodentia	*Dicrostonyx groenlandicus*	6	0	0	0
Rodentia	*Ctenomys minutus*	20	0	0	0
Rodentia	*Ctenomys perrensi*	3	0	0	0
Rodentia	*Ctenomys flamarioni*	3	0	0	0
Rodentia	*Ctenomys pearsoni*	2	0	0	0
Rodentia	*Ctenomys rionegrensis*	8	0	0	0
Rodentia	*Ctenomys torquatus*	4	0	0	0
Rodentia	*Hylaeamys megacephalus*	0	0	0	1
Rodentia	*Peromyscus truei*	0	0	0	1
Rodentia	*Rhipidomys mastacalis*	0	0	0	1
Rodentia	*Marmota flaviventris*	10	0	0	0
Rodentia	*Marmota vancouverensis*	3	0	0	0
Rodentia	*Dipodomys merriami*	0	0	0	2
Rodentia	*Zapus trinotatus*	9	0	0	0
Rodentia	*Cynomys leucurus*	0	0	0	1
Rodentia	*Cynomys parvidens*	11	0	0	0
Rodentia	*Xerospermophilus mohavensis*	13	0	0	0
Rodentia	*Xerospermophilus perotensis*	3	0	0	0
Rodentia	*Urocitellus parryii*	0	0	0	1
Rodentia	*Xerospermophilus polionotus*	1	0	0	0
Rodentia	*Sorex oreopolus*	0	0	0	1
Sirenia	*Trichechus inunguis*	2	0	0	0
Sirenia	*Trichechus manatus*	7	0	0	0

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