

**i. Title:** Multi-dimensional biodiversity hotspots and the future of taxonomic, ecological, and phylogenetic diversity: a case study of North American rodents

**ii. Authors:**

Tara M Smiley<sup>1,2</sup>; Pascal O. Title<sup>1,3</sup>; Miriam L. Zelditch<sup>4</sup>; Rebecca C. Terry<sup>2</sup>

Corresponding Author: Tara M. Smiley, Indiana University; email: [tmsmiley@iu.edu](mailto:tmsmiley@iu.edu)

**iii. Institutional Affiliation:**

<sup>1</sup>Environmental Resilience Institute, Indiana University, Bloomington, Indiana

<sup>2</sup>Department of Integrative Biology, Oregon State University, Corvallis, Oregon

<sup>3</sup>Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan

<sup>4</sup>Museum of Paleontology, University of Michigan, Ann Arbor, Michigan

**iv. Acknowledgements:**

Funding for this research was provided by the National Science Foundation Postdoctoral Research Fellowship in Biology – Biological Collections, Division of Biological Infrastructure, Grant #1612002 awarded to TMS. Additional funding for POT came from the University of Michigan’s Rackham Predoctoral Fellowship. This project was also supported by the Environmental Resilience Institute, funded by Indiana University’s Prepared for Environmental Change Grand Challenge initiative. We are grateful to Diego Verzi and Nate Upham for constructive comments that improved this manuscript. We thank Jesse Laney, Morah West, Elia deJesus, Juniper Grimes, and Bridget Regan at Oregon State University for assistance with data collection.

**v. Biosketch:**

Tara M. Smiley led this work as an NSF postdoctoral research fellow at Oregon State University with co-author Rebecca Terry. Smiley has recently moved to the Environmental Resilience Institute at Indiana University. She is interested in biodiversity patterns across space and time in

**This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/geb.13050](https://doi.org/10.1111/geb.13050)**

This article is protected by copyright. All rights reserved

relation to landscape and climate change. Her research integrates studies from modern and fossil records of mammals in North America, focusing on biogeography, ecomorphology, and diversification history.

Author Manuscript

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31

DR. TARA MAGNOLIA SMILEY (Orcid ID : 0000-0001-5940-1755)

Article type : Research Papers

**GEB Title:** Multi-dimensional biodiversity hotspots and the future of taxonomic, ecological, and phylogenetic diversity: a case study of North American rodents

**Running Title:** Patterns of multi-dimensional diversity

**Keywords:** Biodiversity Gradients, Ecological Diversity, North America, PhyloEndemism, Rodentia, Species Richness

**Abstract:**

**Aim**

We investigate geographic patterns across taxonomic, ecological, and phylogenetic diversity to test for spatial (in)congruency and identify aggregate diversity hotspots in relation to present land-use and future climate. Simulating extinctions of imperiled species, we demonstrate where losses across diversity dimensions and geography are predicted.

**Location**

North America

**Time period**

Present-day, future

**Major taxa studied**

Rodentia

**Methods**

32 Using geographic range maps for rodent species, we quantified spatial patterns for eleven  
33 dimensions of diversity: taxonomic (species, range-weighted), ecological (body size, diet,  
34 habitat), phylogenetic (mean, variance, and nearest-neighbor patristic distances, phylogenetic  
35 distance, genus-to-species ratio) and phyloendemism. We tested for correlations across  
36 dimensions and used spatial residual analyses to illustrate regions of pronounced diversity. We  
37 aggregated diversity hotspots in relation to land-use and climate-change predictions and  
38 recalculated metrics following extinctions of IUCN-listed imperiled species.

39

#### 40 **Results**

41 Topographically-complex western North America hosts high diversity across multiple  
42 dimensions: phyloendemism and ecological diversity exceed predictions based on taxonomic  
43 richness and phylogenetic variance patterns indicate steep gradients in phylogenetic turnover.  
44 While an aggregate diversity hotspot emerges in the west, spatial incongruence exists across  
45 diversity dimensions at the continental scale. Notably, phylogenetic metrics are uncorrelated  
46 with ecological diversity. Diversity hotspots overlap with land-use and climate change, and  
47 extinctions predicted by IUCN status are unevenly distributed across space, phylogeny, or  
48 ecological groups.

49

#### 50 **Main conclusions**

51 Comparison of taxonomic, ecological, and phylogenetic diversity patterns for North American  
52 rodents clearly shows the multifaceted nature of biodiversity. Testing for geographic patterns and  
53 (in)congruency across dimensions of diversity facilitates investigation into underlying ecological  
54 and evolutionary processes. The geographic scope of this analysis suggests that several explicit  
55 regional challenges face North American rodent fauna in the future. Simultaneous consideration  
56 of multi-dimensional biodiversity allows us to assess what critical functions or evolutionary  
57 history we might lose with future extinctions and maximize the potential of our conservation  
58 efforts.

59

60

## INTRODUCTION

61

62

Striking patterns and hotspots of biodiversity in relation to climatic, elevational, and  
geographic gradients are common across the globe (Badgley & Fox, 2000; Myers, Mittermeier,

63 Mittermeier, da Fonseca, & Kent, 2000; Antonelli et al., 2018). This biodiversity encompasses  
64 many aspects of biological complexity, including not only variation in the number of species  
65 present, but also variation in species' ecological attributes, functional roles within ecosystems,  
66 and phylogenetic history (Pagel, May, & Collie, 1991; Purvis & Hector, 2000; Stevens & Tello,  
67 2014). Approaches to quantifying and characterizing variation in biodiversity have increased  
68 dramatically (Rosauer, Laffan, Crisp, Donnellan, & Cook, 2009; Tucker et al., 2017), and it is  
69 now well accepted that integrating across multiple dimensions of biodiversity (e.g., species  
70 richness, phylogenetic, functional ecological) both enriches our understanding of the origin and  
71 maintenance of biodiversity patterns (Davies & Buckley, 2011; Fritz & Rahbek, 2012; Rosauer  
72 & Jetz, 2014) and informs strategies for biodiversity conservation (Humphries, Williams, &  
73 Vane-Wright, 1995; Myers et al., 2000; Dirzo & Raven 2003; Mace, Gittleman, & Purvis, 2003;  
74 Cumming & Child, 2009; Chiarucci, Bacaro, & Scheiner, 2011; Stein et al., 2018). While species  
75 richness is often not a one-for-one surrogate for other dimensions of biodiversity (Safi et al.,  
76 2011; Stevens, Tello, & Gavilanez, 2013; Fergnani & Ruggiero, 2015), the degree to which  
77 geographic variation across multiple dimensions of diversity represents redundant information  
78 versus unique biological patterns remains unresolved (Orme et al., 2005; Devictor et al., 2010;  
79 Huang, Stephens, & Gittleman, 2012; but see Tucker & Cadotte, 2013).

80       Where tested, mismatches between taxonomic richness, phylogenetic diversity, and  
81 functional ecological diversity, exist for some, but not all groups and settings (Devictor et al.,  
82 2010; Stevens & Tello, 2014). Variation in the correlation strength between different dimensions  
83 of biodiversity may correspond with environmental conditions, regional landscape and  
84 biogeographic history, and the composition of the regional species pool (Safi et al., 2011; Davies  
85 & Buckley, 2012; Fritz & Rahbek, 2012; Mazel et al., 2014; Villalobos, Olalla-Tárraga,  
86 Cianciaruso, Rangel, & Diniz-Filho, 2017). Thus identification of areas of spatial (in)congruency  
87 between various dimensions of biodiversity provides powerful insight into the underlying  
88 processes of species diversification (speciation and extinction), biogeographic dynamics (range  
89 shifts and immigration), and community assembly. Biodiversity hotspots that emerge from the  
90 intersection of multiple axes of diversity may additionally represent special conservation targets,  
91 where taxonomic and ecological diversity, phylogenetic history, and ecosystem function can be  
92 simultaneously preserved (Orme et al., 2005; Stein et al., 2018). Demonstrating how these  
93 hotspots are threatened – either through imminent species loss (Barnosky et al., 2011; Ceballos et

94 al., 2015), high velocity of climate change (Loarie et al., 2009; Burrows et al., 2011), or  
95 pervasive land-use changes (Sala et al., 2000) – provides additional context for the prioritization  
96 of biological conservation.

97 Here we assess the geographic patterns of multiple dimensions of species biodiversity  
98 within North American rodents, emphasizing four broad categories of diversity: (1) taxonomic,  
99 (2) geographic range size, (3) ecological, and (4) phylogenetic diversity. By quantifying these  
100 different dimensions, we ask the following questions: (1) Which geographic regions harbor the  
101 highest taxonomic, ecological, and phylogenetic diversity? (2) Are there hotspots of multi-  
102 dimensional diversity? (3) What are the geographic patterns of (in)congruency among  
103 dimensions? (4) Which regions and dimensions are likely to be most affected by current  
104 environmental and climatic change, including predicted species loss? In addressing these  
105 questions, we do not expect to find congruence among all dimensions of biodiversity, and we  
106 expect landscape properties and history to play determining roles in both spatial congruency and  
107 biodiversity hotspots. For example, we predict that the mountains will be regions of high  
108 diversity across multiple axes as a result of both ecological processes (e.g., species  
109 accommodation across heterogeneous habitats) and evolutionary processes (e.g., speciation  
110 across geographic barriers) (e.g., Simpson, 1964; Badgley et al., 2017). However, phylogenetic  
111 diversity need not mirror ecological diversity, as physiographic barriers to gene flow may result  
112 in geographically restricted, but not necessarily ecologically disparate, species. We also predict  
113 that regions with a shared geologic and climate history will exhibit similar patterns regardless of  
114 topographic complexity. For example, we expect both high- and low-relief northern latitudes to  
115 have low species richness due to recent glaciation, low ecological diversity due to strong  
116 environmental filtering, but potentially high phylogenetic variance as taxa from different rodent  
117 families dispersed into the region following glacial retreat. Finally, we expect regions with small  
118 species ranges and highly endemic faunas to be threatened across multiple biodiversity axes by  
119 environmental and climate change. This may not always align with the regions experiencing the  
120 highest rates of climate change; however, in less seasonal climates, even a small amount of  
121 climate change may be detrimental or even insurmountable to already geographically-restricted  
122 taxa (e.g., Deutsch et al., 2008).

123 Study System—The reasons for selecting rodents for a large-scale and multi-faceted  
124 analysis of biodiversity are many. North American rodents represent almost half of continental

125 mammalian species richness and ~5.5% of global extant mammal diversity (Burgin, Colella,  
126 Kahn, & Upham, 2018; Mammal Diversity Database, 2019). Nearly 20% of North American  
127 species are currently threatened (Wilson & Reeder, 2005; IUCN, 2017). By looking at North  
128 America, we are approximating the Nearctic; however, choosing to 1) include all of Mexico  
129 based on a priori knowledge from the paleontological record, in addition to modern distributions  
130 of diversity, demonstrating its importance for rodent evolution and 2) exclude Greenland,  
131 because of its low diversity and present-day ice cover.

132 We focus on this clade because of its excellent phylogenetic coverage (Fabre, Hautier,  
133 Dimitrov, & Douzery, 2012), well-documented body size and geographic range size information,  
134 and detailed species-level descriptions of dietary and habitat preferences. A within-rodent  
135 approach allows us to more finely partition diet and habitat categories than possible for broader  
136 taxonomic studies. North America taxa in particular have detailed information at the species  
137 level that are lacking or inconsistently known in other continental settings with high rodent  
138 diversity (IUCN, 2017). The biogeographic history of this clade has also been well studied in  
139 North America over multiple spatio-temporal scales (Riddle, Jezkova, Hornsby, & Matocq,  
140 2014). Over evolutionary timescales, species richness, ecological diversity, and diversification  
141 rates for rodents have varied in relation to climate and landscape changes (Finarelli & Badgley,  
142 2010; Zelditch, Li, Tran, & Swiderski, 2015; Badgley et al., 2017; Samuels & Hopkins, 2017;  
143 Smiley, 2018). Over Quaternary timescales, range dynamics, dietary shifts, extinctions,  
144 extirpations, and re-colonizations have been documented for rodents in relation to glacial-  
145 interglacial climate oscillations (Lessa, Cook & Patton, 2003; Barnosky, Koch, Feranec, Wing,  
146 & Shabel, 2004; Blois, McGuire, & Hadly, 2010; Grayson, 2011; Jezkova, Olah-Hemmings, &  
147 Riddle, 2011; Terry, Li, & Hadly, 2011; Riddle et al., 2014; Terry, Guerre, & Taylor, 2017).  
148 Finally, over the past century, the influence of climate, land-use, and vegetative change has  
149 further altered present-day rodent communities (Moritz et al., 2008; Rowe, Terry, & Rickart,  
150 2011; Rowe & Terry, 2014; Terry & Rowe, 2015; Walsh et al., 2016). Rodents are additionally  
151 of broad interest, because they serve as a critical food base for many other vertebrate groups  
152 (Wolf & Ripple, 2016). Their top-down effect on plant communities is likewise critical; soil  
153 aeration, seed dispersal and burial are all key functions that rodents play across ecosystem types  
154 (Laundré & Reynolds, 1993; Chambers & MacMahon, 1994). Rodents therefore represent

155 bellwethers of larger-scale biological change, with benefits of small-mammal conservation  
156 cascading up and down the food web.

157 Together, these characteristics make North American rodents an ideal case study to  
158 highlight which aspects of biodiversity – including potentially hidden dimensions and regions of  
159 diversity – are most vulnerable under present and future land-use and climate change due to  
160 anthropogenic influences. Because of links between diversity and stability of ecosystem function  
161 (Tilman & Downing, 1994; Thibaut & Connolly, 2013; Schindler, Armstrong, & Reed, 2015),  
162 understanding the geographic congruence of diversity measures in the context of regional  
163 landscape properties is critical for informing policy and management initiatives at a continental  
164 scale (Cadotte, Dinnage, & Tilman, 2012). Furthermore, understanding whether hotspots of  
165 biodiversity today represent accumulations of evolutionarily distant taxa, the in situ generation of  
166 new species, or some combination of both is important for prioritizing regions for biodiversity  
167 conservation (e.g., Mischler, Knerr, González-Orozco, Thornhill, Laffran & Miller, 2014).  
168 Finally, evaluating whether ecosystems and biodiversity hotspots can remain functionally intact  
169 even with the loss of certain species, is important for looking forward to the coming century  
170 when species loss is inevitable.

171

## 172 MATERIALS AND METHODS

### 173 Analytical Approach

174 To illustrate multiple dimensions of biodiversity within North American rodents, we  
175 generated maps of diversity patterns for 350 species using 100 x 100 km equal-area grid cells on  
176 a North America Albers Conic equal area projection (following recommendations regarding  
177 scale dependence in Hurlbert & Jetz, 2007; Jarzyna & Jetz, 2018). This includes all North  
178 American taxa with range data and excludes extinct and recently synonymized taxa (see  
179 Supporting Information in Appendix S1 for more details). We used the ‘rgeos’ (Bivand &  
180 Rundel, 2018), ‘raster’ (Hijmans, 2017), and ‘sp’ (Pebesma & Bivand, 2005; Bivand, Pebesma,  
181 & Gomez-Rubio, 2013) packages in R to extract and manipulate geographic data as well as to  
182 generate biodiversity maps. All statistical analyses were performed in the R statistical and  
183 computing environment (R Development Core Team, 2017).

184 Taxonomic diversity—Within each grid cell, species lists were compiled based on  
185 overlapping geographic ranges of extant, native species as classified and provided by the IUCN



186 Red List database (IUCN, 2017). To be considered within cell, a species must span at least 10%  
187 of a grid cell, unless it is the only grid cell that species occupies; in which case, it was also  
188 retained for our analysis. We quantified taxonomic diversity, also known as species richness, as  
189 the number of species co-occurring within each grid cell.

190 Ecological diversity—To capture the diversity of functional roles that species play within  
191 their local ecosystems, we collected three primary types of ecological information: i) body size,  
192 ii) diet category, and iii) habitat affinity (Supporting Tables S1.1 and S1.2). Species-level trait  
193 data were compiled from the literature, refined, and cross-checked using a variety of sources,  
194 including volumes on North American mammals (Wilson & Ruff, 1999; Kays & Wilson, 2009),  
195 comprehensive body size databases and references (Silva & Downing, 1995; Smith et al., 2007),  
196 and previous studies (Badgley & Fox, 2000).

197 Because body size has been shown to reflect many aspects of a species' ecology and play  
198 a major role in community structure, function, and dynamics (Brown & Nicoletto, 1991; Smith et  
199 al., 2004; Ernest, 2005), we assessed the number and evenness of body size classes present  
200 within grid cells across the continent. We binned species into ten groups according to Jenks  
201 natural break classification for the logged distribution of body sizes across all North American  
202 species (Supporting Table S1.2) using the 'classInt' package in R (Bivand, 2018). We also  
203 binned species on the basis of dietary functional group (13 categories total, including granivores,  
204 frugivores, insectivores, and succulent specialists) and habitat affinity (30 categories total,  
205 including forest, coastal, tundra, shrubland, and freshwater habitats), both of which are axes  
206 along which niche partitioning and competitive exclusion can occur in rodent communities (e.g.,  
207 Brown & Lieberman, 1973; Price & Brown, 1983). While an individual species may span several  
208 diet and habitat categories, we chose the dominant category represented in the literature and  
209 quantified ecological diversity based on the number of categories filled per grid cell. We then  
210 calculated the evenness of all three ecological measures using Simpson's evenness metric, or the  
211 Probability of Interspecific Encounter (PIE), as formulated by Hurlbert (1971). Species-  
212 depauperate grid cells (i.e., less than five species present) were excluded from analyses.

213 Range-related diversity patterns—We first calculated the mean and minimum  
214 geographic range area of species present in a grid cell. We then combined taxonomic richness  
215 and range data to calculate range-weighted taxonomic richness, a metric that assigns greater

216 proportional weight to spatially-restricted than geographically-widespread species and reflects  
217 endemism (Crisp, Laffan, Linder, & Monro, 2001; Rosauer & Jetz, 2014).

218 Phylogenetic diversity patterns—To investigate phylogenetic diversity for rodents, we  
219 used the maximum likelihood phylogeny generated by Fabre et al. (2012) from a supermatrix of  
220 mitochondrial and nuclear genes (obtained via personal communication). As North American  
221 rodents do not form a monophyletic group, we pruned the phylogeny to our dataset; 99% of  
222 species for which geographic distributions were available were also present in the phylogeny ( $n$   
223 = 348; see Supporting Appendix S1 for additional taxonomic considerations). We used four  
224 metrics to quantify phylogenetic diversity (Faith, 1992; Tucker et al., 2017) for the assemblages  
225 occupying each 100 x 100 km grid cell: i) the mean of all pairwise branch lengths (mean patristic  
226 distance, MPD); ii) the mean of pairwise shortest branch lengths (patristic nearest neighbor  
227 distance, PNN); iii) the variance of pairwise branch lengths (variance in patristic distance, VPD);  
228 and, iv) Faith's Phylogenetic Diversity (PD). MPD and PNN describe the distribution of  
229 divergence dates among species, with PNN specifically highlighting recent divergences. The use  
230 of MPD is further justified because it is not mathematically correlated with richness. VPD  
231 describes the regularity of species composition, or how evenly evolutionary history is distributed  
232 among species within a set (Tucker et al., 2017). In conjunction with ecological diversity, VPD  
233 provides useful information about the overall structure of biodiversity across spatial scales.  
234 While known to correlate strongly with species richness (Fritz & Rahbek, 2012), Faith's PD was  
235 also included and describes the accumulated evolutionary history represented by a set of species  
236 (Faith, 1992). We additionally used a purely taxonomic approach and calculated genus-to-  
237 species ratios (GSR) for each suite of species to demonstrate the distribution of shallower  
238 (species-level) divergences relative to deeper (genus-level) divergences.

239 Finally, we integrated range size data with phylogenetic branch lengths to calculate  
240 phylogenetic endemism (PE; Rosauer et al., 2009), a metric that identifies regions that host both  
241 phylogenetically isolated and spatially restricted biota (Rosauer & Jetz, 2014; Gonzalez-Orozco  
242 et al., 2016). All phylogenetic analyses were conducted in R, using the 'ape' package (Paradis,  
243 Claude, & Strimmer, 2004).

244 Multi-dimensional hotspots and imperiled-species assessment—To assess congruency in  
245 spatial patterns of taxonomic, ecological, and phylogenetic diversity, we applied a Dutilleul's t-  
246 test (Dutilleul, Clifford, Richardson, & Hemon, 1993), which is a modified test of association

247 between spatially autocorrelated variables, using the ‘SpatialPack’ package in R (Osorio,  
248 Vallejos, & Cuevas, 2014). Due to the large number of comparisons conducted, we applied a  
249 Bonferroni sequential adjustment to test for significant relationships (Rice, 1989). For diversity  
250 metrics that were significantly correlated (i.e., adjusted p-value < 0.05) or exhibited a clear linear  
251 relationship with species richness, we also mapped residuals to identify areas where ecological or  
252 phylogenetic diversity differ from expectations based on species richness in a cell (e.g., Fritz &  
253 Rahbek, 2012; Fergnani & Ruggiero, 2015).

254 To identify regions that represent high multi-dimensional biodiversity, we generated  
255 aggregate hotspot maps (e.g., Stein et al., 2018). Hotspots of species richness comprised cells  
256 within the top 10% for taxonomic richness, range-weighted taxonomic richness, and  
257 phylogenetic endemism. Likewise, hotspots of ecological richness comprised cells within the top  
258 10% for body size, diet, and habitat richness. Finally, regions that harbor elevated deep diversity  
259 (top 10% of MPD and VPD) and elevated shallow diversity (bottom 10% of PNN and GSR)  
260 were identified as phylogenetic diversity hotspots.

261 Given that multi-dimensional hotspots likely represent regions of particular conservation  
262 concern, we also relate hotspots to the current and future geography of habitat transformation  
263 (e.g., Sala et al., 2000) and climate change velocity (Loarie et al., 2009; Burrows et al., 2011).  
264 Mapping the geographic distribution of biodiversity hotspots in relation to regions of high human  
265 impact and rapidly shifting climates serves to identify regions disproportionately at risk  
266 (Ohlemüller et al., 2008; Garcia et al., 2014; Finnegan et al., 2015). We assigned human-  
267 impacted habitats to cells for which the maximum land-cover type was cropland, pasture, or  
268 urban using a business-as-usual scenario of modern (1970) and future (2080) land use from the  
269 IMAGE 3.0 database (<https://data.knmi.nl/datasets>). We determined regions of high climate  
270 velocity using the GCM ensemble-based forward velocity datasets for moderate (RCP4.5) and  
271 high (RCP8.5) emissions scenarios (Carroll, Lawler, Roberts, & Hamann, 2015;  
272 <https://adaptwest.databasin.org>). Forward velocity refers to the rate (km/yr) at which organisms  
273 in the current landscape would have to migrate in order to maintain constant climate conditions  
274 in 2080. We designated cells as having a high velocity if they were within the 90<sup>th</sup> percentile of  
275 velocity values under the moderate emissions scenario.

276 Finally, to demonstrate potential losses of biodiversity, be it taxonomic, ecological, or  
277 phylogenetic, we simulated future extinctions by culling currently imperiled rodent species and

278 reanalyzing diversity patterns. We defined imperiled species as those categorized by the IUCN  
279 Red List as Critically Endangered, Endangered or Vulnerable. To demonstrate the impact of  
280 species loss, we compared both geographic diversity patterns and distributions of diversity  
281 metrics across taxa for the current biodiversity state versus a future ‘post’-extinction state.

282

### 283 Sensitivity Analyses

284 Using the following approaches, we additionally tested the sensitivity of our analysis to  
285 two factors: 1) influence of wide-ranging species and 2) choice of phylogeny.

286 Wide-ranging species—To test the sensitivity of these metrics to wide-ranging species  
287 (Jetz & Rahbek, 2002), we performed additional analyses that excluded species with geographic  
288 range sizes above the 90% quantile, such as *Castor canadensis* and *Peromyscus maniculatus*. A  
289 total of 35 species with ranges greater than 2,620,000 km<sup>2</sup> were excluded and all analyses were  
290 re-run to test for statistical over-representation of wide-ranging taxa in correlation tests of spatial  
291 congruence across different dimensions of biodiversity. We note that range-weighted diversity  
292 and phylogenetic endemism measures mitigate the potential impacts of wide-ranging taxa by  
293 down-weighting those taxa in diversity calculations.

294 Phylogeny choice—To test the sensitivity of phylogenetic metrics to tree choice, we  
295 conducted all phylogenetic analyses (MPD, VPD, PNN, PD, PE) using an alternative molecular-  
296 based 4254-taxon mammal phylogeny from Faurby and Svenning (2015a), updated to version  
297 1.2 in the Phylacine database (Faurby, Davis, Pedersen, Schowanek, Antonelli, & Svenning,  
298 2018). From a posterior distribution of 1000 trees, we generated the maximum clade credibility  
299 tree for use in our analyses, calculated with the R package ‘phangorn’ v2.5.5 (Schliep, 2011) and  
300 pruned it to North American rodent taxa. When reanalyzing geographic patterns of phylogenetic  
301 diversity, 36 taxa were excluded due to lack of phylogenetic information in the Faurby and  
302 Svenning tree.

303

304

## RESULTS

305 Taxonomic richness varies considerably over the North American continent, ranging from fewer  
306 than five species per 100 x 100 km grid cell (Arctic) to over 45 species per cell (intermontane  
307 west) (Figure 1a). The species-rich western region (including the Rocky Mountain Front Range,  
308 the Great Basin and the Sierra Madres) also hosts species with small mean and minimum range

309 sizes (Figure 1b). Small geographic ranges contribute to elevated range-weighted taxonomic  
310 richness (Figure 1c) and phylogenetic endemism (Figure 3e), highlighting regions with small  
311 ranging and phylogenetically isolated taxa along the Pacific Coast and in Mexico.

312 Ecological richness metrics (based on body size, diet, and habitat affinity) demonstrate  
313 similar east-to-west gradients in diversity. The number of body size classes varies with longitude  
314 and latitude, peaking in the Great Basin and southern Mexico (Figure 2a). High dietary richness  
315 is found in southwest deserts of the USA, while habitat richness is highest in western regions  
316 with increased topographic relief and habitat heterogeneity (Figure 2b-c). In contrast, ecological  
317 evenness varies little and remains high across the continent for all three metrics (Fig 2d-f),  
318 suggesting that communities are composed of equally-filled body size, diet, and habitat  
319 categories within the local environment. A few notable exceptions are low (0.5-0.7) body size  
320 evenness localized to the Baja Peninsula and southeastern California and a moderate increase  
321 (from 0.6 to 0.8) in dietary evenness from Great Plains to intermontane west communities.

322 Each phylogenetic diversity metric reveals a distinct pattern across North America  
323 (Figure 3). While MPD varies little with geography (Figure 3a), VPD (Figure 3b) is lowest in the  
324 Great Plains (low relief, environmentally homogeneous) and parts of the Great Basin and  
325 southwestern deserts (high relief, environmentally heterogeneous), indicating relatively uniform  
326 distributions of branch lengths independent of absolute branch length in these regions. PNN and  
327 GSR are both low in the intermontane west of the USA, indicating concentrations of recently-  
328 diverged taxa in these regions spanning multiple genera (Figure 3c-d). In contrast, low PNN  
329 values in the eastern USA do not correspond with low GSR values, where fewer species are  
330 found within genera, but these species tend to have at least one within-genus nearest neighbor.  
331 Faith's PD tightly follows the species richness geographic pattern, with highest values along the  
332 southern Rocky Mountain Front Range. Finally, strong gradients in phylogenetic diversity exist  
333 in Canada due to low taxonomic richness, especially in the Arctic.

334 To assess whether different dimensions of biodiversity represent novel or redundant  
335 information, we also tested the spatial congruence of these patterns and, using a Bonferoni  
336 sequential correction, found significant correlations between less than 15% of the diversity  
337 metric pairs (Figure 4a, Supporting Table S1.3). Lack of significant correlation between metrics  
338 is reflected in non-congruent geographic gradients at both continental and regional scales. The  
339 notable exception is Faith's PD which exhibits significant positive correlations ( $r = 0.94$ ,

340 adjusted p-value = 0.001) and similar spatial patterns with species richness and its correlates,  
341 including body size, diet, and habitat richness. The residuals from regression models of  
342 ecological diversity against species richness also exhibit spatial variation, including lower than  
343 expected body size richness in the taxonomically diverse desert southwest (Figure 4b) and higher  
344 than expected dietary richness in the Great Plains and intermontane west (Figure 4c). Likewise,  
345 habitat richness was lower than expected in the Sierra Madres, but higher than expected along  
346 strong regional ecotones (e.g., Northern Great Basin, Rocky Mountain Front Range). While not  
347 significantly correlated using a Bonferroni sequential adjustment, higher species richness  
348 generally corresponded with higher range-weighted species richness and phylogenetic  
349 endemism, and lower GSR at the continental scale ( $r > 0.8$ ). These three metrics include species  
350 richness in their calculation; however, correlation need not be expected (Tucker & Cadotte,  
351 2013; Reig 1989) and spatial differences in gradients, especially the location of high richness,  
352 exists among these metrics (Figure 1 and Fig 3e,f). Phylogenetic endemism was generally  
353 uncorrelated with other phylogenetic metrics and therefore reveals novel information about  
354 geographic patterns of species relatedness and diversity. Finally, phylogenetic diversity metrics  
355 were only weakly correlated, suggesting each metric also reflects a unique aspect of clade  
356 diversity and history.

357       Sensitivity tests that excluded wide-ranging species revealed where our analysis might be  
358 influenced by the over-representation of species with ranges spanning much of the continent.  
359 While we find an increase in the number of significantly correlated relationships among diversity  
360 dimensions (Supporting Table S1.4), the spatial patterns remain similar (Supporting Figure  
361 S1.1). Losses of ecological diversity patterns at high latitudes and in eastern USA are notable,  
362 where taxonomic lists are comprised of numerous wide-ranging taxa. In comparison with the full  
363 dataset, MPD, PNN and VPD also differ in spatial patterns in these northern and eastern regions;  
364 however, phylogenetic diversity hotspots remain in the intermontane West and Mexico, where  
365 species ranges are smaller on average (Figure 1b). Measures of phylogenetic diversity calculated  
366 from the phylogenies of Fabre et al. (2012) and Faurby and Svenning (2015a) exhibited highly  
367 correlated patterns ( $r > 0.89$ ;  $p \ll 0.001$ ). Therefore, all results and discussion herein pertain to  
368 the Fabre et al. (2012) phylogeny; for further information about tree choice and interpretation of  
369 phylogenetic diversity metrics across trees, see Figure S1.2 in the Supporting Information. In

370 combination, these sensitivity analyses show that the results of the (in)congruency analysis  
371 remain robust to the influence of wide-ranging taxa and choice of phylogeny.

372 Despite their different spatial patterns at the continental scale, high diversity values  
373 across multiple metrics are roughly congruent, concentrated in the western USA and Mexico.  
374 Aggregate hotspots of taxonomic (raw and range-weighted) richness and phylogenetic endemism  
375 (Figure 5a) overlap broadly with aggregate hotspots of ecological diversity along body size, diet,  
376 and habitat axes (Figure 5b). In contrast, hotspots of shallow (bottom 10% PNN and GSR) and  
377 deep (top 10% MPD and VPD) phylogenetic diversity are not spatially congruent (Figure 5c).  
378 Summing across all biodiversity hotspots, the Great Basin, the southwest deserts, and the Sierra  
379 Madres capture a high degree of taxonomic, ecological, and phylogenetic diversity (Figure 5d).  
380 Comparing multi-dimensional biodiversity hotspots with regions that have undergone human-  
381 driven land-use change (agriculture, pasture, or urbanization) in the last century (Figure 5e)  
382 reveals considerable overlap: 33.3% and 34.4% of hotspot area overlaps with highly affected  
383 regions due to modern and future human land-use, respectively. Overlap of multi-dimensional  
384 diversity hotspots with regions predicted to experience rapidly changing climates over the  
385 coming decades may also be high, depending on the emissions scenario (Figure 5f); 10.4% and  
386 37.9% of hotspot area overlaps with high climate change velocity under moderate and high CO<sub>2</sub>  
387 emission scenarios, respectively.

388 Under hypothetical future extinctions of imperiled IUCN species due to these and other  
389 drivers, the impact of species loss on taxonomic, ecological, or phylogenetic diversity is  
390 geographically concentrated along the western coast of the USA and Mexico, in southern  
391 Mexico, and in Florida (Figure 6a-b). Typically, only a single species went extinct in a cell;  
392 however, up to three species were lost in southern California and up to six species were lost  
393 within regions of southern Mexico (Supporting Figure S1.3). For cells that experienced  
394 extinction, we found significant differences in several diversity metrics pre- and post-extinction  
395 (Supporting Figure S1.4). Lost species represent a mix of deep and shallow divergence events,  
396 and all but one had restricted geographic range areas (Figure 6a-b). The loss of ecological  
397 diversity varied in geographic extent and intensity, with body size, dietary and habitat richness  
398 loss in certain regions (e.g., southwestern Mexico) but not in others (e.g., Florida) during species  
399 extinction (Figure 6c). Ecological loss was distributed across all body size classes and dietary  
400 categories, but was most pronounced among mid-size rodents and insectivore and carnivore

401 specialists (Figure 6d). Lost species span several different habitat categories; in particular, a  
402 large percentage (64%) of species occupying particularly fragmented and fragile cloud forest  
403 habitats of central Mexico are imperiled.

404

405

## DISCUSSION

406 Our comparison of taxonomic, ecological, and phylogenetic diversity patterns for North  
407 American rodents clearly shows the multifaceted nature of biodiversity. Familiar patterns emerge  
408 from this analysis, such as a strong, positive relationship between topographic complexity and  
409 taxonomic diversity (Simpson, 1964; Badgley & Fox, 2000; Antonelli et al., 2018; Badgley,  
410 Smiley, & Cable, 2018; Quintero and Jetz, 2018). Yet this study adds several new dimensions of  
411 diversity that, in conjunction, suggest potential mechanisms driving elevated species richness in  
412 topographically complex regions and reduced diversity in others.

413

### **Patterns and hotspots of multi-dimensional diversity**

415 As predicted, we find that the influence of topography and environmental heterogeneity  
416 extends beyond species richness to novel dimensions of biodiversity (Figure 5d): high-relief  
417 landscapes and heterogeneous habitats harbor high diversity in rodent body size, dietary, and  
418 habitat classes (Figure 3a-c, Figure 5b), as well as phylogenetic endemism (Figure 3e, Figure  
419 5a). Furthermore, rodent communities in these regions comprise species that span a broader  
420 range of evolutionary history than elsewhere on the continent (Figure 2, Figure 5c). Thus high  
421 regional diversity in western North America not only fuels high local diversity during  
422 community assembly (Ricklefs, 1987; Mittelbach & Schemske, 2015; Ernest, Brown, Thibault,  
423 White, & Goheen, 2008), but also highlights the importance of topographically complex  
424 landscapes as potential species source regions (e.g., “out-of-the-mountains” model; Badgley et  
425 al., 2017) and refugia (Holderegger, Thiel-Egenter, & Whittaker, 2009; Grayson, 2011) over  
426 evolutionary timescales.

427 Previous work has attributed the high taxonomic richness in topographically complex  
428 regions to ecological, evolutionary, and geohistorical mechanisms (Simpson, 1964; Badgley et  
429 al., 2017). We find high dietary and habitat richness (Figure 3a,c), even after removing the effect  
430 of taxonomic diversity (Figure 5c,d), in intermontane regions, adding support to a species  
431 accommodation model for explaining macroecological patterns, with tighter species packing



432 along steep environmental and elevational gradients (Kotler & Brown, 1988; Coblentz &  
433 Riitters, 2004). Evolutionary hypotheses additionally propose that topographic relief increases  
434 the likelihood of population-level divergence and ultimately speciation events, especially during  
435 intervals of climate change and corresponding range shifts (Riddle et al., 2014; Jezkova et al.,  
436 2011; Machac, Graham, & Storch, 2017; Barnosky & Carrasco, 2002; Flantua and Hooghiem  
437 2018; Quintero and Jetz, 2018). Modern and fossil records have demonstrated that tectonically  
438 active landscapes promote diversification pulses and high regional species richness (Cracraft,  
439 1985; Hoorn et al., 2010; Finarelli & Badgley, 2010; Moen & Morlon, 2014; Mulch, 2016;  
440 Smiley, 2018). Thus, isolated mountain ranges and intervening basins can generate and maintain  
441 high regional diversity through increases in both deep and shallow divergence events.

442         These evolutionary and geohistorical hypotheses are supported by our results, and notable  
443 patterns in phylogenetic diversity arise in relation to topographic complexity. In particular,  
444 although MPD does not change substantially across most of the continent, steep gradients in  
445 VPD in the intermontane west indicate high turnover in the phylogenetic makeup of species  
446 assemblages. High variance could reflect the combined influence of speciation, extinction, and  
447 immigration into intermontane regions during intervals of climate change (Davies & Buckley,  
448 2011). Patterns of PNN and GSR additionally illustrate hotspots of ‘young’ diversity (low  
449 values) found across the heterogeneous habitats of western USA and the Mexican highlands  
450 (Figure 3c,f). Thus, our findings are consistent with mountains as sites of recent radiations and  
451 current hotspots of neoendemism (Davis, Koo, Conroy, Patton, & Moritz, 2008; Badgley et al.,  
452 2018; Antonelli et al., 2018). Topographically complex landscapes can furthermore preserve  
453 ‘old’ lineages through various mechanisms (e.g., refugia effect). We find a concentration of  
454 phylogenetically distinct and long-branched taxa with small geographic ranges leading to  
455 increased phyloendemism in the western USA and Mexican highlands (Figure 3e).

456         While our focus on the intermontane west stems from identifying and examining multi-  
457 dimensional hotspots, equally interesting hypotheses could be proposed and tested for regions  
458 that harbor low diversity across multiple dimensions, such as the Great Plains. Likewise, this  
459 analysis is applicable to other topographically-complex landscapes globally. Next steps might  
460 include assessing patterns in other mountain ranges and taxonomic groups to 1) investigate  
461 whether concordant patterns emerge and 2) test if similar ecological and evolutionary drivers of  
462 high diversity in relation to topographic relief and history are at play. In addition, at the spatial

463 scale of our analysis, we are not able to distinguish whether taxa co-occur locally or experience  
464 high turnover along elevational gradients within our grid cells. Incorporating elevational range  
465 data to assess patterns of taxonomic, ecological, and phylogenetic diversity along topographic  
466 gradients (e.g., Quintero and Jetz, 2018) would be a promising future direction.

467

### 468 **Incongruence in geographic patterns sheds light on potential drivers of diversity gradients**

469 While regions of topographic complexity harbor high multi-dimensional biodiversity,  
470 spatial congruence across diversity metrics is not the dominant trend (Figure 4), as predicted and  
471 previously demonstrated at other spatial and taxonomic scales (Devictor et al., 2010; Safi et al.,  
472 2011; Huang et al., 2012; Fritz & Rahbek, 2012; Stevens & Tello, 2014; Stein et al., 2018).

473 While many factors may contribute to spatial incongruency, the geographic scope of our study  
474 allows us to address whether processes of faunal assembly appear localized or if general patterns  
475 emerge across regional scales. Towards this aim, we highlight three observations from our  
476 results: 1) regional diversity is shaped by processes of speciation, immigration, and extinction,  
477 and the relative contribution of each may lead to incongruency in some regions but not in others;  
478 2) phylogenetic and ecological diversity measures are not interchangeable; and, 3) diversity and  
479 evenness patterns in the desert southwest depart from regional patterns.

480 Our findings, especially the wedge-shaped relationship between taxonomic richness and  
481 MPD, PNN, and VPD, reflect high variability across local and regional assemblages in  
482 phylogenetic diversity, especially among taxonomically impoverished regions. As predicted, the  
483 Arctic exhibits high phylogenetic variance, in part due to the temporally and spatially  
484 asynchronous immigration and refugia histories of disparate phylogenetic lineages into the  
485 region following the end-Pleistocene glacial retreat that, via extinctions, ‘wiped’ the slate clean  
486 for incoming taxa (e.g., Lessa et al., 2003; Lyons, 2003; Shafer, Cullingham, Côté, & Coltman,  
487 2010). This history of extinction and assembly via immigration contrasts sharply with the pattern  
488 of high phylogenetic variance found elsewhere on the continent (e.g., desert southwest) due to a  
489 combination of recently diverged taxa (which likely diverged in situ) co-existing with deep,  
490 endemic lineages. Further examination of the lack of correspondence between different  
491 biodiversity measures and phylogenetic diversity residuals (Supporting Figure S1.5) may help to  
492 illuminate the diversification and immigration processes that help generate and maintain  
493 biodiversity gradients.

494 Early emphasis on phylogenetic diversity rested on the assumption that closely related  
495 species exhibit high functional overlap due to phylogenetic signal (Faith, 1992). Thus, regions of  
496 high phylogenetic diversity, especially phylogenetic variance, were assumed to capture a higher  
497 degree of ecological diversity and promote functional stability of ecosystems (Cadotte et al.,  
498 2012). However, we and others (e.g., Fritz & Purvis, 2010, Devictor et al., 2010), do not find that  
499 expected correspondence between phylogenetic and ecological diversity (Figure 4), especially  
500 across space (Figure 2 and 3), stressing the importance of placing these measures in geographic  
501 context. Furthermore, phylogenetic diversity measures are not interchangeable across our  
502 dataset, nor are ecological diversity measures, each representing distinct information about the  
503 evolutionary makeup and history of a local assemblage (Figs. 3 and 5a,c). Spatial structure  
504 within the residuals of ecological versus taxonomic richness demonstrate regions of ‘functional’  
505 deficits (Safi et al., 2011; Fergnani & Ruggiero, 2015), or areas where more species are  
506 presumably packed into a smaller ecological space (negative residuals in Figure 4b-d).  
507 Conversely, regions with high ecological diversity for the number of species present (positive  
508 residuals in Figure 4b-d) may reflect communities that fill more of the available body size,  
509 dietary or habitat space.

510 A good example of how geographic incongruency informs ecological hypotheses across  
511 spatial scales is in the desert southwest. Rodent communities in the desert southwest have long  
512 been used to test hypotheses centered on community ecology, such as competitive exclusion,  
513 niche partitioning, and energetics and resource utilization (e.g., Bowers & Brown, 1982; Holling,  
514 1992; Ernest, 2005); however, our analysis reveals that the granivore-dominated communities  
515 occurring in this region may follow different assembly rules than elsewhere in North America.  
516 Ecological evenness varies surprisingly little at the continental scale, suggesting that despite  
517 highly structured richness patterns, ecological roles are partitioned relatively uniformly across  
518 body size and functional ecological classes, regardless of how densely packed those classes are  
519 locally. In contrast, the southern desert region – characterized by mosaic habitats, high-relief  
520 terrain, and elevated taxonomic richness and turnover (Figure 1) – departs notably from these  
521 patterns. Body size richness, in particular, is lower than expected based on the number of species  
522 present (Figure 4b) and strikingly low body size evenness is found in the desert southwest and  
523 around the Gulf of California (Figure 2d). Integrating across different dimensions of diversity  
524 elucidates important geographic variation in the structure of faunal assemblages and

525 demonstrates that the drivers of local patterns (e.g., size-mediated utilization of resources  
526 facilitating coexistence of highly competitive desert granivores; Bowers & Brown, 1982; Ernest,  
527 2005) may not be generalizable at broader spatial scales. Assembling a multi-dimensional  
528 viewpoint of biodiversity gradients and their drivers based on North American rodents is a useful  
529 starting point, and broadening the taxonomic or geographic scope of analyses (e.g., Fergnani &  
530 Ruggiero, 2015) will help us to understand the generality of patterns emerging from this well-  
531 known and diverse group.

532

### 533 **Conserving species, ecological diversity, and evolutionary history**

534 The threats to biodiversity are numerous, with losses portended not only for taxonomic  
535 richness, but also for evolutionary history and ecosystem functioning (Dirzo & Raven, 2003;  
536 Cardinale et al., 2006; Dobson et al., 2006; Davis & Buckley, 2011; Stein et al., 2018). Analyses  
537 that consider multiple dimensions of biodiversity thus allow us to ask what we might be losing,  
538 aside from a raw species count, with future extinctions, and therefore maximize the potential of  
539 our conservation efforts. It is clear that phylogenetic and ecological diversity promote ecosystem  
540 stability and resilience in myriad ways (Cadotte et al., 2012; Davies, Urban, Rayfield, Cadotte, &  
541 Peres-Neto, 2016). Greater diversity in existing form and function, as well as in evolutionary  
542 lability and depth, across species within communities translate to a broader range of potential  
543 niches and thus increased capacity of communities and their species to respond to changing  
544 climates, environments, and resource availability (Hooper et al., 2005; Purvis, Cardillo, Grenyer,  
545 & Collen, 2005). Preserving regions with deep and shallow phylogenetic diversity and diverse  
546 evolutionary modes (e.g., Davies, 2015) furthermore protects both past evolutionary heritage and  
547 future potential centers of species generation. Conservation aimed at protecting (phylo-)endemic  
548 species is additionally critical, as these species capture biodiversity components with little  
549 representation elsewhere in terms of geographic and phylogenetic space (Rosauer & Jetz, 2014;  
550 Myers et al., 2000; Ceballos & Ehrlich, 2006).

551 Biodiversity scenarios can be forecast over the coming century based on the current  
552 trajectory of individual taxa (i.e., IUCN Red List Status). We find that future losses felt along  
553 phylogenetic and ecological axes are concentrated in the western USA, and notably throughout  
554 Mexico, with the highest losses experienced among geographically-restricted species (Figure 6a-  
555 c). While certain small rodent clades are at risk of being lost entirely to extinction, imperiled

556 species are distributed throughout the rodent phylogeny (Figure 6b). Likewise, loss of ecological  
557 diversity is not spread evenly across body size, dietary, and habitat categories. While most  
558 ecological categories experience some degree of loss, the greatest impacts are felt by mid-size  
559 rodents, rodents at higher-trophic levels, and rodents occupying higher elevation habitats in the  
560 tropics (Figure 6d). These findings provide further evidence that not all species are at equal risk  
561 of extinction (Ohlemüller et al., 2008; Ripple et al., 2017). Non-uniform species loss across  
562 ecological categories influences ecological evenness as well, possibly compounding negative  
563 impacts on ecosystem function (Chiarucci et al., 2011). In particular, the loss of functional  
564 redundancy places greater burden on the remaining members of the community, with potentially  
565 more disastrous consequences if those species also then go extinct (Tilman, Wedin, & Knops,  
566 1996; Tilman, Knops, & Wedin, 1997).

567 Looking to the coming century via projections of land-use and climate change, we find  
568 that anthropogenic impacts will be felt in many regions that represent multi-dimensional  
569 biodiversity hotspots today (Figure 5d-e). It is important to note that today's snapshot of  
570 biodiversity has already been highly influenced by anthropogenic drivers over both long (Faurby  
571 & Svenning, 2015b; Smith, Elliott-Smith, Lyons, & Payne, 2018) and shallow (Parmesan &  
572 Yohe, 2003; Weinzettel, Vačkář, & Medková, 2018) timescales. Climate change velocity, or the  
573 rate at which species would have to move to maintain their current climate conditions, reveals  
574 especially looming challenges to species response. Not surprisingly, these effects will be more  
575 intense and geographically widespread under higher emission scenarios (Figure 5f; Carroll et al.,  
576 2015). In addition to the direct influence of land-use and climate stressors, indirect and  
577 synergistic interactions among different local, regional, and global change factors may lead to  
578 unpredictable biodiversity outcomes (Sala et al., 2000; Newbold et al., 2016). For example, with  
579 habitat fragmentation and increased urbanization, species are increasingly left without suitable  
580 corridors at the regional scale to track thermal niche requirements during climate change  
581 (Bennett, 2003; McGuire, Lawler, McRae, Nuñez, & Theobald, 2016). Thus, as the window of  
582 opportunity for action begins to close, understanding the geographic context of our existing  
583 biodiversity hotspots, and the multiple dimensions of biodiversity that they represent, is key to  
584 safeguarding them into the future.

585

586 DATA ACCESSIBILITY

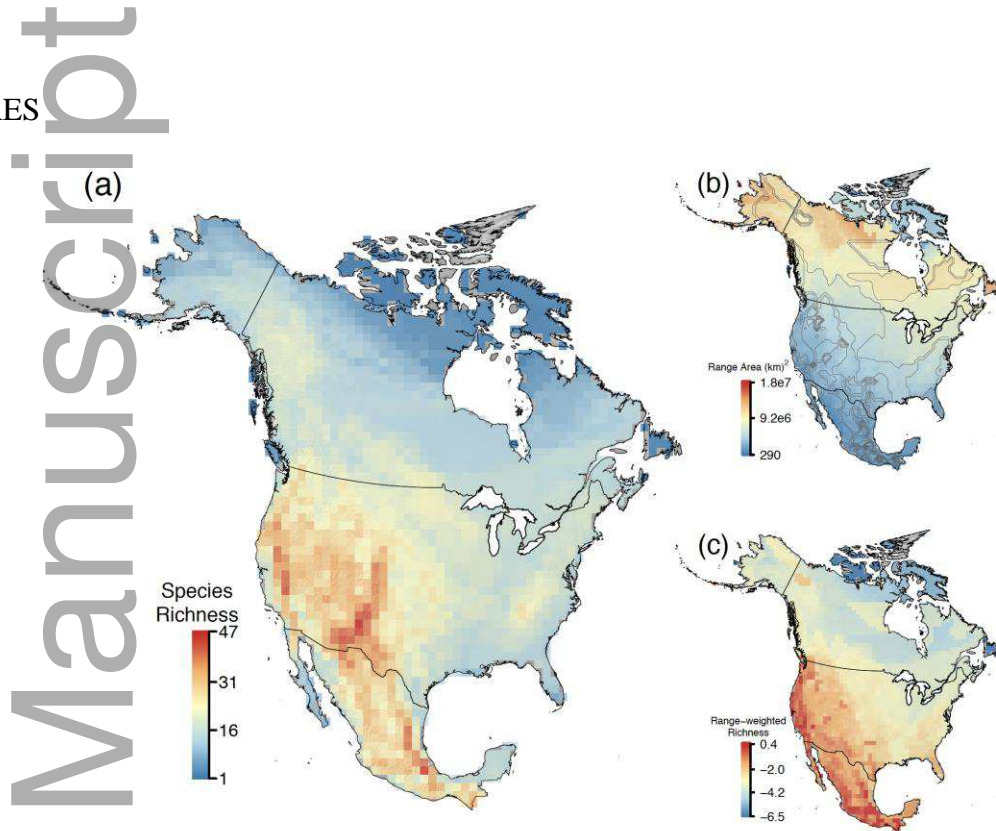
587 Data associated with this manuscript are openly available in the Dryad repository at  
588 <https://doi.org/10.5061/dryad.4xgxd2559>.

589

590

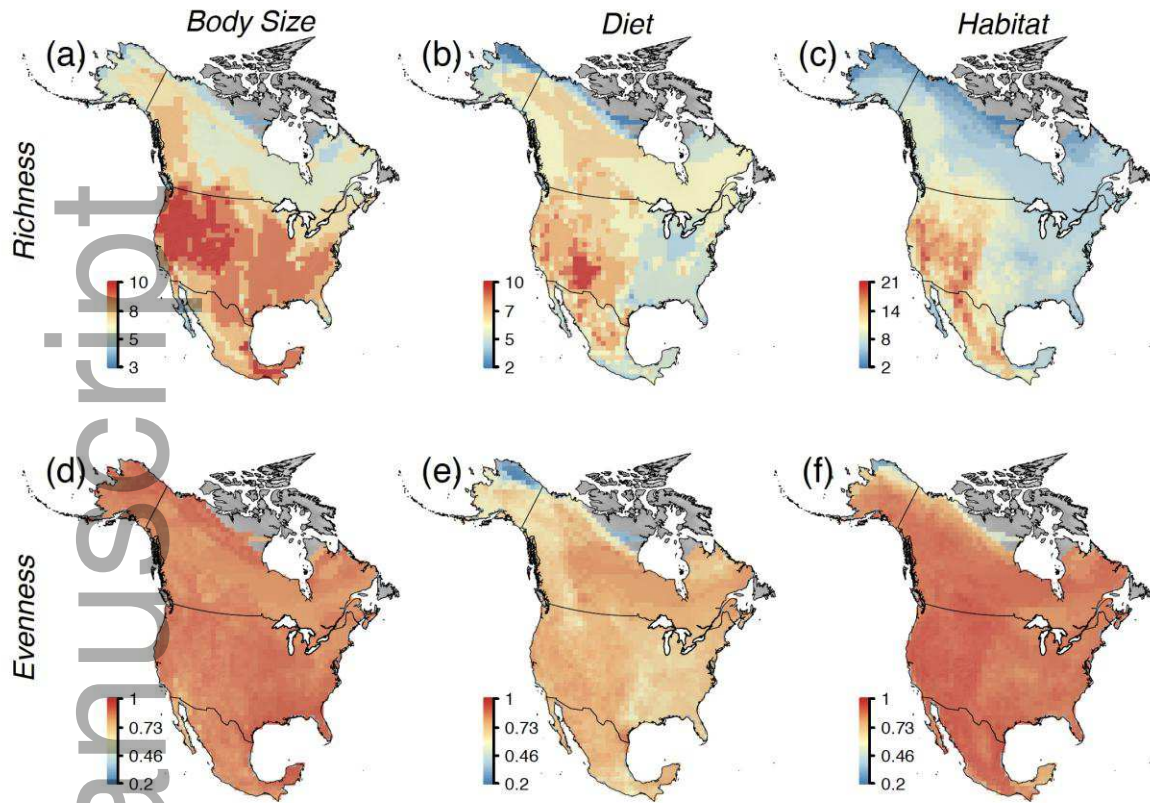
591

592 FIGURES



593

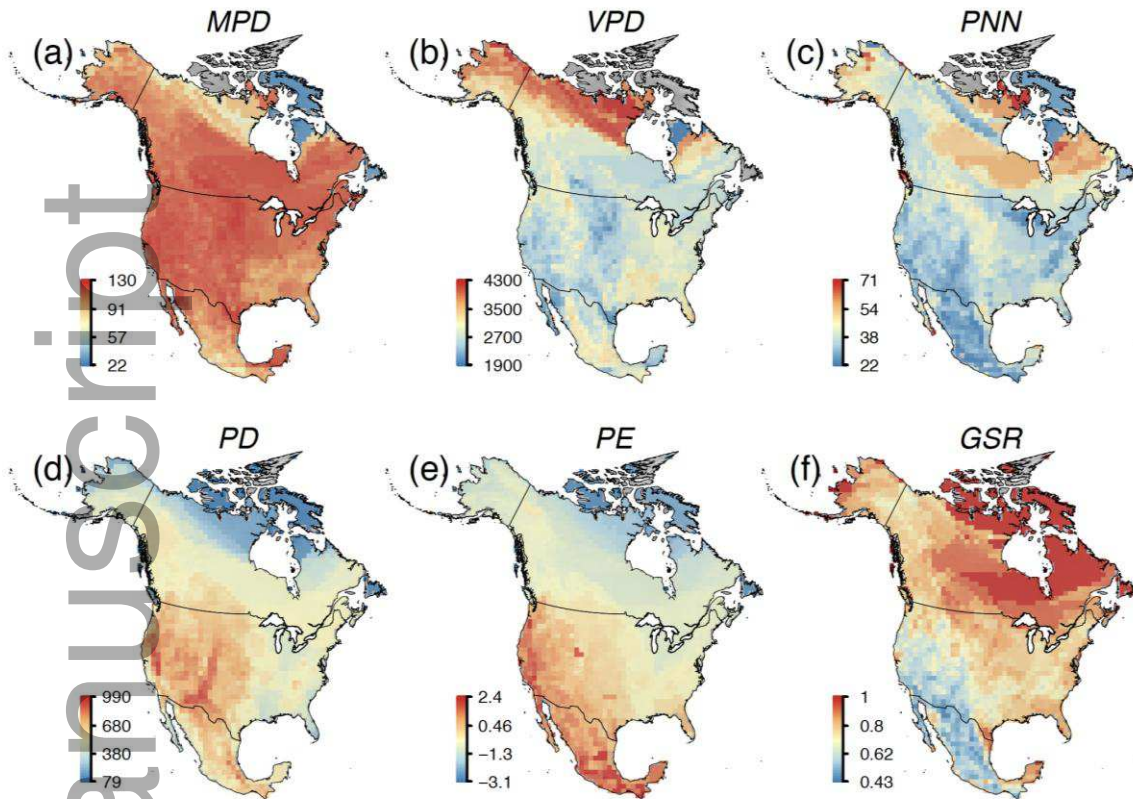
594 **Figure 1.** Maps of North American rodent diversity metrics: (a) taxonomic richness, (b) mean  
595 geographic range size for each suite of species present within a grid cell overlain by contour lines  
596 representing the log of the minimum geographic range size to illustrate a higher concentration of  
597 smaller rodent ranges in the western US and Mexico, and (c) range-weighted taxonomic richness  
598 (log scale).



599

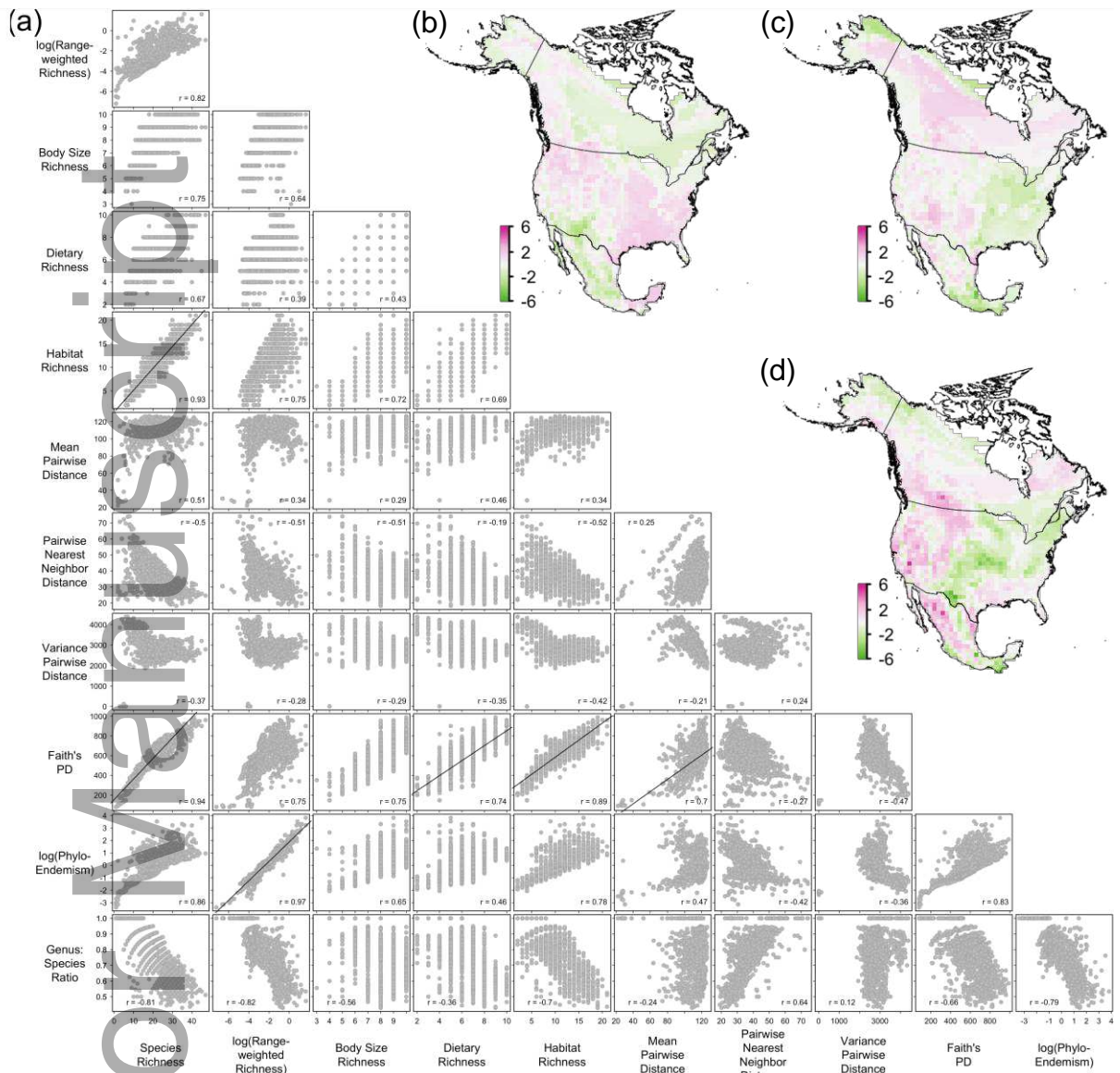
600 **Figure 2.** For North American rodent species, categorical richness (a-c) and Simpson's evenness  
 601 (d-f) for three indices of ecological diversity, calculated for cells with a minimum of five species  
 602 present. Indices include body size class, determined using Jenks natural breaks optimization from  
 603 the North American rodent body-size distribution (a, d), diet category (b, e), and habitat affinity  
 604 (c, f).

605

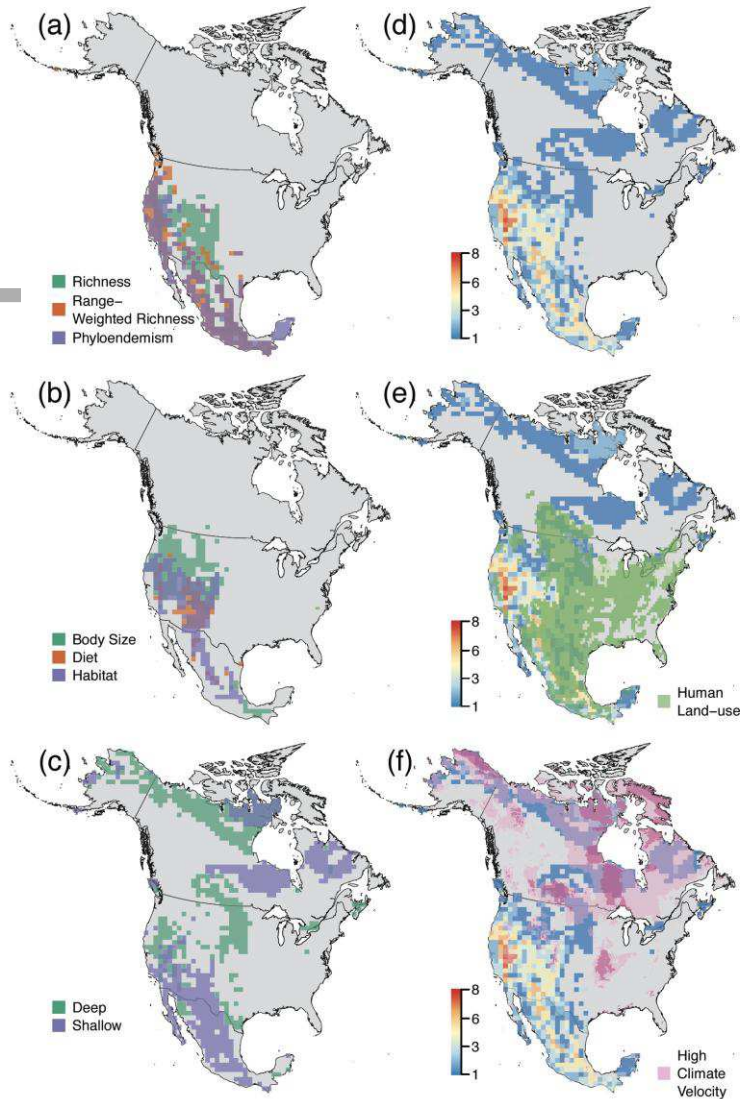


606  
 607 **Figure 3.** Six phylogenetic diversity metrics calculated for each suite of North American rodents  
 608 present in a 100 x 100 km grid cell: (a) mean pairwise distance (MPD), (b) variance of pairwise  
 609 distances (VPD), (c) mean pairwise nearest neighbor distance (PNN), (d) Faith's phylogenetic  
 610 diversity (PD), (e) phylogenetic endemism (PE; log scale), and (d) genus-to-species ratio (GSR).

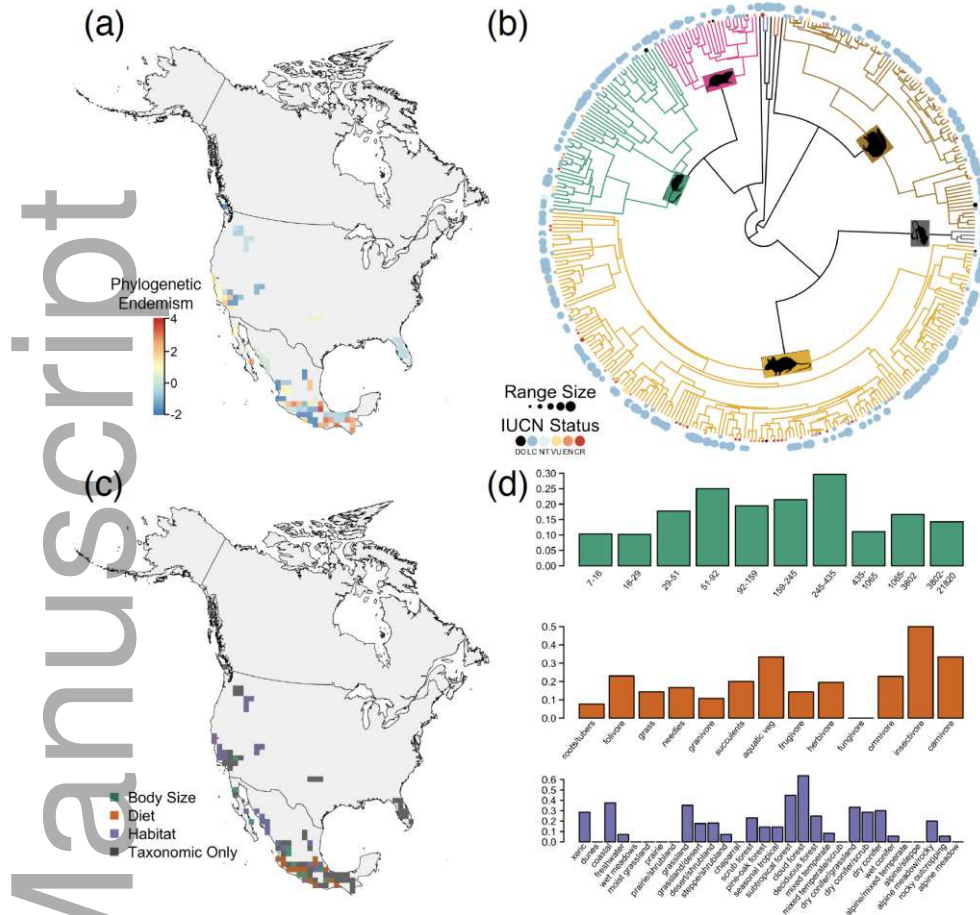




611  
 612 **Figure 4.** (a) Pairwise correlations among biodiversity metrics. Correlation coefficients ( $r$ ) and  
 613 significance are determined using a Dutilleul's t-test, with linear regression lines shown for  
 614 significant correlations, according to a Bonferroni sequential correction (adjusted p-value <  
 615 0.05), only. (b-d): Maps of residuals from a regression model of (b) body size richness, (c)  
 616 dietary category richness, and (d) habitat affinity richness against taxonomic richness.



617  
 618 **Figure 5.** Multi-dimensional hotspots for cells with the top 10% of values for: (a) taxonomic  
 619 richness, log(range-weighted taxonomic richness), and log(phylogenetic endemism); and, (b)  
 620 ecological diversity, including body size, diet, and habitat richness. (c) Multi-dimensional  
 621 hotspots of shallow (bottom 10% PNN and GSR) and deep (top 10% MPD and VPD)  
 622 phylogenetic diversity. For (a-c), the hotspot locations are unique to each metric; however;  
 623 colors are transparent to illustrate regions of hotspot overlap. (d) Aggregate (sum) hotspot map  
 624 for all diversity metrics. This map is overlain by: (e) cells dominated by human land use  
 625 (cropland, pasture, urban) in 1970 and projected into 2080 (each a translucent green layer) and  
 626 (f) cells experiencing high climate velocity (now to 2080) under moderate and high emissions  
 627 scenarios (each a translucent pink layer, the high emissions scenario being more widespread).



628  
 629 **Figure 6.** The geographic regions facing the greatest change under future species extinction are  
 630 represented by (a) the difference in phylogenetic endemism after the removal of imperiled taxa,  
 631 where imperiled refers to Vulnerable (VU), Endangered (EN), and Critically Threatened (CR)  
 632 IUCN status. (b) Phylogenetic endemism captures branch length data from the phylogenetic tree  
 633 of rodents (pruned from Fabre et al., 2012 to North American taxa used in this study) and  
 634 geographic range area. In the phylogeny, branch colors correspond to the major rodent families,  
 635 circle size at the end of each branch is relative to species' range area (points are jittered to better  
 636 see variation), and color indicates species' IUCN status. (c) Cells with species extinction are  
 637 shown in dark gray, with cells that further experience loss in ecological diversity (loss of one or  
 638 more body size classes, diet or habitat categories) are colored accordingly. (d) The proportion  
 639 lost for each ecological category after extinction of imperiled species within those cells.

640 REFERENCES

641

642 Antonelli, A., Kissling, W. D., Flantua, S. G. A., Bermúdez, M. A., Mulch, A., Muellner-Riehl,  
643 A. N., ... Hoorn, C. (2018). Geological and climatic influences on mountain biodiversity.  
644 Nature Geoscience, 11, 718–725.

645 Badgley, C., & Fox, D. L. (2000). Ecological biogeography of North American mammals:  
646 species density and ecological structure in relation to environmental gradients. Journal of  
647 Biogeography, 27, 1437–1467.

648 Badgley, C., Smiley, T. M., Terry, R., Davis, E. B., DeSantis, L. R. G., Fox, D. L., ... Yanites,  
649 B. J. (2017). Biodiversity and Topographic Complexity: Modern and Geohistorical  
650 Perspectives. Trends in Ecology and Evolution, 32, 211–226.

651 Badgley, C., Smiley, T. M., & Cable, R. (2018). Mountains, Climate and Mammals. In Hoorn,  
652 C., Perrigo, A. & Antonelli, A. (Eds.), Mountains, Climate and Biodiversity, (pp. 201–216).  
653 Hoboken, NJ: Wiley-Blackwell.

654 Barnosky, A. D., & Carrasco, M.A. (2002). Effects of Oligo-Miocene global climate changes on  
655 mammalian species richness in the northwestern quarter of the USA. Evolutionary Ecology  
656 Research, 4, 811–841.

657 Barnosky, A. D., Koch, P. L., Feranec, R. S., Wing, S. L., & Shabel, A. B. (2004). Assessing the  
658 causes of late Pleistocene extinctions on the continents. Science, 306, 70–75.

659 Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T.B., ... Ferrer,  
660 E. A. (2011). Has the Earth’s sixth mass extinction already arrived? Nature, 470, 51–57.

661 Bennett, A. F. (2003). Linkages in the landscape: the role of corridors and connectivity in  
662 wildlife conservation (2<sup>nd</sup> ed.). IUCN.

663 Bivand, R. S (2018). ‘classInt’: Choose univariate class intervals. R package version 0.3-1.

664 Bivand, R. S., Pebesma, E. & Gomez-Rubio, V. (2013). Applied spatial data analysis with R (2<sup>nd</sup>  
665 ed.). New York, NY: Springer.

666 Bivand, R. S., & Rundel, C. (2018). ‘rgeos’: Interface to geometry engine – open source  
667 (“GEOS”). R package version 0.4-2.

668 Blois, J. L., McGuire, J. L., & Hadly, E.A. (2010). Small mammal diversity loss in response to  
669 late-Pleistocene climatic change. Nature, 465, 771–774.

670 Bowers, M. A., & Brown, J. H. (1982). Body size and coexistence in desert rodents: Chance or  
671 community structure? Ecology, 63, 391–400.

- 672 Brown, J. H., & Lieberman, G. A. (1973). Resource Utilization and Coexistence of Seed Eating  
673 Desert Rodents in Sand Dune Habitats. *Ecology*, 54, 788–797.
- 674 Brown, J. H., & Nicoletto, P. F. (1991). Spatial Scaling of Species Composition - Body Masses  
675 of North-American Land Mammals. *The American Naturalist*, 138, 1478–1512.
- 676 Burgin, C. J., Colella, J. P., Kahn, P. L., & Upham, N. S. (2018). How many species of mammals  
677 are there? *Journal of Mammalogy*, 99, 1–11.
- 678 Burrows, M. T., Schoeman, D. S., Buckley, L. B., Moore, P., Poloczanska, E. S., Brander, K. M.,  
679 ... Richardson, A.J. (2011). The pace of shifting climate in marine and terrestrial  
680 ecosystems. *Science*, 334, 652–655.
- 681 Cadotte, M. W., Dinnage, R., & Tilman, D. (2012). Phylogenetic diversity promotes ecosystem  
682 stability. *Ecology*, 93, S223–S233.
- 683 Cardinale, B. J., Srivastava, D. S., Emmett Duffy, J., Wright, J. P., Downing, A. L., Sankaran,  
684 M., & Jouseau, C. (2006). Effects of biodiversity on the functioning of trophic groups and  
685 ecosystems. *Nature*, 443, 989–992.
- 686 Carroll, C., Lawler, J. J., Roberts, D. R., & Hamann, A. (2015). Biotic and climatic velocity  
687 identify contrasting areas of vulnerability to climate change. *PLoS ONE*, 10, e0140486–18.
- 688 Ceballos, G., & Ehrlich, P. R. (2006). Global mammal distributions, biodiversity hotspots, and  
689 conservation. *Proceedings of the National Academy of Sciences*, 103, 19374–19379.
- 690 Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. M.  
691 (2015). Accelerated modern human-induced species losses: Entering the sixth mass  
692 extinction. *Science Advances*, 1, e1400253–6.
- 693 Chambers, J. C., & MacMahon, J.A. (1994). A day in the life of a seed - movements and fates of  
694 seeds and their implications for natural and managed systems. *Annual Review of Ecology  
695 and Systematics*, 25, 263–292.
- 696 Chiarucci, A., Bacaro, G., & Scheiner, S.M. (2011). Old and new challenges in using species  
697 diversity for assessing biodiversity. *Philosophical Transactions of the Royal Society B:  
698 Biological Sciences*, 366, 2426–2437.
- 699 Coblenz, D. D., & Riitters, K. H. (2004). Topographic controls on the regional-scale  
700 biodiversity of the south-western USA. *Journal of Biogeography*, 31, 1125–1138.
- 701 Cracraft, J. (1985). Biological diversification and its causes. *Annals of the Missouri Botanical  
702 Garden*, 72, 794–822.

703 Crisp, M. D., Laffan, S., Linder, H. P., & Monro, A. (2001). Endemism in the Australian  
704 flora. *Journal of Biogeography*, 28, 183–198.

705 Cumming, G. S., & Child, M. F. (2009). Contrasting spatial patterns of taxonomic and functional  
706 richness offer insights into potential loss of ecosystem services. *Philosophical Transactions*  
707 *of the Royal Society B: Biological Sciences*, 364, 1683–1692.

708 Davies, T. J. (2015). Losing history: how extinctions prune features from the tree of life.  
709 *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370, 20140006.

710 Davies, T. J., & Buckley, L. B. (2011). Phylogenetic diversity as a window into the evolutionary  
711 and biogeographic histories of present-day richness gradients for mammals. *Philosophical*  
712 *Transactions of the Royal Society B: Biological Sciences*, 366, 2414–2425.

713 Davies, T. J., & Buckley, L. B. (2012). Exploring the phylogenetic history of mammal species  
714 richness. *Global Ecology and Biogeography*, 21, 1096–1105.

715 Davies, T. J., Urban, M. C., Rayfield, B., Cadotte, M. W., & Peres-Neto, P.R. (2016).  
716 Deconstructing the relationships between phylogenetic diversity and ecology: a case study  
717 on ecosystem functioning. *Ecology*, 97, 2212–2222.

718 Davis, E. B., Koo, M. S., Conroy, C. J., Patton, J. L., & Moritz, C. (2008). The California  
719 Hotspots Project: identifying regions of rapid diversification of mammals. *Molecular*  
720 *Ecology*, 17, 120–138.

721 Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., &  
722 Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across  
723 latitude. *Proceedings of the National Academy of Sciences*, 105(18), 6668–6672.

724 Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W. & Mouquet, N. (2010) Spatial  
725 mismatch and congruence between taxonomic, phylogenetic and functional diversity: the  
726 need for integrative conservation strategies in a changing world. *Ecology Letters*, 13, 1030–  
727 1040.

728 Dirzo, R., & Raven, P. H. (2003). Global State of Biodiversity and Loss. *Annual Review of*  
729 *Environment and Resources*, 28, 137–167.

730 Dobson, A., Lodge, D., Alder, J., Cumming, G. S., Keymer, J., McGlade, J., ... Xenopoulos, M.  
731 A. (2006). Habitat loss, trophic collapse, and the decline of ecosystem services. *Ecology*, 87,  
732 1915–1924.

- 733 Dutilleul, P., Clifford, P., Richardson, S., & Hemon, D. (1993). Modifying the t-test for assessing  
734 the correlation between two spatial processes. *Biometrics*, 49, 305–314.
- 735 Ernest, S. K. M. (2005). Body size, energy use, and community structure of small mammals.  
736 *Ecology*, 86, 1407–1413.
- 737 Ernest, S. K. M., Brown, J. H., Thibault, K. M., White, E. P., & Goheen, J.R. (2008). Zero sum,  
738 the niche, and metacommunities: Long-term dynamics of community assembly. *The*  
739 *American Naturalist*, 172, E257–E269.
- 740 Fabre, P.-H., Hautier, L., Dimitrov, D., & Douzery, E. J. P. (2012). A glimpse on the pattern of  
741 rodent diversification: a phylogenetic approach. *BMC Evolutionary Biology*, 12, 88.
- 742 Faith, D.P. (1992). Conservation evaluation and phylogenetic diversity. *Biological Conservation*,  
743 61, 1–10.
- 744 Faurby, S., & Svenning, J. C. (2015a). A species-level phylogeny of all extant and late  
745 Quaternary extinct mammals using a novel heuristic-hierarchical Bayesian  
746 approach. *Molecular Phylogenetics and Evolution*, 84, 14–26.
- 747 Faurby, S., & Svenning, J. C. (2015b). Historic and prehistoric human-driven extinctions have  
748 reshaped global mammal diversity patterns. *Diversity and Distributions*, 21, 1155–1166.
- 749 Faurby, S., Davis, M., Pedersen, R. Ø., Schowanek, S. D., Antonelli, A., & Svenning, J.C.  
750 (2018). PHYLACINE 1.2: The phylogenetic atlas of mammal macroecology. *Ecology*, 99,  
751 2626.
- 752 Fergnani, P. N., & Ruggiero, A. (2015). Ecological diversity in South American mammals: their  
753 geographical distribution shows variable associations with phylogenetic diversity and does  
754 not follow the latitudinal richness gradient. *PloS one*, 10(6), e0128264.
- 755 Finarelli, J. A. & Badgley, C. (2010). Diversity dynamics of Miocene mammals in relation to the  
756 history of tectonism and climate. *Proceedings of the Royal Society of London. Series B:*  
757 *Biological Sciences*, 277, 2721–2726.
- 758 Finnegan, S., Anderson, S. C., Harnik, P. G., Simpson, C., Tittensor, D. P., Byrnes, J. E., ...  
759 Pandolfi, J.M. (2015). Paleontological baselines for evaluating extinction risk in the modern  
760 oceans. *Science*, 348, 567–570.
- 761 Flantua, S. G., & Hooghiemstra, H. (2018). Historical connectivity and mountain biodiversity. In  
762 Hoorn, C., Perrigo, A. & Antonelli, A. (Eds.), *Mountains, Climate and Biodiversity*, (pp.  
763 171-186). Hoboken, NJ: Wiley-Blackwell.

764 Fritz, S. A., & Purvis, A. (2010). Phylogenetic diversity does not capture body size variation at  
765 risk in the world's mammals. *Proceedings of the Royal Society of London. Series B:*  
766 *Biological Sciences*, 277, 2435–2441.

767 Fritz, S. A., & Rahbek, C. (2012). Global patterns of amphibian phylogenetic diversity. *Journal*  
768 *of Biogeography*, 39, 1373–1382.

769 Garcia, R. A., Araújo, M. B., Burgess, N. D., Foden, W. B., Gutsche, A., Rahbek, C., & Cabeza,  
770 M. (2014). Matching species traits to projected threats and opportunities from climate  
771 change. *Journal of Biogeography*, 41, 724–735.

772 González-Orozco, C. E., Pollock, L. J., Thornhill, A. H., Mishler, B. D., Knerr, N., Laffan, S.  
773 W., ... Gruber, B. (2016). Phylogenetic approaches reveal biodiversity threats under climate  
774 change. *Nature Climate Change*, 6, 1110–1114.

775 Grayson, D. K. (2011). *The Great Basin: A Natural Prehistory*. Berkeley, CA: University of  
776 California Press.

777 Hijmans, R. J. (2017). Raster: geographic data analysis and modeling. R package version 2.5–2.

778 Holderegger, R., Thiel-Egenter, C., & Whittaker, R. (2009). A discussion of different types of  
779 glacial refugia used in mountain biogeography and phylogeography. *Journal of*  
780 *Biogeography*, 36, 476–480.

781 Holling, C. S. (1992). Cross-scale morphology, geometry, and dynamics of ecosystems.  
782 *Ecological monographs*, 62, 447–502.

783 Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., ... Wardle, D. A.  
784 (2005). Effects of biodiversity on ecosystem functioning: A consensus of current  
785 knowledge. *Ecological Monographs*, 75, 3–35.

786 Hoorn, C., Wesselingh, F. P., ter Steege, H., Bermudez, M. A., Mora, A., Sevink, J., ...  
787 Antonelli, A. (2010). Amazonia through time: Andean uplift, climate change, landscape  
788 evolution, and biodiversity. *Science*, 330, 927–931.

789 Huang, S., Stephens, P. R., & Gittleman, J.L. (2012). Traits, trees and taxa: global dimensions of  
790 biodiversity in mammals. *Proceedings of the Royal Society of London. Series B: Biological*  
791 *Sciences*, 279, 4997–5003.

792 Humphries, C. J., Williams, P. H., & Vane-Wright, R. I. (1995). Measuring Biodiversity Value  
793 for Conservation. *Annual Review of Ecology and Systematics*, 26, 93–111.



794 Hurlbert, S. H. (1971). The non-concept of species diversity: a critique and alternative  
795 parameters. *Ecology*, 52, 577–586.

796 Hurlbert, A. H., & Jetz, W. (2007). Species richness, hotspots, and the scale dependence of range  
797 maps in ecology and conservation. *Proceedings of the National Academy of Sciences*, 104,  
798 13384–13389.

799 IUCN 2017. The IUCN Red List of Threatened Species. Version 2017–5.2.  
800 <http://www.iucnredlist.org>. Downloaded on 04 July 2017.

801 Jarzyna, M. A. & Jetz, W. (2018). Taxonomic and functional diversity change is scale  
802 dependent. *Nature Communications*, 9, 2565.

803 Jezkova, T., Olah-Hemmings, V., & Riddle, B. R. (2011). Niche shifting in response to warming  
804 climate after the last glacial maximum: inference from genetic data and niche assessments in  
805 the chisel-toothed kangaroo rat (*Dipodomys microps*). *Global Change Biology*, 17, 3486–  
806 3502.

807 Jetz, W., & Rahbek, C. (2002). Geographic range size and determinants of avian species  
808 richness. *Science*, 297, 1548–1551.

809 Kays, R. W., & Wilson, D. E. (2009). *Mammals of North America*. Princeton, NJ: Princeton  
810 University Press.

811 Kotler, B. P., & Brown, J. S. (1988). Environmental heterogeneity and the coexistence of desert  
812 rodents. *Annual Review of Ecology and Systematics*, 19, 281–307.

813 Laundre, J. W., & Reynolds, T. D. (1993). Effects of soil structure on burrow characteristics of  
814 five small mammal species. *Great Basin Naturalist*, 53, 358–366.

815 Lessa, E. P., Cook, J. A., & Patton, J. L. (2003). Genetic footprints of demographic expansion in  
816 North America, but not Amazonia, during the Late Quaternary. *Proceedings of the National  
817 Academy of Sciences*, 100(18), 10331–10334.

818 Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackerly, D. (2009). The  
819 velocity of climate change. *Nature*, 462, 1052–1055.

820 Lyons, S. K. (2003). A quantitative assessment of the range shifts of Pleistocene mammals.  
821 *Journal of Mammalogy*, 84, 385–402.

822 Mace, G. M., Gittleman, J. L., & Purvis, A. (2003). Preserving the tree of life. *Science*, 300,  
823 1707–1709.

824 Machac, A., Graham, C. H., & Storch, D. (2017). Ecological controls of mammalian  
825 diversification vary with phylogenetic scale. *Global Ecology and Biogeography*, 27, 32–46.

826 Mammal Diversity Database. (2019). [www.mammaldiversity.org](http://www.mammaldiversity.org). American Society of  
827 Mammalogists. Accessed 2019-08-18

828 Mazel, F., Guilhaumon, F., Mouquet, N., Devictor, V., Gravel, D., Renaud, J., ... Thuiller, W.  
829 (2014). Multifaceted diversity-area relationships reveal global hotspots of mammalian  
830 species, trait and lineage diversity. *Global Ecology and Biogeography*, 23, 836–847.

831 McGuire, J. L., Lawler, J. J., McRae, B. H., Nuñez, T. A., & Theobald, D. M. (2016). Achieving  
832 climate connectivity in a fragmented landscape. *Proceedings of the National Academy of  
833 Sciences*, 113, 7195–7200.

834 Mishler, B. D., Knerr, N., González-Orozco, C. E., Thornhill, A. H., Laffan, S. W., & Miller, J.  
835 T. (2014). Phylogenetic measures of biodiversity and neo- and paleo-endemism in Australian  
836 Acacia. *Nature Communications*, 5, 4473.

837 Mittelbach, G. G., & Schemske, D. W. (2015). Ecological and evolutionary perspectives on  
838 community assembly. *Trends in Ecology and Evolution*, 30, 241–247.

839 Moen, D., & Morlon, H. (2014). Why does diversification slow down? *Trends in Ecology and  
840 Evolution*, 29, 190–197.

841 Moritz, C., Patton, J. L., Conroy, C. J., Parra, J. L., White, G. C., & Beissinger, S. R. (2008).  
842 Impact of a century of climate change on small-mammal communities in Yosemite National  
843 Park, USA. *Science*, 322, 261–264.

844 Mulch, A. (2016). Stable isotope paleoaltimetry and the evolution of landscapes and life. *Earth  
845 and Planetary Science Letters*, 433, 180–191.

846 Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G., & Kent, J. (2000).  
847 Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858.

848 Newbold, T., Hudson, L. N., Arnell, A. P., Contu, S., De Palma, A., Ferrier, S., ... Purvis, A.  
849 (2016). Has land use pushed terrestrial biodiversity beyond the planetary boundary? A  
850 global assessment. *Science*, 353, 288–291.

851 Ohlemüller, R., Anderson, B. J., Araújo, M. B., Butchart, S. H. M., Kudrna, O., Ridgely, R. S., &  
852 Thomas, C.D. (2008). The coincidence of climatic and species rarity: high risk to small-  
853 range species from climate change. *Biology Letters*, 4, 568–572.

854 Orme, C. D. L., Davies, R. G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V. A., ... Owens,  
855 I. P. F. (2005). Global hotspots of species richness are not congruent with endemism or  
856 threat. *Nature*, 436, 1016–1019.

857 Osorio, F., Vallejos, R., & Cuevas, F. (2014). *SpatialPack: Package for analysis of spatial data*. R  
858 package version 0.2-3.

859 Pagel, M. D., May, R. M., & Collie, A. R. (1991). Ecological aspects of the geographical  
860 distribution and diversity of mammalian species. *The American Naturalist*, 137, 791–815.

861 Paradis, E., Claude, J., & Strimmer, K. (2004). APE: analyses of phylogenetics and evolution in  
862 R language. *Bioinformatics*, 20, 289–290.

863 Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts  
864 across natural systems. *Nature*, 421, 37–42.

865 Pebesma, E. J., & Bivand, R. S. (2005). Classes and methods for spatial data in R. *R news*, 5, 9–  
866 13.

867 Price, M. V., & Brown, J. H. (1983). Patterns of morphology and resource use in North  
868 American desert rodent communities. *Great Basin Naturalist Memoirs*, 7.8, 117–134.

869 Purvis, A., & Hector, A. (2000). Getting the measure of biodiversity. *Nature*, 405, 212–219.

870 Purvis, A., Cardillo, M., Grenyer, R., & Collen, R. (2005). Correlates of extinction risk:  
871 phylogeny, biology, threat and scale. In Purvis, A., Gittleman, J. L. & Brooks, T. M. (Eds.)  
872 *Phylogeny and Conservation* (pp. 295-316). Cambridge, MA: Cambridge University Press.

873 Quintero, I., & Jetz, W. (2018). Global elevational diversity and diversification of birds. *Nature*,  
874 555(7695), 246.

875 R Development Core Team. (2017). *R: A language and environment for statistical computing*.  
876 Vienna, Austria: R Foundation for Statistical Computing.

877 Rice, W. R. (1989). Analyzing tables of statistical tests. *Evolution* 43, 223–225

878 Ricklefs, R. E. (1987). Community diversity: relative roles of local and regional processes.  
879 *Science*, 235, 167–171.

880 Riddle, B. R., Jezkova, T., Hornsby, A. D., & Matocq, M. D. (2014). Assembling the modern  
881 Great Basin mammal biota: insights from molecular biogeography and the fossil record.  
882 *Journal of Mammalogy*, 95, 1107–1127.

883 Ripple, W. J., Wolf, C., Newsome, T. M., Hoffmann, M., Wirsing, A. J., & McCauley, D. J.  
884 (2017). Extinction risk is most acute for the world's largest and smallest vertebrates.  
885 *Proceedings of the National Academy of Sciences*, 114, 10678–10683.

886 Rosauer, D. F., & Jetz, W. (2014). Phylogenetic endemism in terrestrial mammals. *Global*  
887 *Ecology and Biogeography*, 24, 168–179.

888 Rosauer, D. F., Laffan, S. W., Crisp, M. D., Donnellan, S. C., & Cook, L. G. (2009).  
889 Phylogenetic endemism: a new approach for identifying geographical concentrations of  
890 evolutionary history. *Molecular Ecology*, 18, 4061–4072.

891 Rowe, R. J., & Terry, R. C. (2014). Small mammal responses to environmental change:  
892 integrating past and present dynamics. *Journal of Mammalogy*, 95, 1157–1174.

893 Rowe, R. J., Terry, R. C., & Rickart, E. A. (2011). Environmental change and declining resource  
894 availability for small-mammal communities in the Great Basin. *Ecology*, 92, 1366–1375.

895 Safi, K., Cianciaruso, M. V., Loyola, R. D., Brito, D., Armour-Marshall, K., & Diniz-Filho, J. A.  
896 F. (2011). Understanding global patterns of mammalian functional and phylogenetic  
897 diversity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366,  
898 2536–2544.

899 Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., ... Wall, D. H.  
900 (2000). Global biodiversity scenarios for the year 2100. *Science*, 287, 1770–1774.

901 Samuels, J. X., & Hopkins, S. S. B. (2017). The impacts of Cenozoic climate and habitat changes  
902 on small mammal diversity of North America. *Global and Planetary Change*, 149, 36–52.

903 Schindler, D. E., Armstrong, J. B., & Reed, T.E. (2015). The portfolio concept in ecology and  
904 evolution. *Frontiers in Ecology and the Environment*, 13, 257–263.

905 Schliep, K. P. (2011). phangorn: Phylogenetic analysis in R. *Bioinformatics*, 27, 592–593.

906 Shafer, A. B. A., Cullingham, C. I., Côté, S. D., & Coltman, D. W. (2010). Of glaciers and  
907 refugia: a decade of study sheds new light on the phylogeography of northwestern North  
908 America. *Molecular Ecology*, 19, 4589–4621.

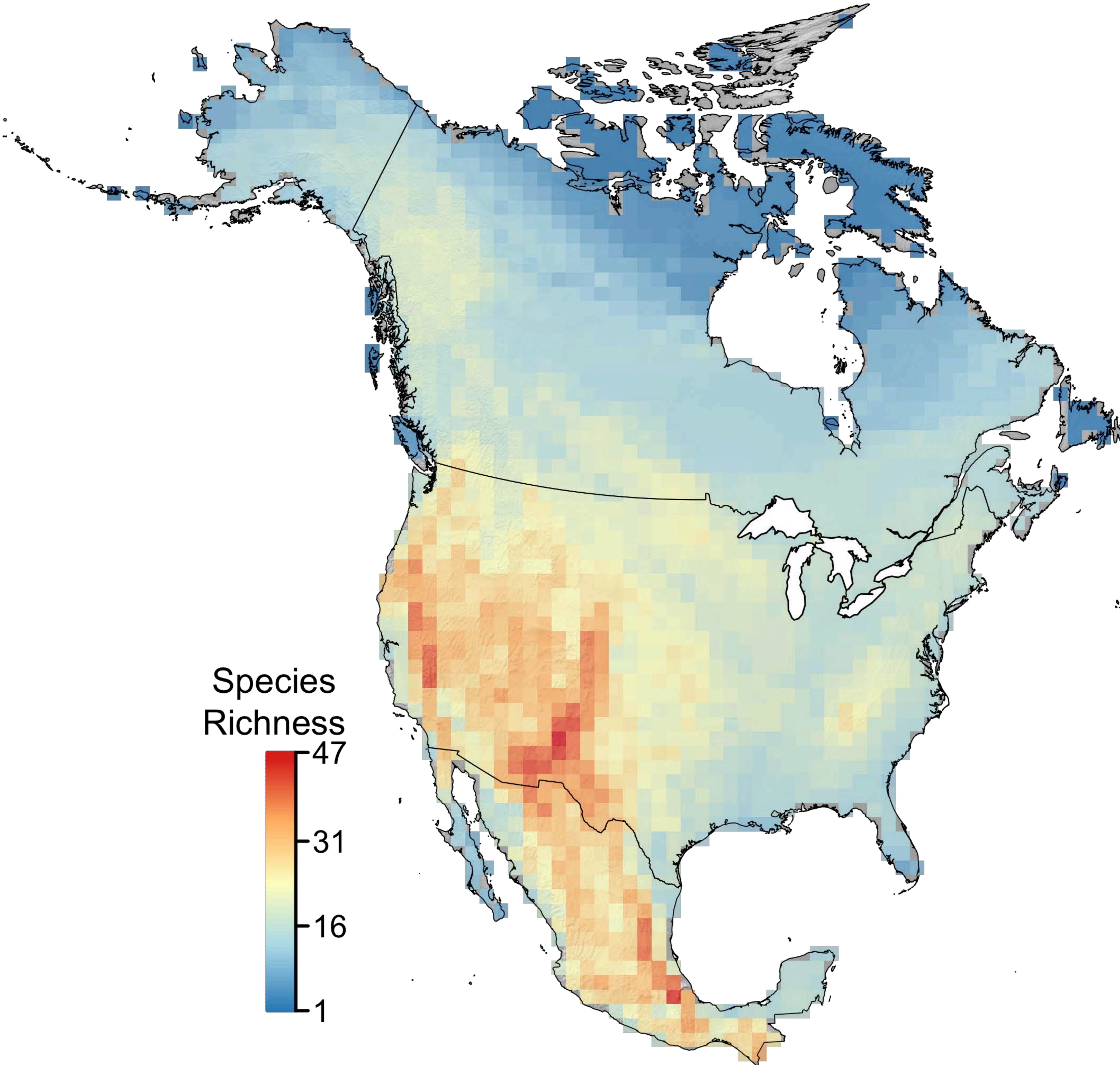
909 Simpson, G. G. (1964). Species density of North American recent mammals. *Systematic*  
910 *Zoology*, 13, 57–73.

911 Silva-Aliaga, M., & Downing, J. A. (1995). *CRC Handbook of Mammalian Body Masses*. Boca  
912 Raton, FL: CRC Press.

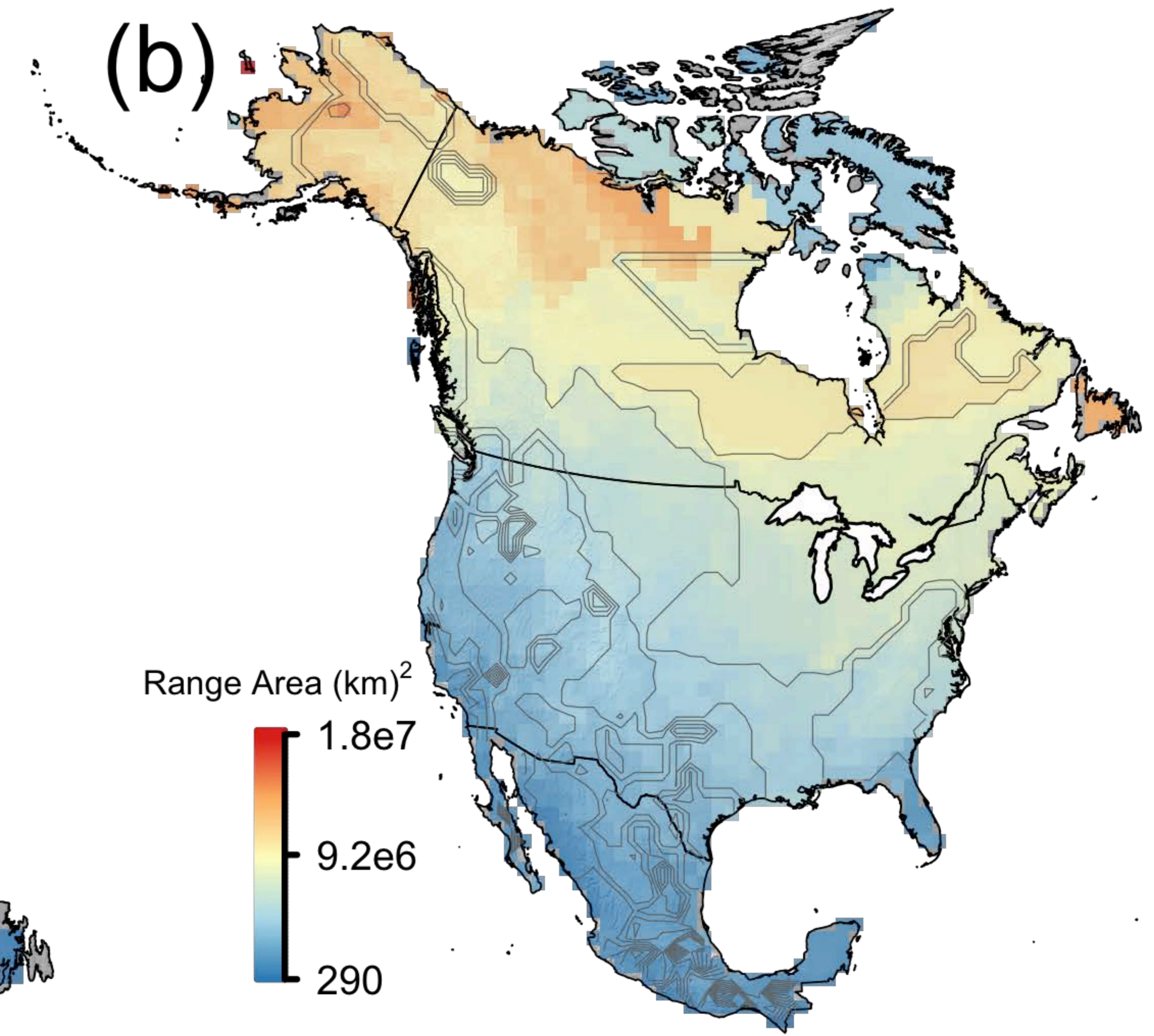
- 913 Smiley, T. M. (2018). Detecting diversification rates in relation to preservation and tectonic  
914 history from simulated fossil records. *Paleobiology*, 44, 1–24.
- 915 Smiley, T. M., Title, P. O., Zelditch, M. L., & Terry, R. C. (2019). Multi-dimensional  
916 biodiversity hotspots and the future of taxonomic, ecological, and phylogenetic diversity: a  
917 case study of North American rodents, Dryad, Dataset,  
918 <https://doi.org/10.5061/dryad.4xgxd2559>.
- 919 Smith, F. A., Brown, J. H., Haskell, J. P., Lyons, S. K., Alroy, J., Charnov, E. L., ... Willig,  
920 M.R. (2004). Similarity of mammalian body size across the taxonomic hierarchy and across  
921 space and time. *The American Naturalist*, 163, 672–691.
- 922 Smith, F. A., Lyons, S. K., Ernest, S. K. M., Jones, K. E., Kaufman, D. M., Dayan, T., ...  
923 Haskell, J.P. (2007). Macroecological database of mammalian body mass. MOM  
924 version, 3(1).
- 925 Smith, F. A., Smith, R. E. E., Lyons, S. K., & Payne, J. L. (2018). Body size downgrading of  
926 mammals over the late Quaternary. *Science*, 360, 310–313.
- 927 Stein, R. W., Mull, C. G., Kuhn, T. S., Aschliman, N. C., Davidson, L. N. K., Joy, J. B., ...  
928 Mooers, A. O. (2018). Global priorities for conserving the evolutionary history of sharks,  
929 rays and chimaeras. *Nature Ecology & Evolution*, 2, 288–298.
- 930 Stevens, R. D., & Tello, J. S. (2014). On the measurement of dimensionality of biodiversity.  
931 *Global Ecology and Biogeography*, 23, 1115–1125.
- 932 Stevens, R. D., Tello, J. S., & Gavilanez, M. M. (2013). Stronger tests of mechanisms underlying  
933 geographic gradients of biodiversity: Insights from the dimensionality of biodiversity. *PLoS*  
934 *ONE*, 8, e56853–11.
- 935 Terry, R. C., & Rowe, R. J. (2015). Energy flow and functional compensation in Great Basin  
936 small mammals under natural and anthropogenic environmental change. *Proceedings of the*  
937 *National Academy of Sciences*, 112, 9656–9661.
- 938 Terry, R. C., Li, C. L., & Hadly, E. A. (2011). Predicting small-mammal responses to climatic  
939 warming: autecology, geographic range, and the Holocene fossil record. *Global Change*  
940 *Biology*, 17, 3019–3034.
- 941 Terry, R. C., Guerre, M. E., & Taylor, D. S. (2017). How specialized is a diet specialist? Niche  
942 flexibility and local persistence through time of the Chisel-toothed kangaroo rat. *Functional*  
943 *Ecology*, 31, 1921–1932.

- 944 Thibaut, L. M., & Connolly, S. R. (2013). Understanding diversity-stability relationships:  
945 Towards a unified model of portfolio effects. *Ecology Letters*, 16, 140–150.
- 946 Tilman, D., & Downing, J.A. (1994). Biodiversity and stability in grasslands. *Nature*, 367, 363–  
947 365.
- 948 Tilman, D., Wedin, D., & Knops, J. (1996). Productivity and sustainability influenced by  
949 biodiversity in grassland ecosystems. *Nature*, 379, 718–720.
- 950 Tilman, D., Knops, J., & Wedin, D. (1997). The influence of functional diversity and  
951 composition on ecosystem processes. *Science*, 277, 1300–1302.
- 952 Tucker, C. M., & Cadotte, M. W. (2013). Unifying measures of biodiversity: understanding  
953 when richness and phylogenetic diversity should be congruent. *Diversity and Distributions*,  
954 19, 845–854.
- 955 Tucker, C. M., Cadotte, M. W., Carvalho, S. B., Davies, T. J., Ferrier, S., Fritz, S. A., ... Mazel,  
956 F. (2017). A guide to phylogenetic metrics for conservation, community ecology and  
957 macroecology. *Biological Reviews*, 92, 698–715.
- 958 Villalobos, F., Olalla-Tárraga, M. Á., Cianciaruso, M. V., Rangel, T. F., & Diniz-Filho, J. A. F.  
959 (2016). Global patterns of mammalian co-occurrence: phylogenetic and body size structure  
960 within species ranges. *Journal of Biogeography*, 44, 136–146.
- 961 Walsh, R. E., Aprígio Assis, A. P., Patton, J. L., Marroig, G., Dawson, T. E., & Lacey, E. A.  
962 (2016). Morphological and dietary responses of chipmunks to a century of climate change.  
963 *Global Change Biology*, 22, 3233–3252.
- 964 Weinzettel, J., Vačkář, D., & Medková, H. (2018). Human footprint in biodiversity hotspots.  
965 *Frontiers in Ecology and the Environment*, 16, 447–452.
- 966 Wilson, D. E., & Reeder, D. M. (2005). *Mammal species of the World. A Taxonomic and*  
967 *Geographic Reference* (3<sup>rd</sup> ed.). Baltimore, MD: Johns Hopkins University Press.
- 968 Wilson, D. E., & Ruff, S. (1999). *The Smithsonian book of North American mammals*.  
969 Washington DC: Smithsonian Institution Press.
- 970 Wolf, C., & Ripple, W. J. (2017). Range contractions of the world's large carnivores. *Royal*  
971 *Society Open Science*, 4, 170052–11.
- 972 Zelditch, M. L., Li, J., Tran, L. A. P., & Swiderski, D. L. (2015). Relationships of diversity,  
973 disparity, and their evolutionary rates in squirrels (Sciuridae). *Evolution*, 69, 1284–1300.

(a)



(b)



(c)

