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Species are not most abundant in the center of their geographic
range or climatic niche

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<https://doi.org/10.6084/m9.figshare.5023232>. Data are available for eBird data (Sullivan *et al.*, 2009), EPA-EMAP data (<https://www.epa.gov/emap/>), NAWQA data (Knouft & Anthony (2016a); <https://water.usgs.gov/nawqa>), Forest Inventory and Analysis data (Woudenberg *et al.*, 2010) (<https://www.fia.fs.fed.us/>), and the mammal community database Thibault *et al.* (2011). While authors should cite the original data sources, we also provide data used in the analyses and analytic code.

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Abstract

1 The pervasive idea that species should be most abundant in the center of their
2 geographic range or center of their climatic niche is a key assumption in many
3 existing ecological hypotheses and has been declared a general macroecological
4 rule. However, empirical support for decreasing population abundance with increasing
5 distance from geographic range or climatic niche center (*distance-abundance* relationships)
6 remains fairly weak. We examine over 1400 bird, mammal, fish, and tree species to
7 provide a thorough test of *distance-abundance* relationships, and their associations
8 with species traits and phylogenetic relationships. We failed to detect consistent
9 *distance-abundance* relationships, and found no association between *distance-abundance*
10 slope and species traits or phylogenetic relatedness. Together, our analyses suggest
11 that *distance-abundance* relationships may be rare, difficult to detect, or are an
12 oversimplification of the complex biogeographical forces that determine species
13 spatial abundance patterns.

14 Introduction

15 A shared common goal of macroecology, biogeography, and population ecology
16 is to understand the distribution of species abundances across geographic space
17 (Gaston & Blackburn, 2003; Vandermeer & Goldberg, 2013). One such species
18 abundance pattern is the tendency for species to be most abundant in the center of
19 their geographic ranges (Hengeveld & Haeck, 1982; Holt *et al.*, 1997; Brown, 1984;
20 McGill & Collins, 2003). This phenomenon, sometimes referred to as the *abundant*
21 *center hypothesis* (Sagarin *et al.*, 2006), is one of many *distribution-abundance*
22 relationships in macroecology, which attempt to relate species abundance patterns
23 to geographic extent (e.g., occupancy, geographic range area, etc.). Under the
24 umbrella of *distribution-abundance* relationships, the way both *distribution* and
25 *abundance* are quantified can have a large influence on the resulting relationship.
26 For instance, quantifying *distribution* as the number of occupied spatial grid
27 cells typically yields positive relationships with abundance (abundance-occupancy
28 relationships; (Gaston & Blackburn, 2003)), but variation in this relationship exists
29 when measured at different spatial scales, or if *distribution* is defined as geographic
30 extent (Blackburn *et al.*, 2006). *Distance-abundance* relationships are a subset of
31 *distribution-abundance* relationships that relate the distance from the center of a
32 species geographic range to local population sizes, which tests the hypothesis that
33 species are most abundant at their range centers. Further, the *distance-abundance*
34 relationship is a common assumption of theoretical modeling efforts (Gaston &
35 Blackburn, 2003; Sagarin *et al.*, 2006), has been used to inform conservation and
36 management decisions (Borregaard & Rahbek, 2010), and has served as the basis
37 for many biogeographic and macroecological hypotheses (Sagarin *et al.*, 2006).

38 However, empirical support for *distance-abundance* relationships is mixed (Sagarin
39 & Gaines, 2002; Pironon *et al.*, 2016), with no clear causal basis (Borregaard &
40 Rahbek, 2010). Studies on trees (Murphy *et al.*, 2006; Ren *et al.*, 2013) and coastal
41 plants (Samis & Eckert, 2007) failed to detect *distance-abundance* relationships,
42 while evidence has been found for a small number of animal species (Martínez-Meyer
43 *et al.*, 2013). The variable support for *distance-abundance* relationships may
44 relate to how distance is quantified, the spatial scale of studies, or ecological
45 and biogeographic differences in species groups through conserved traits related
46 to population growth and dispersal (Flügge *et al.*, 2012). Logistical constraints
47 have typically restricted researchers to examine *distance-abundance* relationships
48 at smaller spatial scales and for a limited number of populations (Sagarin & Gaines,
49 2002), which may not fully capture abundance patterns across species' geographic
50 ranges. Understanding associations between species-level covariates may provide
51 much needed insight into *when* a *distance-abundance* relationship is likely to be
52 observed. For instance, species body size may be associated with the slope of the
53 *distance-abundance* relationship, as macroecological patterns have suggested that
54 body size is closely related to metabolic rate (Nagy, 2005), range size (Diniz-Filho
55 *et al.*, 2005), and is central to many macroecological studies (see (Smith & Lyons,
56 2013)).

57 Another confounding influence on the generality of *distance-abundance* relationships
58 is the considerable variation in how distance is quantified, suggesting the need
59 for an integrative and unified approach to examinations of *distance-abundance*
60 relationships (McGill & Collins, 2003). Distance may be measured from geographic
61 range edge or center (see Table 2 of (Sagarin & Gaines, 2002)), where range
62 center may be quantified in a number of ways (Borregaard & Rahbek, 2010).

63 Recently, Martínez-Meyer *et al.* (2013) demonstrated that the lack of a relationship
64 between local population abundance and geographic distance from range centers
65 of eleven animal species belied a clear relationship between species abundance
66 and environmental distance from species niche centers. The use of environmental
67 distance provides a link between species niche requirements and corresponding
68 geographic distribution (Pulliam, 2000), and potentially explains the limited support
69 for *distance-abundance* relationships to date. Further, this tests a slightly different
70 assumption that is central to niche theory; species should be most abundant under
71 optimal niche conditions (Weber *et al.*, 2016). Together, these issues may underlie
72 the limited support for *distance-abundance* relationships, and highlight a clear
73 knowledge gap in a fundamental area of ecological research (Sagarin *et al.*, 2006).

74 A final note on the ambiguity of *distance-abundance* relationships relates to the
75 quantification of abundance itself. The inherent difficulty in measuring population
76 abundance has resulted in the use of standardized counts of individuals in place
77 of overall abundance. That is, although *abundance* is the commonly applied term,
78 *density* is a perhaps more sensible term, and, in most cases, the only possible
79 measure. In keeping with previous terminology, we use the term *abundance*, but
80 it is important to note that perhaps *density* would be more accurate.

81 To address the degree of empirical support for *distance-abundance* relationships,
82 we proposed a simple test: if species are most abundant at their range or niche
83 centers, then a negative correlation should exist between species abundance and
84 distance from either geographic or niche center. To this end, we used a number of
85 extensive datasets on natural populations to examine *distance-abundance* relationships,
86 and how they can be influenced by species-level traits and evolutionary relationships.
87 First, we investigated the relationship between distance—measured as either geographic

88 distance or climatic niche distance—and species abundance for a diverse set of
89 mammals, birds, fishes, and trees distributed across a broad latitudinal gradient
90 through the Americas. When data were available, species *distance-abundance*
91 correlations were related to species body size and range size in order to determine
92 the presence of a species-level trait basis for *distance-abundance* relationships.
93 Lastly, we related *distance-abundance* correlation coefficients to measures of phylogenetic
94 distance to determine associations between the strength of *distance-abundance*
95 relationships and species evolutionary history. We found very little support for
96 *distance-abundance* relationships when distance was defined as either geographic
97 distance from range center or environmental distance from niche center. Further,
98 we failed to detect associations between the *distance-abundance* relationship slope
99 and species body size, geographic range area, climatic niche area, or phylogenetic
100 relatedness. Together, our findings suggest that *distance-abundance* relationships
101 may be rare, difficult to detect, or are an oversimplification of the complex biogeographical
102 forces that determine species spatial abundance patterns.

103 **Methods**

104 **Data sources**

105 To examine the relationship between species abundance and the distance from
106 species geographic range center or climatic niche center, we used estimates from
107 databases based on published work (Thibault *et al.*, 2011), aggregated data from
108 large-scale citizen science efforts (Sullivan *et al.*, 2009), and government-sponsored
109 repeated sampling efforts (Woudenberg *et al.*, 2010). As we noted above, these
110 estimates are, strictly speaking, estimates of density, not abundance. Data spanned

111 a broad latitudinal gradient (see Figure S8) and a diverse set of taxa, including
112 mammals (MCDB; (Thibault *et al.*, 2011)), birds (eBird database (Sullivan *et al.*,
113 2009)), tree seedlings (USDA Forest Inventory and Analysis database; FIA (Woudenberg
114 *et al.*, 2010)), and fish species (EPA Environmental Monitoring and Assessment
115 Program – EPA-EMAP; <https://www.epa.gov/emap/> and a subset of the USGS
116 National Water Quality Assessment – NAWQA; (Knouft & Anthony, 2016a);
117 <https://water.usgs.gov/nawqa>).

118
119 The total number of species examined represents the largest investigation of
120 *distance-abundance* relationships to date, including a total of bird ($n = 1109$), fish
121 ($n = 63$), mammal ($n = 81$), and tree ($n = 166$) species for which enough data
122 were available to calculate *distance-abundance* correlations. Further, the number of
123 observations tended to be large, including over a million total observations among
124 the data sources (birds = 593,288; trees = 389,850; fishes = 9,375; and mammals
125 = 20,412).

126
127 We limited the scope of our analyses to species occurring in the Americas
128 with more than 10 sampled populations, resulting in a data set consisting of over
129 118,000 sampled and georeferenced localities (see Figure S8 for sampling locations).
130 We discuss the sensitivity of our results to this threshold in the Supplemental
131 Materials. Also, the spatial extent of the eBird data was constrained to the
132 Americas, while the other data sources occupied either the Americas (Mammal
133 Community Database) or were restricted to the United States (tree and fish
134 data). For datasets restricted to the United States (USDA-FIA tree seedlings and
135 fish data from the EPA-EMAP and NAWQA data), we discarded species whose

136 northernmost or southernmost abundance was greater than the mean abundance
137 observed over all sampled populations for that species. This was an effort to remove
138 species whose geographic range exceeds the sampled range. Sampled populations
139 on distant islands were removed, as these potentially dispersal-limited populations
140 may strongly influence *distance-abundance* relationships. Lastly, migratory status
141 might influence species range estimation in the eBird data. We examine this
142 further in the Supplemental Materials, demonstrating our results are robust to the
143 inclusion/exclusion of migratory species.

144 **Species abundance estimation**

145 Species abundance was estimated from sampling data; either repeated samples of
146 variable (MCDB) or standardized (USDA-FIA) plot sizes, rarefied estimates of
147 abundance based on repeated sampling (NAWQA), or acoustic and visual surveys
148 (eBird). For these analyses, species abundance was estimated as the number
149 of individuals within a sampling area, standardized by either sampling area or
150 sampling intensity. This approach results in standardized species counts most akin
151 to a measure of species density, as abundance may not be sensibly measured at
152 the scale we examine here. There is also little assurance that sampling was equal
153 across study sites or across species, as this is an impossibly high bar given the
154 spatial scale examined. However, we accounted for sampling biases in a number of
155 ways. First, some data sources were based on rigorous national efforts, which
156 used standardized plot sizes (USDA FIA data), which means that abundance
157 estimates are comparable across space. That is, even if estimates do not capture
158 true abundance, abundance estimates will be proportional to true abundance as
159 a function of sampling design. Other data sources contained sufficient detail to

160 allow for rarefaction (NAWQA; Knouft & Anthony (2016a)), a form of statistical
161 standardization of sampling effort. For data based on published literature (MCDB
162 data), raw species abundance was standardized by the number of trap nights, a
163 commonly used measure of sampling effort (Richards & Schnute, 1986). Lastly,
164 abundance estimates from citizen science efforts (eBird) were standardized by the
165 duration of time spent sampling, while data for which duration was not available
166 was discarded. While other factors (e.g., time of day, length of transect, etc.) may
167 also influence observations, these variables were less often recorded by users.

168 **Distance calculation**

169 We examined the *distance-abundance* relationship by measuring the distance of
170 all sampled populations from a central point (Figure 1a), which was represented
171 either as the geographic center of the species range, or the species climatic niche
172 center. The geographic range center was determined by finding the center point
173 of a convex hull around observed populations. Meanwhile, the climatic niche
174 center was determined by first translating the multivariate climate space into a
175 two dimensional space comparable to geographic space. To do this, we calculated
176 the first two Principal Components (PCA) of the set of 56 BioClim/WorldClim
177 variables (Hijmans *et al.*, 2005), translating geographic points into climatic niche
178 space, and finding the center of the convex hull of points in niche space (Kriticos
179 *et al.*, 2014; Dallas & Drake, 2017). WorldClim variables ($n = 36$) contain monthly
180 information on minimum and maximum temperature and precipitation, while the
181 BioClim variables ($n = 19$) are derived quantities (e.g., temperature seasonality,
182 mean annual precipitation). Together, these climate data (plus altitude) represent
183 the best available data for defining species niches and modeling species geographic

184 distributions (Barbet-Massin & Jetz, 2014). While species likely vary in their
185 sensitivities to these variables, previous work has demonstrated high predictive
186 accuracy from models trained on these climatic covariates (Barbet-Massin & Jetz,
187 2014).

188
189 The first two PCA axes explained 77% of the variation in the global climate
190 (Dallas & Drake, 2017). We make the assumption that favorable climatic conditions
191 will result in larger population sizes, as we don't have detailed information on
192 species growth responses to various environmental variables. This is a common
193 assumption of niche modeling efforts, and evidence suggests that climatic suitability
194 does capture aspects of local abundance (VanDerWal *et al.*, 2009). Geographic
195 distance from species range centers was calculated as Haversine distance, while
196 distance in species niche space was calculated using Euclidean distance between
197 points in niche space created by the two PCA niche axes. We used Pearson's
198 correlations to quantify the relationship between distance and abundance (Figure
199 1a and b), and explore the possibility of non-linear relationships by using Spearman's
200 rank correlation coefficients in the Supplemental Materials.

201 **Range area, niche area, body size, and phylogeny**

202 The slope of the *distance-abundance* relationship could be associated with species
203 traits or with overall geographic range or climatic niche area. This could, in
204 part, explain the variable support for *distance-abundance* relationships. To explore
205 variation in *distance-abundance* relationships as a function of species ecology or
206 distribution, we examined relationships between the slope of the *distance-abundance*
207 relationship and species geographic range, climatic niche area, body size, and

208 phylogenetic relatedness.

209

210 Species geographic range size and climatic niche area were determined by
211 calculating the area of the minimum convex polygon that encompassed all sampling
212 locations for a given species either in space (i.e., geographic range size) or in
213 the phase space of the first two climatic niche axes (i.e., niche area). Species
214 body size estimates were obtained in terms of mass for bird (Myhrvold *et al.*,
215 2015) and mammal (Jones *et al.*, 2009) species, length for fish species (Froese &
216 Pauly, 2000), and height for tree species (Kattge *et al.*, 2011). Species body size
217 and range size, either geographic range area or niche area, were related to the
218 slope of the *distance-abundance* relationship obtained from a best fit linear model
219 relating species abundance to either geographic or niche distance. Some species
220 were not sampled in enough unique geographic locations ($n < 4$) or environments to
221 estimate geographic or niche area accurately, resulting in slightly reduced numbers
222 of species that could be used to examine relationships between slope of the *distance-abundance*
223 relationship and species traits. This number was also reduced for some species
224 where estimates of body size were unavailable (see Table 1). We explore the
225 sensitivity of *distance-abundance* relationships to the number of occurrence points
226 in the Supplementary Materials. For the set of species for which data were available
227 (n column of Table 1), we fit linear models to each taxa (mammal, bird, fish, and
228 tree species) including species body mass, estimated geographic range size, and
229 climatic niche area as covariates.

230

231 Phylogenetic data were obtained from the mammal (Bininda-Emonds *et al.*,
232 2007) and bird (Myhrvold *et al.*, 2015) phylogenetic supertrees. Branch lengths

233 were not included in the avian supertree, but were calculated using the well-established
234 *Grafen* method (Grafen, 1989). Taxonomic dissimilarity was used instead of
235 phylogenetic distance for trees and fishes. We used Moran's I to determine if
236 the slope of the *distance-abundance* relationship contained a phylogenetic (or
237 taxonomic) signal. Taxonomic data was accessed using *taxize* (Chamberlain &
238 Szöcs, 2013; Chamberlain *et al.*, 2016), and *ape* was used for the calculation of
239 Moran's I statistic (Paradis *et al.*, 2004). Some species in the data were not found
240 in the supertree or through *taxize*, constraining our analyses to 713 bird, 48 fish,
241 39 mammal, and 152 tree species.

242 Results

243 Distance-abundance relationships

244 *Distance-abundance* relationships were rarely observed when measuring distance
245 as geographic distance from a species range center (Figure 2a) and environmental
246 distance from a species niche center (Figure 2b). The mean correlation coefficients
247 between geographic distance and species abundance were near zero for birds ($\bar{\rho}_{bird}$
248 = -0.015), fishes ($\bar{\rho}_{fish}$ = -0.041), mammals ($\bar{\rho}_{mammal}$ = 0.002), and trees ($\bar{\rho}_{tree}$
249 = 0.015). Significant correlations, both positive and negative, were detected for
250 some bird ($n_+ = 151$; $n_- = 123$), fish ($n_+ = 1$; $n_- = 3$), mammal ($n_+ = 2$; n_-
251 = 2), and tree ($n_+ = 35$; $n_- = 8$) species. However, these significant correlations
252 tended to occur for species with limited sampling (Figure S6). Further, relative
253 to the number of species examined the percent of significant *distance-abundance*
254 relationships in bird ($p_+ = 0.12$; $p_- = 0.10$), fish ($p_+ = 0.02$; $p_- = 0.06$), mammal
255 ($p_+ = 0.04$; $p_- = 0.04$), and tree ($p_+ = 0.12$; $p_- = 0.03$) species was quite

256 low, and positive relationships –indicating higher abundance at range edges– were
257 just as common as negative relationships. These findings were robust to using
258 Spearman’s correlation coefficients to capture potentially non-linear relationships
259 between distance and abundance (Figure S4) and when defining species range and
260 climatic niche centroids (and subsequent distance to centroid) based on occurrence
261 data instead of abundance data (Figure S3). Lastly, we failed to detect consistently
262 strong relationships between geographic distance to species range centroids and
263 environmental distance to species niche centroids (Figure 3), though these relationships
264 did tend to be positive.

265
266 Examining the *distance-abundance* relationship in terms of environmental distance
267 from the niche centroid did not increase the detectability of *distance-abundance*
268 relationships; environmental distance from centroid and species abundance had
269 near zero correlation coefficients for birds ($\bar{\rho}_{bird} = -0.010$), fishes ($\bar{\rho}_{fish} = 0.018$),
270 mammals ($\bar{\rho}_{mammal} = -0.068$), and trees ($\bar{\rho}_{tree} = 0.009$). Similar to when distance
271 was measured as geographic distance from species range centers, significant correlations,
272 both positive and negative, were detected only rarely for bird ($n_+ = 109$; $n_- =$
273 101), fish ($n_+ = 2$; $n_- = 1$), mammal ($n_+ = 1$; $n_- = 1$), and tree ($n_+ = 34$; $n_- =$
274 15) species. As with geographic *distance-abundance* relationships, these numbers
275 represented small portions of the number of species tested, and the percent of
276 significant *distance-abundance* relationships in bird ($p_+ = 0.09$; $p_- = 0.08$), fish
277 ($p_+ = 0.04$; $p_- = 0.02$), mammal ($p_+ = 0.02$; $p_- = 0.02$), and tree ($p_+ = 0.11$;
278 $p_- = 0.05$) species was quite low, and positive relationships –indicating higher
279 abundance at climatic niche edges– were just as common as negative relationships.

280 **Ecological and phylogenetic covariates to distance-abundance slope**

281 Species body size, geographic range area, and climatic niche area were unrelated to
282 the slope of the relationship between species population abundance and geographic
283 distance to range center or environmental distance from niche center (Table 1).
284 Further, we failed to detect evidence for a phylogenetic signal in the *distance-abundance*
285 slope for any species group, regardless of whether distance was defined in terms
286 of geographic distance from species range centroid or niche distance from species
287 niche center (Table 2).

288 **Discussion**

289 The assumption that species abundance—or perhaps more properly termed *density*—is
290 highest at the geographic range or climatic niche center is a central assumption
291 of many hypotheses in macroecology (Gaston & Blackburn, 2003; Brown, 1984)
292 and population ecology (Pulliam, 2000), with qualitative evidence for the pattern
293 dating back to the formation of ecology as a discipline (Gause, 1930; Whittaker,
294 1952). However, empirical support remains limited, for a number of factors including
295 variation in environmental conditions, incomplete sampling of species ranges, or
296 interactions with competitors and parasites (Sagarin *et al.*, 2006; Borregaard &
297 Rahbek, 2010). We suggested a simple test of the *distance-abundance* relationship;
298 if species are most abundant in the center of their spatial range, then a negative
299 correlation should exist between species abundance and distance from either geographic
300 or niche centroid. We failed to detect a signal of *distance-abundance* relationships
301 using a dataset consisting of over 118,000 sampled populations across over 1400
302 species across a wide range of species, including birds, mammals, trees, and

303 fishes. Further, we have provided the first attempt to relate the strength of
304 the *distance-abundance* correlation to species traits, range size, and evolutionary
305 history. We failed detect any influence of body size, range size, or evolutionary
306 history on the correlation between species abundance and spatial or environmental
307 distance. Together, our findings suggest that *distance-abundance* relationships
308 may not be as general as previously believed, and that hypotheses and models
309 based upon the assumption that species abundance is highest in the interior of a
310 species geographic range or niche may need to be reconsidered.

311
312 Some previous studies have found support for *distance-abundance* relationships
313 (references within Pironon *et al.* (2016); Sagarin & Gaines (2002)), and the closely
314 related relationship between mean abundance and species range size (Gaston *et al.*,
315 2000), leading to classification of *distance-abundance* relationships as a general rule
316 in macroecology (Hengeveld & Haeck, 1982). However, several recent studies have
317 failed to detect any effect of spatial distance from species range center or to species
318 niche edges on species local abundance (see meta-analysis by Sagarin & Gaines
319 (2002)). More recently, researchers have begun to explore the conditions under
320 which *distance-abundance* relationships should be observed. For instance, several
321 recent studies have recongized that geographic distance may simply be a surrogate
322 for environmental distance, in which niche constraints are responsible for the
323 relationship between distance from a species range center and abundance (Knouft
324 & Anthony, 2016a; Martínez-Meyer *et al.*, 2013). However, we failed to detect
325 strong associations between distance and species abundance regardless whether
326 distance was measured as geographic distance or environmental distance. Further,
327 we arrived at different conclusions than Knouft & Anthony (2016a), though we

328 used the same data on freshwater fish abundance (Knouft & Anthony, 2016b).
329 This disparity stems from a key difference between our conceptual approaches;
330 Knouft & Anthony (2016a) uses a model selection procedure to examine if principal
331 component axes representing climatic variation can explain local abundance, while
332 we examine the shape of decay relationship between local abundance and geographic
333 or environmental distance. While relating climatic conditions to species abundance
334 is important to understand patterns of species abundance, the application of
335 regression analyses from niche modeling may not be appropriate to address macroecological
336 *rules* like the *distance-abundance* relationship, as the ability to predict species
337 abundance as a function of climatic covariates does not directly test if species
338 abundance declines from a species range or niche center.

339

340 There are at least two classes of mechanisms that reduce the probability of
341 observing a *distance-abundance* relationship. First, species abundances may not be
342 strongly constrained by the environmental variables measured here. This suggests
343 that unmeasured environmental variation may underlie *distance-abundance* relationships,
344 or that species interactions and community structure may be more important
345 in regulating population abundance than the environment. Second, the spatial
346 distribution of abundance, and subsequent *distance-abundance* relationships, may
347 be limited by dispersal boundaries or unmeasured ecological interactions. For
348 instance, coasts and mountain ranges represent obvious barriers to species spread.
349 Species abundance may be highest at the barrier (Brown *et al.*, 1996), with the
350 putative explanation being directional dispersal against a barrier, and an environment
351 capable of sustaining relatively high species abundance. To address this in our
352 analyses, we discarded species with greater than average abundance at sampling

353 limits present in the USDA FIA seedling data and the eBird data (sampling
354 locations in Figure S8). Though we used the most extensive data available,
355 temporal variation in abundance, changing environmental conditions, and the role
356 of interspecific interactions with competitors and natural enemies (Robinson *et al.*,
357 2010; Hastings *et al.*, 1997; Frick *et al.*, 2010) may further confound detection of
358 *distance-abundance* relationships. Understanding how interspecific interactions,
359 natural enemies, environmental forces, and dispersal barriers influence the existence
360 of *distance-abundance* relationship remains an open question; one, when answered,
361 may provide an underlying basis for the emergence of the macroecological pattern.

362
363 Macroecological relationships, such as those examining spatial abundance patterns,
364 are interesting due to their perceived generality (Brown, 1984; McGill & Collins,
365 2003; Lennon & Locey, 2017). However, the development of macroecological *laws* is
366 confounded when researchers use different measures of abundance or distribution.
367 This confusion may promote the construction of hypotheses which assume these
368 general relationships. Clear definitions of terms used to refer to macroecological
369 variables (e.g., distribution, abundance), the application of mechanistic approaches
370 to the study of macroecological relationships (Eckert *et al.*, 2008; Alexander *et al.*,
371 2016), and closer examination of hypotheses assuming the existence of *distance-abundance*
372 relationships are necessary to determine support for *distance-abundance* relationships,
373 and macroecological relationships in general.

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378 eBird), species occurrences (GBIF), species traits (Pantheria, fishbase, Amniote
379 database), and phylogenies (bird and mammal supertrees) used in this manuscript.
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References

- Alexander, J.M., Diez, J.M., Hart, S.P. & Levine, J.M. (2016). When climate reshuffles competitors: a call for experimental macroecology. *Trends in Ecology & Evolution*, 31, 831–841.
- Barbet-Massin, M. & Jetz, W. (2014). A 40-year, continent-wide, multispecies assessment of relevant climate predictors for species distribution modelling. *Diversity and Distributions*, 20, 1285–1295.
- Bininda-Emonds, O.R., Cardillo, M., Jones, K.E., MacPhee, R.D., Beck, R.M., Grenyer, R., Price, S.A., Vos, R.A., Gittleman, J.L. & Purvis, A. (2007). The delayed rise of present-day mammals. *Nature*, 446, 507–512.
- Blackburn, T.M., Cassey, P. & Gaston, K.J. (2006). Variations on a theme: sources of heterogeneity in the form of the interspecific relationship between abundance and distribution. *Journal of Animal Ecology*, 75, 1426–1439.
- Borregaard, M.K. & Rahbek, C. (2010). Causality of the relationship between geographic distribution and species abundance. *The Quarterly Review of Biology*, 85, 3–25.
- Brown, J.H. (1984). On the relationship between abundance and distribution of species. *American Naturalist*, 124, 255–279.
- Brown, J.H., Stevens, G.C. & Kaufman, D.M. (1996). The geographic range: size, shape, boundaries, and internal structure. *Annual review of ecology and systematics*, 27, 597–623.

- 403 Chamberlain, S. (2017). *spocc: Interface to Species Occurrence Data Sources*. R
404 package version 0.6.2.9140.
- 405 Chamberlain, S., Szocs, E., Boettiger, C., Ram, K., Bartomeus, I., Baumgartner,
406 J., Foster, Z. & O'Donnell, J. (2016). *taxize: Taxonomic information from*
407 *around the web*. R package version 0.7.8.
- 408 Chamberlain, S.A. & Szöcs, E. (2013). *taxize: taxonomic search and retrieval in*
409 *R. F1000Research*, 2.
- 410 Dallas, T. & Drake, J. (2017). The world is nearly flat: Species distributions and
411 the dimensionality of the future global environment. *in review*.
- 412 Diniz-Filho, J.A.F., Carvalho, P., Bini, L.M. & Tôrres, N.M. (2005). Macroecology,
413 geographic range size–body size relationship and minimum viable population
414 analysis for new world carnivora. *Acta Oecologica*, 27, 25–30.
- 415 Eckert, C., Samis, K. & Loughheed, S. (2008). Genetic variation across species
416 geographical ranges: the central–marginal hypothesis and beyond. *Molecular*
417 *ecology*, 17, 1170–1188.
- 418 Flügge, A.J., Olhede, S.C. & Murrell, D.J. (2012). The memory of spatial patterns:
419 changes in local abundance and aggregation in a tropical forest. *Ecology*, 93,
420 1540–1549.
- 421 Frick, W.F., Pollock, J.F., Hicks, A.C., Langwig, K.E., Reynolds, D.S., Turner,
422 G.G., Butchkoski, C.M. & Kunz, T.H. (2010). An emerging disease causes
423 regional population collapse of a common north american bat species. *Science*,
424 329, 679–682.

- 425 Froese, R. & Pauly, D. (2000). *FishBase 2000: Concepts Designs and Data Sources*.
426 vol. 1594. WorldFish.
- 427 Gaston, K.J. & Blackburn, T.M. (2003). Dispersal and the interspecific
428 abundance-occupancy relationship in british birds. *Global Ecology and*
429 *Biogeography*, 12, 373–379.
- 430 Gaston, K.J., Blackburn, T.M., Greenwood, J.J., Gregory, R.D., Quinn, R.M. &
431 Lawton, J.H. (2000). Abundance–occupancy relationships. *Journal of Applied*
432 *Ecology*, 37, 39–59.
- 433 Gause, G. (1930). Studies on the ecology of the Orthoptera. *Ecology*, 11, 307–325.
- 434 Grafen, A. (1989). The phylogenetic regression. *Philosophical Transactions of the*
435 *Royal Society of London. Series B, Biological Sciences*, 326, 119–157.
- 436 Hastings, A., Harrison, S. & McCann, K. (1997). Unexpected spatial patterns in
437 an insect outbreak match a predator diffusion model. *Proceedings of the Royal*
438 *Society of London B: Biological Sciences*, 264, 1837–1840.
- 439 Hengeveld, R. & Haeck, J. (1982). The distribution of abundance. I. Measurements.
440 *Journal of Biogeography*, pp. 303–316.
- 441 Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005). Very
442 high resolution interpolated climate surfaces for global land areas. *International*
443 *Journal of Climatology*, 25, 1965–1978.
- 444 Holt, R., Lawton, J., Gaston, K. & Blackburn, T. (1997). On the relationship
445 between range size and local abundance: Back to basics. *Oikos*, 78, 183–190.

- 446 Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., O'Dell, J., Orme, C.D.L., Safi, K.,
447 Sechrest, W., Boakes, E.H., Carbone, C. *et al.* (2009). Pantheria: a species-level
448 database of life history, ecology, and geography of extant and recently extinct
449 mammals. *Ecology*, 90, 2648–2648.
- 450 Kattge, J., Diaz, S., Lavorel, S., Prentice, I., Leadley, P., Bönisch, G., Garnier,
451 E., Westoby, M., Reich, P.B., Wright, I. *et al.* (2011). TRY—a global database
452 of plant traits. *Global Change Biology*, 17, 2905–2935.
- 453 Knouft, J.H. & Anthony, M.M. (2016a). Climate and local abundance in freshwater
454 fishes. *Royal Society Open Science*, 3, 160093.
- 455 Knouft, J.H. & Anthony, M.M. (2016b). Data from: Climate and
456 local abundance in freshwater fishes. *Dryad Digital Repository*, p.
457 <http://dx.doi.org/10.5061/dryad.1d1t5>.
- 458 Kriticos, D.J., Jarošik, V. & Ota, N. (2014). Extending the suite of bioclim
459 variables: a proposed registry system and case study using principal components
460 analysis. *Methods in Ecology and Evolution*, 5, 956–960.
- 461 Lennon, J.T. & Locey, K.J. (2017). Macroecology for microbiology. *Environmental*
462 *Microbiology Reports*, 9, 38–40.
- 463 Martínez-Meyer, E., Díaz-Porrás, D., Peterson, A.T. & Yáñez-Arenas, C. (2013).
464 Ecological niche structure and rangewide abundance patterns of species. *Biology*
465 *Letters*, 9, 20120637.
- 466 McGill, B. & Collins, C. (2003). A unified theory for macroecology based on spatial
467 patterns of abundance. *Evolutionary Ecology Research*, 5, 469–492.

- 468 Murphy, H.T., VanDerWal, J. & Lovett-Doust, J. (2006). Distribution of
469 abundance across the range in eastern north american trees. *Global Ecology*
470 *and Biogeography*, 15, 63–71.
- 471 Myhrvold, N.P., Baldrige, E., Chan, B., Sivam, D., Freeman, D.L. & Ernest, S.
472 (2015). An amniote life-history database to perform comparative analyses with
473 birds, mammals, and reptiles. *Ecology*, 96, 3109–3109.
- 474 Nagy, K.A. (2005). Field metabolic rate and body size. *Journal of Experimental*
475 *Biology*, 208, 1621–1625.
- 476 Paradis, E., Claude, J. & Strimmer, K. (2004). APE: analyses of phylogenetics
477 and evolution in R language. *Bioinformatics*, 20, 289–290.
- 478 Pironon, S., Papuga, G., Villellas, J., Angert, A.L., García, M.B. & Thompson,
479 J.D. (2016). Geographic variation in genetic and demographic performance: new
480 insights from an old biogeographical paradigm. *Biological Reviews*.
- 481 Pulliam, H.R. (2000). On the relationship between niche and distribution. *Ecology*
482 *letters*, 3, 349–361.
- 483 Ren, H., Condit, R., Chen, B., Mi, X., Cao, M., Ye, W., Hao, Z. & Ma, K. (2013).
484 Geographical range and local abundance of tree species in china. *PLoS ONE*, 8,
485 e76374.
- 486 Richards, L.J. & Schnute, J.T. (1986). An experimental and statistical approach
487 to the question: is cpue an index of abundance? *Canadian Journal of Fisheries*
488 *and Aquatic Sciences*, 43, 1214–1227.

- 489 Robinson, R.A., Lawson, B., Toms, M.P., Peck, K.M., Kirkwood, J.K., Chantrey,
490 J., Clatworthy, I.R., Evans, A.D., Hughes, L.A., Hutchinson, O.C. *et al.* (2010).
491 Emerging infectious disease leads to rapid population declines of common british
492 birds. *PLoS ONE*, 5, e12215.
- 493 Sagarin, R.D. & Gaines, S.D. (2002). The “abundant centre” distribution: to what
494 extent is it a biogeographical rule? *Ecology Letters*, 5, 137–147.
- 495 Sagarin, R.D., Gaines, S.D. & Gaylord, B. (2006). Moving beyond assumptions
496 to understand abundance distributions across the ranges of species. *Trends in*
497 *Ecology & Evolution*, 21, 524–530.
- 498 Samis, K.E. & Eckert, C.G. (2007). Testing the abundant center model using
499 range-wide demographic surveys of two coastal dune plants. *Ecology*, 88,
500 1747–1758.
- 501 Smith, F.A. & Lyons, S.K. (2013). *Animal body size: linking pattern and process*
502 *across space, time, and taxonomic group*. University of Chicago Press.
- 503 Sullivan, B.L., Wood, C.L., Iliff, M.J., Bonney, R.E., Fink, D. & Kelling, S.
504 (2009). ebird: A citizen-based bird observation network in the biological sciences.
505 *Biological Conservation*, 142, 2282–2292.
- 506 Thibault, K.M., Supp, S.R., Giffin, M., White, E.P. & Ernest, S. (2011).
507 Species composition and abundance of mammalian communities. *Ecology*, 92,
508 2316–2316.
- 509 Vandermeer, J.H. & Goldberg, D.E. (2013). *Population ecology: first principles*.
510 Princeton University Press.

- 511 VanDerWal, J., Shoo, L.P., Johnson, C.N. & Williams, S.E. (2009). Abundance
512 and the environmental niche: environmental suitability estimated from niche
513 models predicts the upper limit of local abundance. *The American Naturalist*,
514 174, 282–291.
- 515 Weber, M.M., Stevens, R.D., Diniz-Filho, J.A.F. & Grelle, C.E.V. (2016). Is there
516 a correlation between abundance and environmental suitability derived from
517 ecological niche modelling? A meta-analysis. *Ecography*.
- 518 Whittaker, R.H. (1952). A study of summer foliage insect communities in the
519 great smoky mountains. *Ecological Monographs*, 22, 1–44.
- 520 Woudenberg, S.W., Conkling, B.L., OConnell, B.M., LaPoint, E.B., Turner,
521 J.A. & Waddell, K.L. (2010). The forest inventory and analysis database:
522 Database description and users manual version 4.0 for phase 2. *Gen. Tech.*
523 *Rep. RMRS-GTR-245. Fort Collins, CO: US Department of Agriculture, Forest*
524 *Service, Rocky Mountain Research Station.*

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Table 1: Species body size, geographic range area ($\log \text{km}^2 + 1$), and climatic niche area ($\log \text{area} + 1$) explained very little of the variation in *distance-abundance* slope, treating distance either as geographic distance from species range center (models identified by subscript G) or environmental distance from species climatic niche center (identified by subscript E). Due to limited data availability, species body size was estimated as mass (g) for mammals and birds, length (cm) for fish, and height (m) for trees. The number of species for which data were available is given by n . β are model coefficients (with standard errors SE), and t and p are the t -statistic and p -value associated with model coefficients.

Taxa	Variable	n	β_G	SE_G	t	p	R^2	β_E	SE_E	t	p	R^2
Birds	Body mass	1047	-0.001	0.003	-0.397	0.69	0.03	-0.004	0.003	-1.058	0.29	0.002
	Range size	1137	0.024	0.005	4.680	<0.001		-0.002	0.010	-0.205	0.84	
	Niche area	1137	-0.007	0.010	-0.672	0.50		0.006	0.005	1.174	0.24	
Trees	Height	48	-0.006	0.014	-0.410	0.68	0.03	-0.004	0.014	-0.299	0.77	0.13
	Range size	48	0.011	0.006	1.810	0.07		0.003	0.018	0.174	0.86	
	Niche area	48	-0.006	0.018	-0.338	0.74		-0.008	0.006	-1.332	0.18	
Mammals	Body mass	39	0.019	0.054	0.345	0.73	0.04	-0.041	0.045	-0.915	0.37	0.06
	Range size	42	-0.070	0.062	-1.136	0.26		-0.098	0.082	-1.207	0.24	
	Niche area	42	0.078	0.098	0.795	0.43		0.051	0.051	0.991	0.33	
Fishes	Length	209	-0.016	0.031	-0.529	0.60	0.02	0.040	0.034	1.174	0.25	0.01
	Range size	294	0.037	0.071	0.522	0.60		0.112	0.140	0.796	0.43	
	Niche area	294	-0.025	0.127	-0.195	0.85		-0.111	0.078	-1.419	0.16	

Table 2: We failed to detect a phylogenetic signal in the relationship between spatial distance from either the geographic (G) or niche (E) centroid for any species group examined. The analysis uses a permutation approach of Moran's I values to test for the presence of a phylogenetic signal in *distance-abundance* relationships.

Taxa	obs $_G$	exp $_G$	sd $_G$	p	obs $_E$	exp $_E$	sd $_E$	p
Birds	0.001	-0.001	0.02	0.80	-0.01	-0.001	0.02	0.72
Trees	-0.003	-0.004	0.002	0.70	-0.004	-0.004	0.002	0.65
Mammals	-0.03	-0.004	0.03	0.48	0.02	-0.004	0.03	0.46
Fishes	-0.02	-0.016	0.01	0.52	-0.02	-0.016	0.01	0.82

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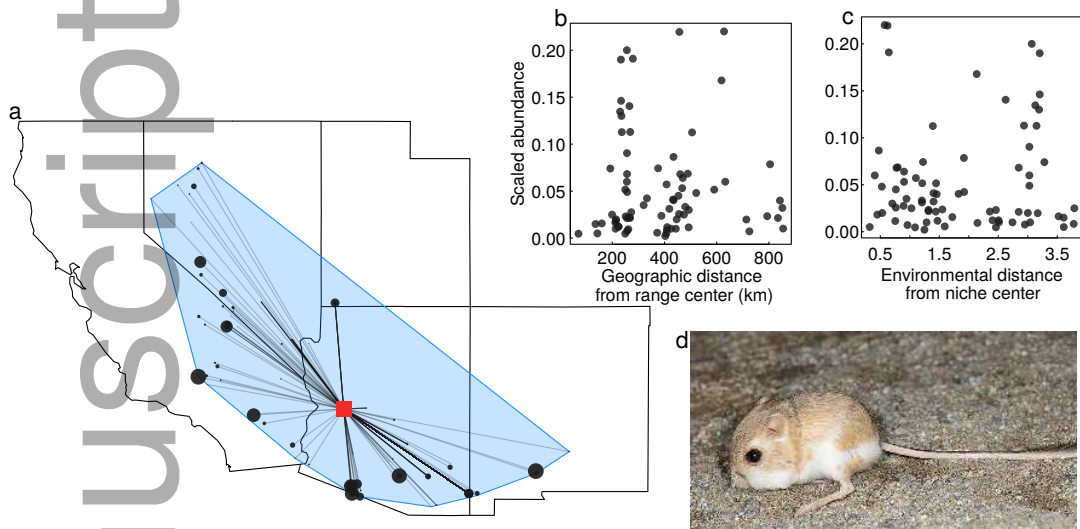
Figure 1: An example of the spatial distribution of abundance for *Dipodomys merriami*, whose range is outlined by a blue convex polygon, and whose center is denoted by a red square (panel a). Lines connecting this centroid to each population – black points with population size proportional to point size – provide a means to measure geographic distance. The relationship between scaled abundance of *D. merriami* and geographic (b) and environmental (c) distance provide an instance of the lack of a clear *distance-abundance* relationship. Photograph of *D. merriami* (d) is by Marshal Hedin.

Figure 2: *Distance-abundance* correlations for over 1600 species reveal a lack of support for the hypothesis that populations should have the highest abundance in the a) center of their geographic distribution or b) in the interior of their niche. Distance from the geographic or niche center was calculated either as spatial distance (a) or Euclidean distance in climatic niche space from species niche centroid (b).

Figure 3: Pearson's correlation coefficients between spatial and environmental distance from geographic or niche centers reveals that geographic distance and niche distance are often only weakly related, and can even be negatively related, corresponding to a situation where nearby environmental conditions are less similar than those in geographically distant areas.

527 **Figures**

528 **Figure 1**

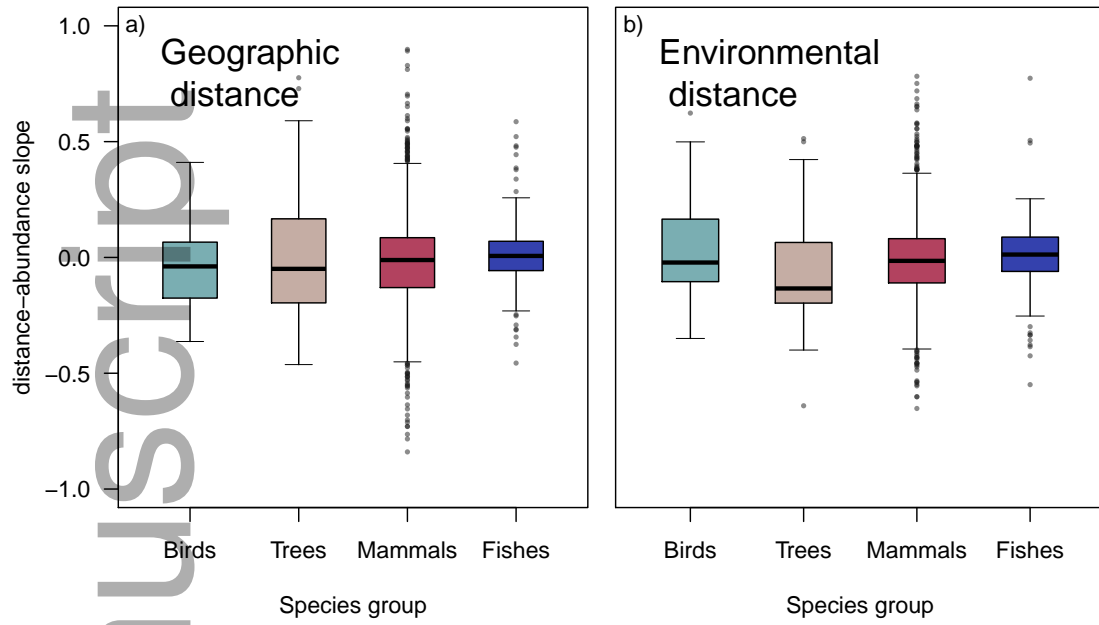


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Figure 2

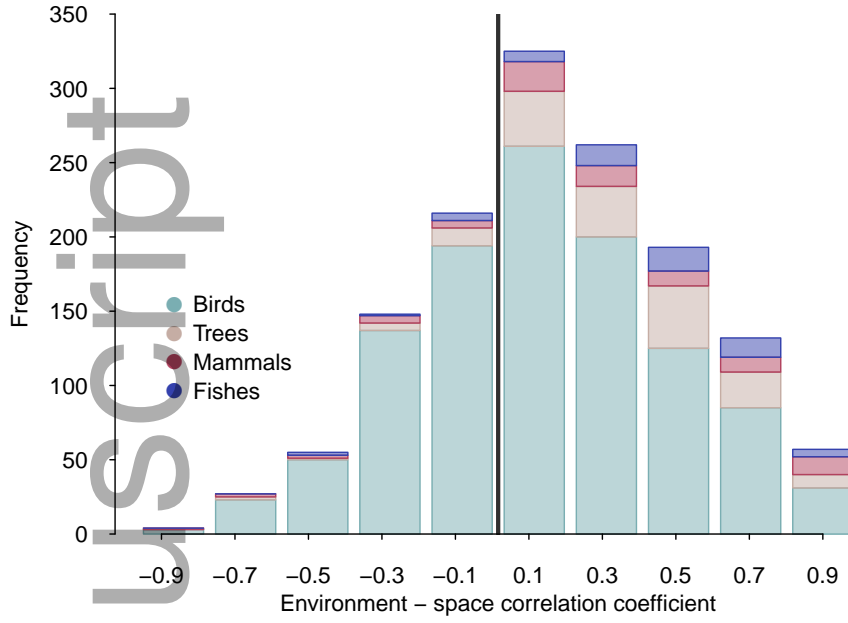


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Figure 3



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534 Supplemental Material

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541

542 Comparing geographic range coverage with occupancy data

543 An assumption of the main text analyses was that the range of each species –
544 or at least that the centroid of the species range – was adequately estimated
545 by the sampled populations. However, this could not be the case given the
546 data constraints. To investigate this further, we calculated species range and
547 niche centroids using freely available occurrence data obtained from the Global
548 Biodiversity Information Facility using the R package `spocc` (Chamberlain, 2017).
549 Species geographic range and niche centroids were estimated by forming a minimum
550 convex hull around the sampling occurrence points, which were truncated to
551 include the Americas for mammals and birds, and just North America for trees
552 and fishes. This allowed us the opportunity to compare species range estimates
553 from abundance and occurrence data. We found that occurrence data tended to
554 estimate larger range areas (Figure S1), measured as the area of the minimum
555 convex polygon encompassing all sampled points.

556

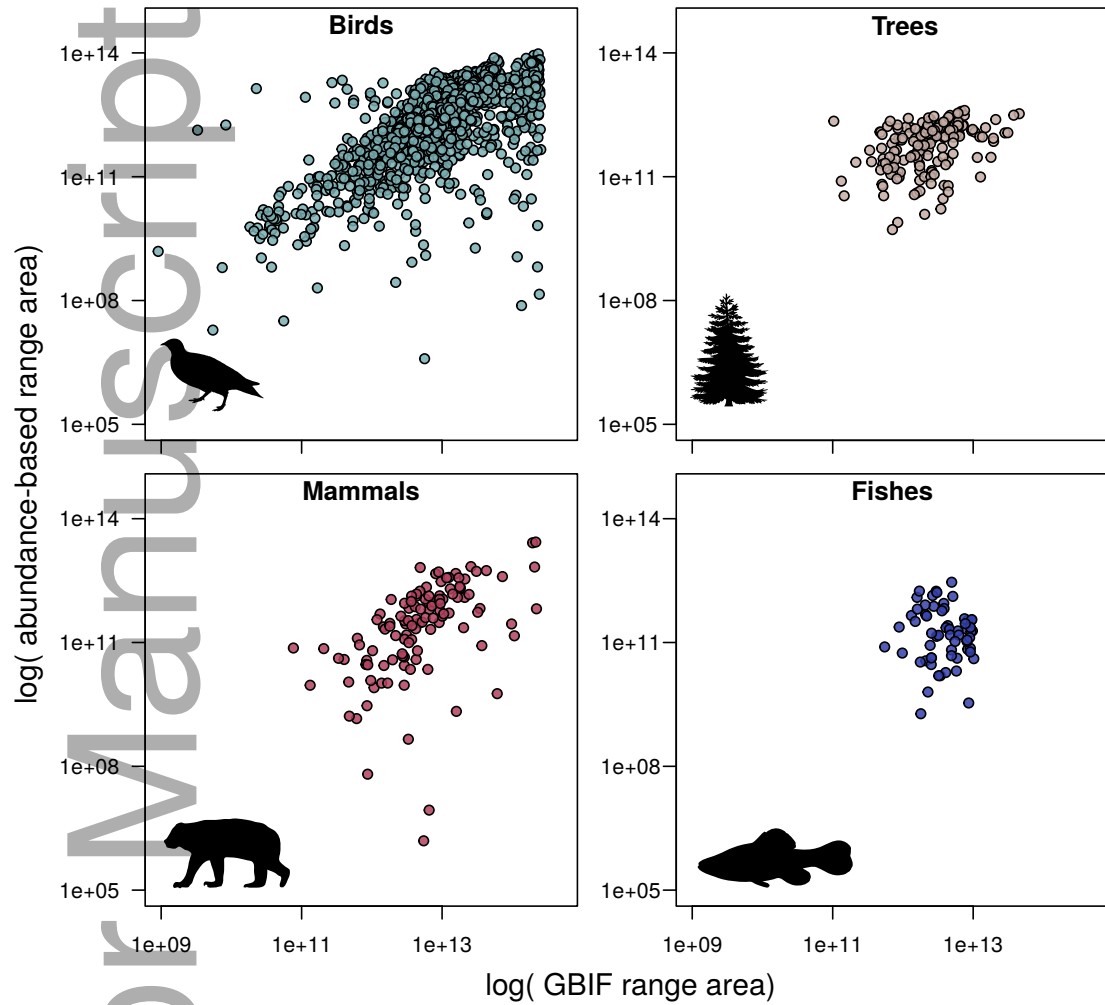


Figure S1: A comparison of species range area estimates from abundance-based data and occurrence data from the Global Biodiversity Information Facility (GBIF). Silhouettes were obtained from Phylopic.

557 Further examination of the difference between range size estimates from occurrence
558 and abundance data demonstrated that this difference was unrelated to the observed
559 *distance-abundance* slope (Figure S2).

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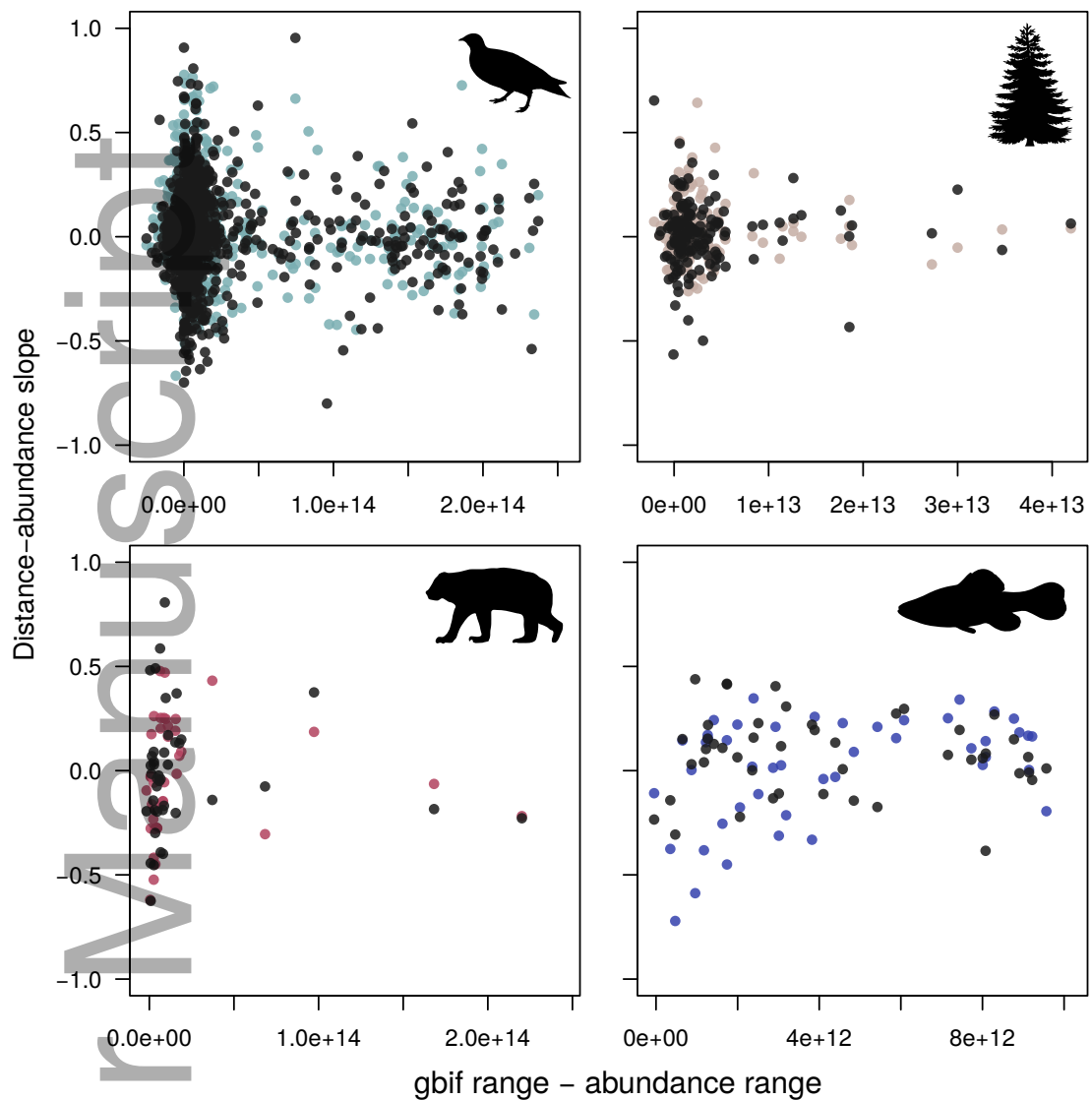


Figure S2: *Distance-abundance* relationships were unrelated to the absolute value of the difference between species range size as estimated from GBIF occurrence data and range size estimated from abundance data. Points are colored by how *distance-abundance* relationships were quantified; either as Haversine distance from species range centers (colored points), or climatic distance from niche center (grey points). Silhouettes were obtained from Phylopic.

560 Distance from each sampled population to the GBIF-estimated centroid was
561 then used as our distance measure, and was related to population abundance
562 as in the main text. Our main text findings are robust to this change, with
563 *distance-abundance* relationships still quite weak and rarely observed (Figure S3).
564 Further, we found a similar lack of predictive power of species traits, range size,
565 and climatic niche area when calculating species range/niche centroids using GBIF
566 data (Table S1).

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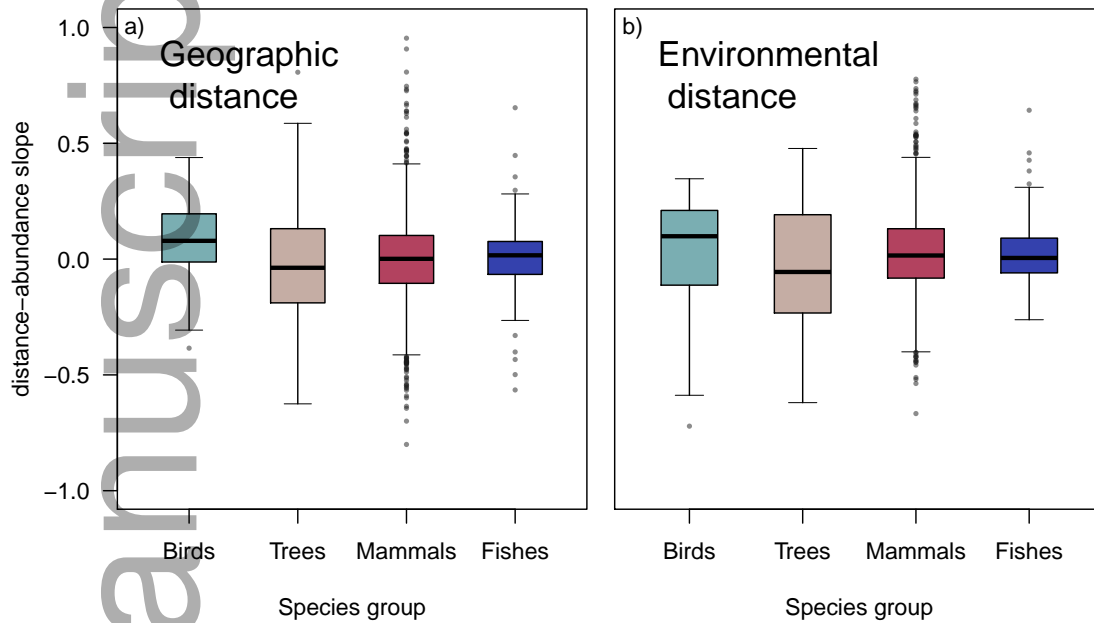


Figure S3: *Distance-abundance* correlations for over 1600 species reveal a lack of support for the hypothesis that populations should have the highest abundance in the *a)* center of their geographic distribution or *b)* in the interior of their niche. Distance from the geographic or niche center was calculated either as spatial distance (*a)* or Euclidean distance in climatic niche space from species niche centroid (*b)* based on species occurrence data from GBIF.

Table S1: Species body size, geographic range area ($\log \text{km}^2 + 1$), and climatic niche area ($\log \text{area} + 1$) explained very little of the variation in *distance-abundance* slope, treating distance either as geographic distance from species range center (models identified by subscript G) or environmental distance from species climatic niche center (identified by subscript E). Due to limited data availability, species body size was estimated as mass (g) for mammals and birds, length (cm) for fish, and height (m) for trees. The number of species for which data were available is given by n . β are model coefficients (with standard errors SE), and t and p are the t -statistic and p -value associated with model coefficients.

Taxa	Variable	n	β_G	SE_G	t	p	R^2	β_E	SE_E	t	p	R^2
Birds	Body mass	1047	-0.00	0.00	-0.91	0.36	0.01	-0.01	0.00	-2.43	0.02	0.01
	Range size	1137	0.02	0.01	3.34	< 0.01		-0.03	0.01	-2.93	< 0.01	
	Niche area	1137	-0.03	0.01	-2.54	0.01		0.02	0.01	2.97	< 0.01	
Trees	Height	48	-0.03	0.01	-1.82	0.07	0.03	0.04	0.01	3.37	0.00	0.12
	Range size	48	-0.01	0.01	-0.94	0.35		-0.03	0.02	-1.95	0.05	
	Niche area	48	0.00	0.02	0.22	0.82		-0.01	0.01	-0.94	0.35	
Mammals	Body mass	39	0.12	0.06	2.13	0.04	0.13	-0.02	0.05	-0.42	0.68	0.21
	Range size	42	-0.04	0.06	-0.68	0.50		0.22	0.08	2.62	0.01	
	Niche area	42	0.07	0.10	0.72	0.48		-0.07	0.05	-1.29	0.20	
Fishes	Length	209	-0.09	0.04	-2.23	0.03	0.17	0.08	0.05	1.71	0.10	0.20
	Range size	294	0.02	0.09	0.28	0.78		0.09	0.17	0.56	0.58	
	Niche area	294	-0.09	0.14	-0.65	0.52		-0.09	0.10	-0.87	0.39	

567 **Relaxing the assumption of a linear *distance-abundance* relationship**

568 The Pearson's correlation coefficient used in the main text assumes a linear relationship
569 between distance and abundance. This is potentially too constraining. To address
570 this, we re-analyzed the *distance-abundance* relationships using Spearman's rank
571 correlation coefficients, which are able to capture non-linear – though still monotonic
572 – relationships. We find no difference in our main text results when Spearman's
573 correlation coefficient was used to assess *distance-abundance* relationships (Figure
574 S4). Further, we found a similar lack of predictive power of species traits, range
575 size, and climatic niche area when quantifying *distance-abundance* relationships
576 using Spearman's rank correlations instead of Pearson's correlations (Table S2).

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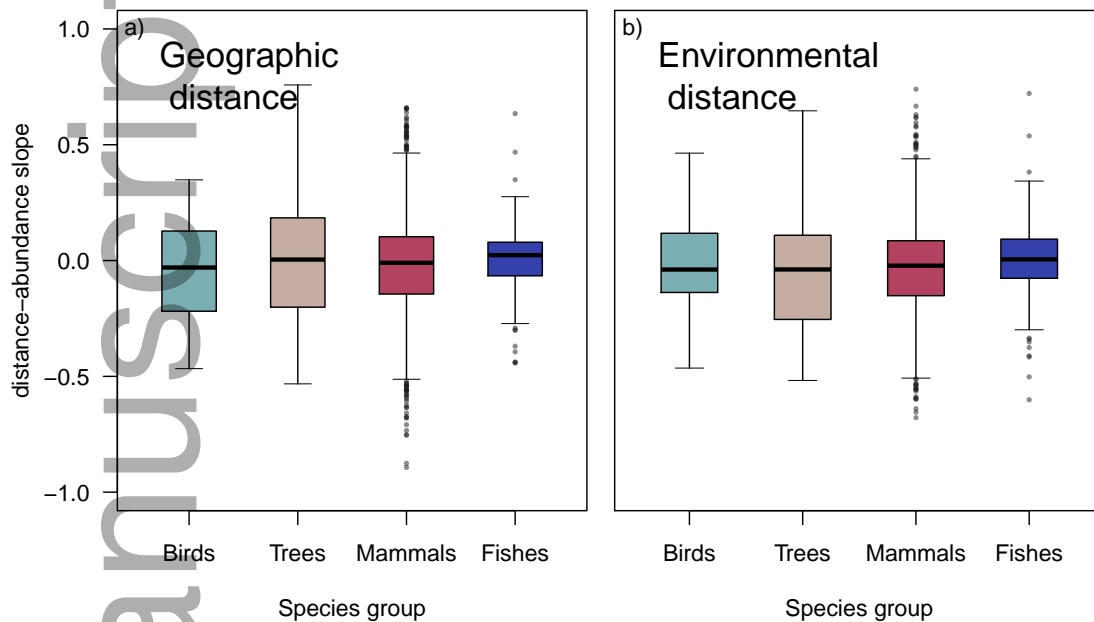


Figure S4: *Distance-abundance* correlations, using Spearman's rank correlations to capture potentially non-linear relationships, for over 1600 species reveal a lack of support for the hypothesis that populations should have the highest abundance in the *a*) center of their geographic distribution or *b*) in the interior of their niche. Distance from the geographic or niche center was calculated either as spatial distance (*a*) or Euclidean distance in climatic niche space from species niche centroid (*b*).

Table S2: Species body size, geographic range area ($\log \text{ km}^2 + 1$), and climatic niche area ($\log \text{ area} + 1$) explained very little of the variation in *distance-abundance* slope, treating distance either as geographic distance from species range center (models identified by subscript G) or environmental distance from species climatic niche center (identified by subscript E). Due to limited data availability, species body size was estimated as mass (g) for mammals and birds, length (cm) for fish, and height (m) for trees. The number of species for which data were available is given by n . β are model coefficients (with standard errors SE), and t and p are the t -statistic and p -value associated with model coefficients.

Taxa	Variable	n	β_G	SE_G	t	p	R^2	β_E	SE_E	t	p	R^2
Birds	Body mass	1047	-0.01	0.00	-1.83	0.07	0.02	-0.01	0.00	-2.56	0.01	0.01
	Range size	1137	0.03	0.01	4.21	< 0.01		-0.00	0.01	-0.25	0.81	
	Niche area	1137	-0.01	0.01	-1.05	0.30		0.01	0.01	1.04	0.30	
Trees	Height	48	-0.01	0.01	-0.53	0.60	0.03	0.02	0.02	1.09	0.28	0.02
	Range size	48	0.02	0.01	1.46	0.15		-0.02	0.02	-0.75	0.46	
	Niche area	48	0.00	0.02	0.09	0.93		-0.00	0.01	-0.26	0.80	
Mammals	Body mass	39	0.04	0.06	0.70	0.49	0.07	-0.06	0.05	-1.19	0.24	0.04
	Range size	42	-0.07	0.06	-1.14	0.26		-0.03	0.10	-0.27	0.79	
	Niche area	42	0.05	0.10	0.45	0.66		0.00	0.06	0.01	0.99	
Fishes	Length	209	-0.04	0.05	-0.73	0.47	0.04	0.03	0.05	0.61	0.55	0.11
	Range size	294	0.06	0.11	0.50	0.62		0.20	0.17	1.17	0.25	
	Niche area	294	-0.10	0.18	-0.57	0.57		-0.15	0.10	-1.40	0.17	

577 **The influence of migration in bird *distance-abundance* relationships**

578 Migratory birds present a challenge to range size estimation, and consequent
579 determination of *distance-abundance* relationships. To examine how our findings
580 were influenced by migratory bird species, we obtained migratory status of bird
581 species from Bird Life International (Selenium code to obtain this information is
582 available in the Supplemental Materials). Migratory bird species did not have
583 different *distance-abundance* relationships relative to partial migrants (altitudinal
584 migrants and nomadic species) or non-migrants (Figure S5).

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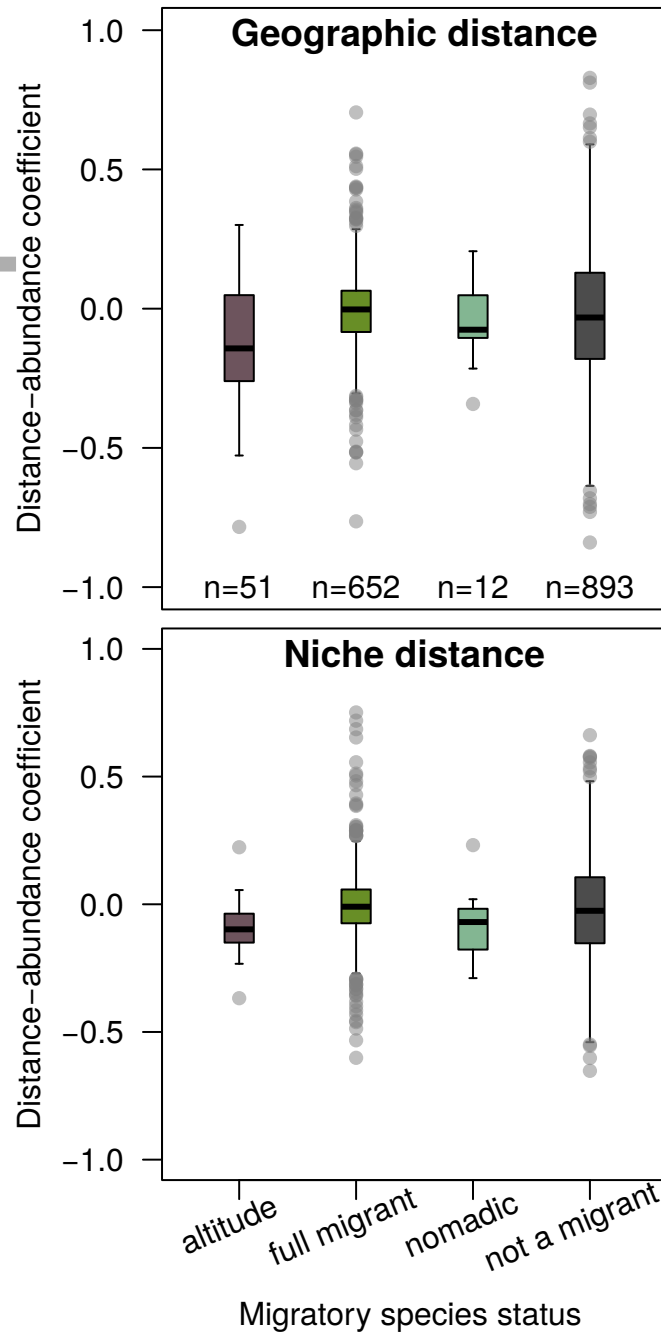


Figure S5: The *distance-abundance* relationship—defined by Pearson’s correlation coefficients between population abundance and geographic (left) or climatic niche (right) distance from species geographic range or niche center—were unaffected by migratory status for over 1200 bird species.⁴⁶

585 **Sensitivity of distance-abundance correlation to sample size**

586 The number of populations sampled was related to the magnitude of calculated
587 *distance-abundance* correlations, with larger positive and negative correlation values
588 commonly corresponding to less well-sampled species (Figure S6). For a full list
589 of species names and analytical code, see our corresponding data supplement
590 (<https://doi.org/10.6084/m9.figshare.5023232>). A map of sampling sites shows
591 the distribution of sites considered in our analyses (Figure S8). We included some
592 island populations for birds, as dispersal was likely not limiting. Interestingly,
593 the potential link between populations isn't a necessity for *distance-abundance*
594 relationships to hold (e.g, clear climatic tolerances could result in *distance-abundance*
595 relationships independent of population processes like dispersal).

596 Sample size could also influence the relationship between environmental distance
597 to niche centroid and geographic distance to range centroids. We failed to detect an
598 influence of number of sampled populations and corresponding environment-space
599 correlation coefficient (Figure S7).

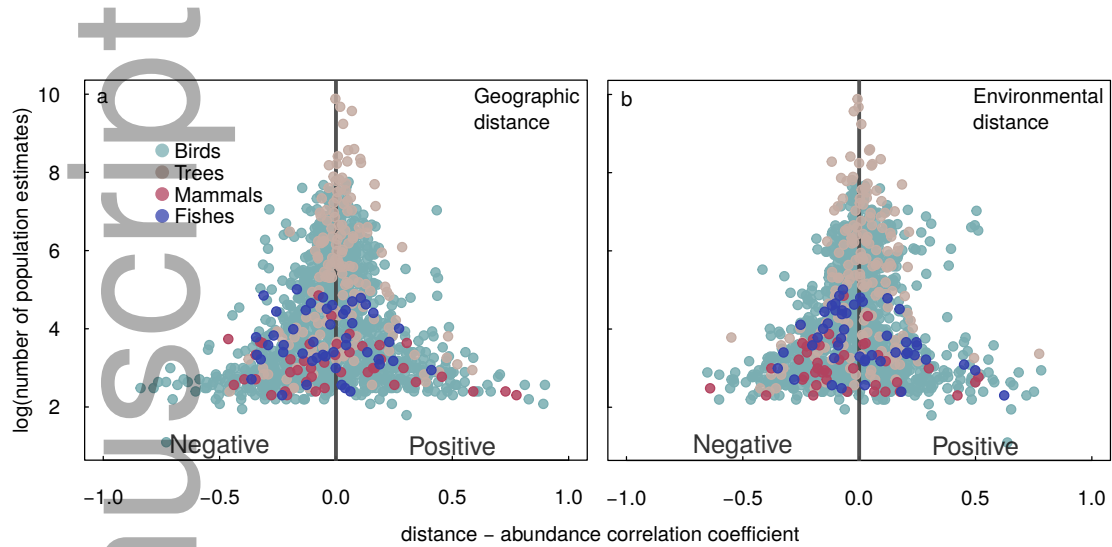


Figure S6: *Distance-abundance* correlation coefficients as a function of the number of sites the species was found in for each species taxa (different colored points). This suggests that strongly negative and positive correlations between *a*) geographic distance from the species range center and *b*) environmental distance from the niche center may be related to the number of species population estimates. That is, sites that were sampled more were more likely to have correlation coefficients near 0, while less well-sampled sites were responsible for the larger positive or negative *distance-abundance* slopes.

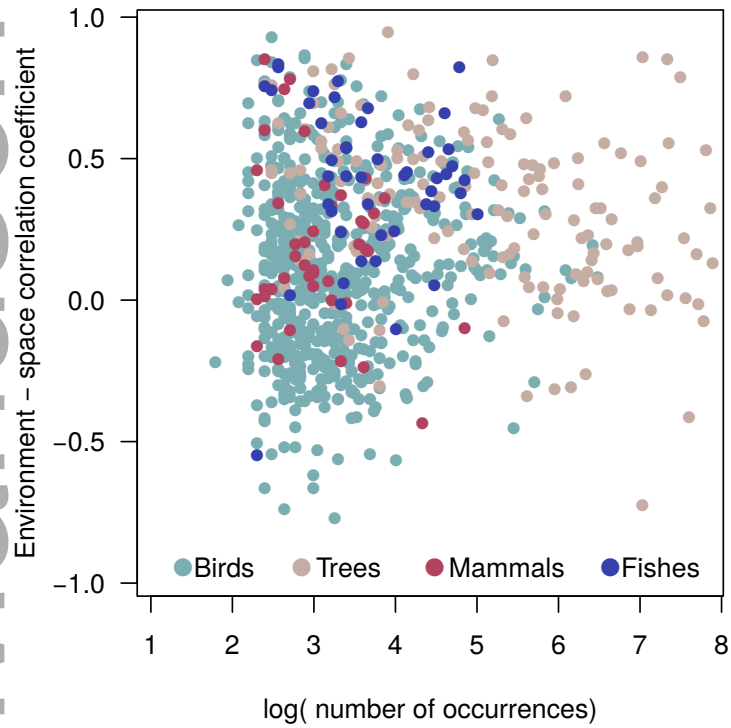


Figure S7: The correlation between distance from the geographic range or climatic niche center for all sampled populations (y-axis) was not strongly related with the number of sampled populations.

600 **Sampling locations**

601 A map showing the spatial locations of sampled locations used in the analyses is
602 provided in Figure S8.

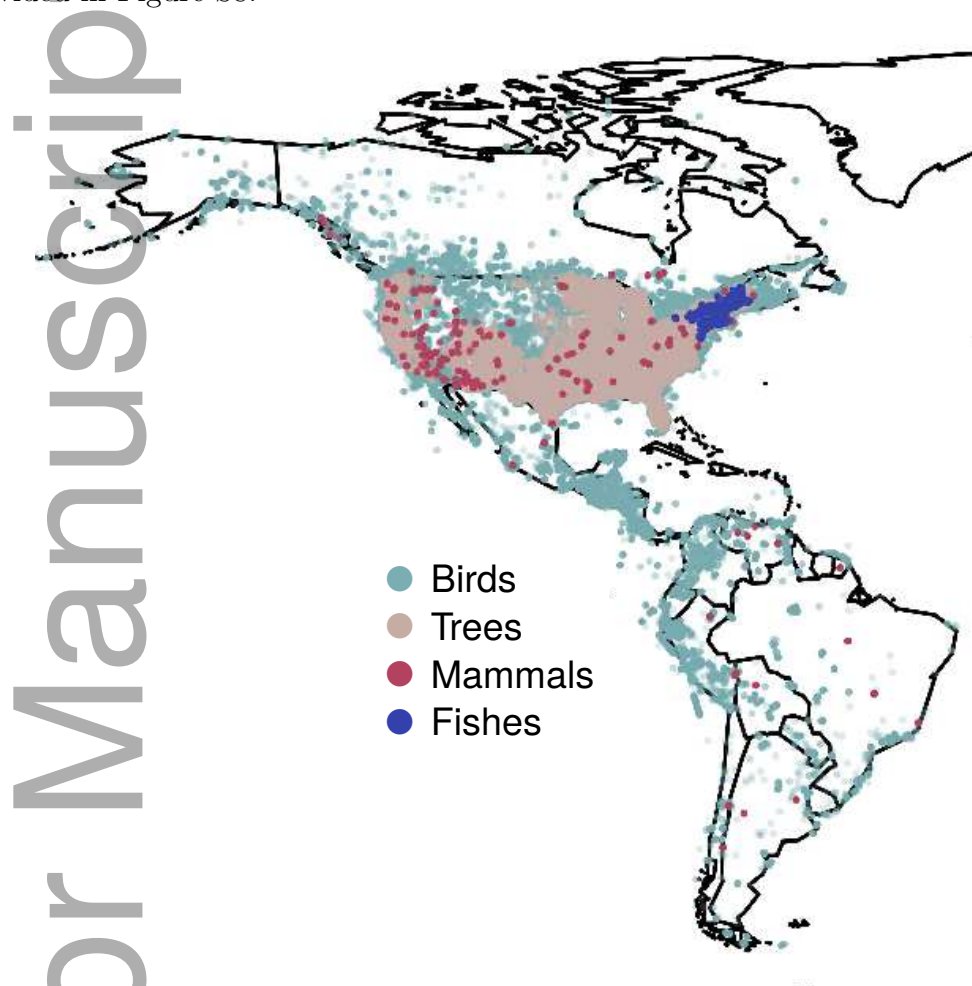


Figure S8: The spatial distribution of sampling sites throughout the Americas.

See main text for information on data sources.