

1   **Title:** The mismatch in distributions of vertebrates and the plants that they disperse

2   **Running head:** Distribution of seed dispersal mutualisms

3   Jacob W. Dittel<sup>1</sup>, Christopher M. Moore<sup>2</sup>, and Stephen B. Vander Wall<sup>3</sup>

4   **Keywords:** Seed dispersal, mutualism, scatter-hoarding, frugivory, species co-distributions, coevolution

5   **Article Type:** Letters

6   **Abstract Length:** 140

7   **Article Length:** 4,507

8   **Number of citations:** 58

9   **Number of Figures:** 3

10   **Number of Tables:** 2

11

12   <sup>1</sup>Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR, USA

13   97331. Email: Jacob.dittel@oregonstate.edu Phone: (920)904-1145

14   <sup>2</sup>Department of Biology, Case Western Reserve University, Cleveland, OH, USA 44106.

15   Email: life.dispersing@gmail.com

16   <sup>3</sup>Department of Biology, University of Nevada Reno, Reno, NV, USA 89557.

17   Email: sv@unr.edu

18   **Statement of authorship:** JD, CM, and SV conceived the original project idea. Plant  
19   data were compiled and analyzed by CM and SV, and JD compiled animal and  
20   environmental data. JD standardized and formatted all geographical data, and JD and  
21   CM performed all statistical analyses. JD wrote the first draft of the manuscript, and all  
22   authors contributed significantly to the revisions.  
23

24 **ABSTRACT**

25 Little is known about how mutualistic interactions affect the distribution of species  
26 richness on broad geographic scales. It has been predicted that the richness of species  
27 involved in obligate mutualisms should be positively associated across their range.  
28 Whereas, if mutualisms are facilitative, the distribution of mutualists should be correlated  
29 with other factors. This study is the first study to compare the co-distribution of mutualist  
30 species in general and seed dispersal mutualisms specifically. We used geographic  
31 distributions of plant and animal mutualists to investigate the co-distribution and patterns  
32 of seed dispersal mutualisms. We found the mutualism between dispersers and plants  
33 does not account for the distribution of either group. In fact, there is a mismatch of  
34 richness between plants and the animals that disperse their seeds. Environmental factors  
35 are better predictors of both animal distribution and seed dispersal mutualisms across  
36 North America.

37 **INTRODUCTION**

38       The broadest spatial scale of ecology examines patterns of diversity based on the  
39       geographic distributions of species (MacArthur 1972). Geographic distributions of  
40       species are important (i) to infer lower-level community-, population-, and physiological-  
41       based processes and (ii) as the ultimate comparison against which lower-level processes  
42       are compared (Bowyer *et al.* 1997; Somero 2005; Siefert *et al.* 2013). Indeed, there is a  
43       preponderance of studies of species richness at broad geographic scales (Oberdoff *et al.*  
44       1995; Rahbek & Graves 2001; Hawkins *et al.* 2003a; Rahbek *et al.* 2007) that have  
45       facilitated our understanding of why species are found where they are, a central tenet  
46       within the domain of ecology (Scheiner & Willig 2008). Most commonly, species  
47       distributions are compared with environmental variables, which are presumed  
48       determinants of species distributions. Environmental variables are only one determinant  
49       of species' distributions, however; the other determinant—species interactions—is a key,  
50       understudied determinant of species' distributions.

51       When species or guilds interact, we expect the geographic distributions of the  
52       pairs to be correlated. For pairwise interaction types where a species or guild benefits  
53       from another species or guild, we expect a positive relationship in distributions of  
54       abundance and richness due to the increase in fitness where they overlap (Svenning *et al.*  
55       2014). This should be especially true in the case of mutualisms, where both sides of the  
56       interaction share an increase in fitness from being together (Bronstein 2015). In the case  
57       of seed dispersal mutualisms, for example, the distribution of plants and the animals that  
58       disperse their seeds should be similar. In terms of diversity, this further implies that the  
59       richness of plant species should maintain an equal or similar richness of animal species

60 (Knops *et al.* 1999). Ultimately, this suggests for seed dispersal mutualisms that the  
61 richness of animal-dispersed plants *ought to be* correlated with the richness of their  
62 animal dispersers, and vice versa. To our knowledge, this prediction has never been  
63 tested on any appreciable geographic scale.

64 Seed dispersal is a critical stage in the life history of plants (Howe & Smallwood  
65 1982; Herrera 1985; Terborgh 1990), and plants have evolved a variety of environmental  
66 and biotic methods to disperse their seeds. Of those plants that are actively dispersed by  
67 animal mutualists, the mutualistic interactions are presumed to be asymmetrical—plants  
68 are obligate mutualists dependent on guilds of dispersing animals, whereas animals are  
69 facultative mutualists partially depending on the plants they disperse. Many studies have  
70 described the richness of animal species (e.g., Jetz & Rahbek 2002; Kissling *et al.* 2007,  
71 2009) and plant species (Kreft & Jetz 2007; Vander Wall & Moore 2016) at geographic  
72 scales and their relationship with various environmental variables. Yet despite the  
73 importance and commonality of these seed dispersal mutualisms, their distribution and  
74 prevalence are still poorly known globally (Vander Wall *et al.* submitted; Willson *et al.*  
75 1990; Almeida-Neto *et al.* 2008). One factor limiting the testing of hypotheses of seed  
76 dispersal mutualism diversity, and the effects of plant diversity on animal diversity in  
77 general, has been the lack of plant data (Hawkins & Pausas 2004). Recently, Vander Wall  
78 & Moore (2016) described the distribution of plants dispersed by animal mutualists in  
79 North America. They found that plants with seed-dispersal mutualists appear to be more  
80 sensitive to environmental conditions than plants dispersed non-mutualistically but it is  
81 unknown whether the species richness of animal dispersers contributes to this pattern. In  
82 this study, we build upon Vander Wall and Moore's (2106) finding to determine how the

83 diversity of seed dispersing animals affects the diversity of animal-dispersed plants  
84 and/or if seed dispersal mutualism are related to environmental variables.

85 Given our theoretical predictions that species and guilds involved in mutualisms  
86 should be positively associated across their geographic distribution, we investigated the  
87 composite distribution of terrestrial bird and mammal seed dispersers in across North  
88 America. The ultimate goal of this study was to determine how the richness of seed  
89 dispersing animals varies across North America and how that composite distribution  
90 matches up with the distribution of the plants that they disperse. To do so, we  
91 investigated whether the richness of seed dispersing animals is correlated with broad  
92 ecological and environmental variables, including the richness of the plants that they  
93 disperse. We hypothesize that if the mutualisms are obligate, as is presumed between  
94 plants being obligate mutualists of the seed dispersers, then the richness distribution of  
95 the plants would show a stronger relationship with seed dispersers compared with  
96 environmental variables. Alternatively, if the mutualisms between plants and seed  
97 dispersing animals is facultative or diffuse, as is presumed between the animals that  
98 disperse the plants, then we expect a stronger relationship between the richness  
99 distribution of animals and environmental variables compared with the plants. We  
100 methodologically used GIS and spatial statistics to investigate if plant mutualist  
101 abundance or environmental factors were correlated with seed dispersing animals and  
102 seed dispersing mutualisms. We surprisingly found that there is a mismatch between the  
103 richness of seed dispersing animals and the plants they disperse. Environmental variables  
104 were more often correlated with the distribution of seed dispersing animals and better

105 explained the distribution of seed dispersing mutualisms than the richness of either plant  
106 or animal mutualists.

107

108 **MATERIALS AND METHODS**

109 *Assignment of species to seed dispersing guilds*

110 To determine how the distribution of vertebrate seed dispersers compares to the  
111 plants that they disperse, we first assigned the birds and mammals of North America  
112 (north of Mexico) to two seed dispersing guilds: frugivorous and scatter-hoarding seed  
113 dispersers. Animals were considered frugivorous seed dispersers if they consume fruits  
114 containing seeds as a significant portion of their diet, and the seeds remain viable after  
115 being either regurgitated or passed through the digestive tract. Scatter-hoarding of seeds,  
116 which frequently results in a mutualism with plants, is limited to the bird family Corvidae  
117 and the mammal order Rodentia in North America (Vander Wall 1990) . A species was  
118 considered a scatter-hoarder if seeds are a significant portion of its diet, it scatter-hoards  
119 them in soil, and there is a reasonable expectation that some of those seeds germinate.  
120 Hereafter, we use the terms frugivore and scatter-hoarder to mean species that are  
121 mutualist seed dispersers. Full details of species assignment can be found in appendix  
122 S1a.

123  
124 *Data acquisition and preparation*

125 We prepared for our analyses by first creating comparable datasets. We had four  
126 groups of data: animal mutualists, environmental variables, plant mutualists, and the  
127 difference between animal and plant mutualists. The animal mutualists consisted of seven  
128 subguilds: all animal mutualists, frugivorous, scatter-hoarding, frugivorous mammals,

129 frugivorous birds, scatter-hoarding rodents, and scatter-hoarding birds. Species data  
130 consisted of a polygon of the geographic distribution involved in the type of mutualism.  
131 Bird distribution data were obtained from BirdLife International and NatureServe  
132 (Ridgley *et al.* 2007; BirdLife International and NaturServe 2014). Mammal distribution  
133 data were obtained from the International Union for Conservation of Nature Red List  
134 (IUCN 2012). These polygons were overlaid, richness was summed, and the resulting file  
135 was rasterized to generate animal mutualist species richness at each grid cell of a master  
136 raster.

137 The environmental variables consisted of four datasets: mean actual  
138 evapotranspiration (mm/yr; hereafter AET), elevation (m), mean precipitation (mm/year;  
139 hereafter precipitation) and latitude (degrees). AET was obtained from the Global-AET  
140 Database (Trabucco & Zomer 2010), elevation was obtained from Natural Earth (2017),  
141 and precipitation was obtained from Bioclim (Hijmans *et al.* 2005). These environmental  
142 variables were chosen because they have been found to be important predictors in  
143 previous studies of species distributions (Pearson & Dawson 2003). AET is a proxy for  
144 terrestrial productivity (Mackey & Currie 2001), and has been found to be associated  
145 with bird and plant distributions (Karr 1976; Hawkins *et al.* 2003b; Kissling *et al.* 2009).  
146 Precipitation is predicted to be important for scatter-hoarding behaviors, with the  
147 behavior being more frequent in semi-arid and arid ecosystems rather than mesic ones  
148 (Vander Wall & Jenkins 2011). Lastly, we included elevation because there are large  
149 elevational gradients in western North America and species richness generally decreases  
150 with an increase in elevation (Rahbek 1995). Each environmental variable was obtained

151 as a raster and bilinear interpolation was used to conform the extent and resolution of the  
 152 original raster to our master raster.

153       The plant mutualists consisted of seven datasets: plant mutualists, plants in  
 154 frugivory mutualism, plants in scatter-hoarding mutualism, plants in frugivory mutualism  
 155 with mammals, plants in frugivory mutualism with birds, plants in scatter-hoarding  
 156 mutualism with rodents, and plants in scatter-hoarding mutualism with birds. Each plant  
 157 dataset was obtained from a previous study that identified plants in dispersal mutualism  
 158 at 197 sites across North America, north of Mexico (Vander Wall & Moore 2016). For  
 159 this study, we used the plant species richness per site that are dispersed by frugivores or  
 160 scatter hoarders. (See Vander Wall & Moore (2016) for details on their methods and  
 161 dispersal mode determination.) We interpreted the point values and estimated values  
 162 across our geographic range of interest. Specifically, we used ordinary kriging to  
 163 interpolate values to our master raster using R library, automap (Hiemstra *et al.* 2009).  
 164 The difference between animal and plant mutualists were for the same seven modes listed  
 165 above. Because the means and variances were very different between animal and plant  
 166 mutualists, we calculated z-scores (eqn. 1) between them, and subtracted the z-score of  
 167 plant from animal mutualists at each point to create a value ( $Z_{\text{diff}}$ ) used in data analysis  
 168 described below.

$$169 \quad Z = \frac{\bar{X} - X_{\text{obs}}}{\sigma(X)} \quad (1)$$

170 Where  $\bar{X}$  is the mean richness,  $X_{\text{obs}}$  is the richness at the specific point, and  $\sigma(X)$  is the  
 171 standard deviation of the richness of either animal or plant mutualists. Further  
 172 explanation on how the rasters for the  $Z_{\text{diff}}$  were created, including details of extent can  
 173 be found in Appendix S1b.

174 *Data analysis*

175 Data analysis was broken into three major categories: all seed dispersing  
176 mutualists, frugivorous animals, and scatter-hoarding animals. Within each major  
177 category, we had two general comparisons: (1) animal mutualists and plant mutualists  
178 and (2)  $Z_{\text{diff}}$  and environmental variables. Due to high heteroscedasticity in the plant  
179 richness, data-weighted least squares regression models were created using the squared  
180 residuals of area adjusted plant richness as weights. Despite richness being count data, a  
181 Poisson distribution was not necessary because the data did not deviate from a normal  
182 distribution. Spatial autocorrelation is a common occurrence in range map and atlas  
183 survey data (Dormann *et al.* 2007) and was present in the environmental variables, but  
184 none of the richness of either plants or animals. To adjust for spatial autocorrelation,  
185 generalized least squares models (GLS) were built for each comparison using a Gaussian  
186 spatial correlation. Data were transformed with a natural log when necessary.

187 We then conducted two types of Monte Carlo simulations to test the hypothesis  
188 that there is no relationship between data within our groups of variables: a complete  
189 randomization and a spatially-structured randomization. The complete randomization  
190 permuted grid cells across the continent, which allowed us to test the hypothesis that  
191 observations are random. The structured randomization statistically fit a spatial  
192 autocorrelation model (variogram), and then generated a random field with the same  
193 degree of spatial autocorrelation using the Random Fields package in R (Schlather *et al.*  
194 2013, 2015). Given that we know that geographic data are spatially autocorrelated, this  
195 allowed us to test the hypothesis that, given our observed levels of spatial autocorrelation,  
196 the observed data are random. We calculated Spearman's correlation coefficient,  $\rho$ , for

197 each of 1000 interactions for the complete and structured randomizations. We then  
198 calculated the proportion of the complete or structured randomizations that were more  
199 extreme than the observed correlation,  $\rho^*$  as an estimated  $p$ -value,  $\hat{p}$ . R code used to  
200 conduct the analyses can be found at the following url:  
201 <https://github.com/dispersing/SpatialRandomizations>. Every complete randomization  
202 failed to detect a random distribution; thus, rendering the analysis uninformative.  
203 (Supplementary Information S6–S9 shows the full results of the complete  
204 randomizations.) Therefore, every Monte Carlo simulation reference henceforth is  
205 specific to the spatially-structured tests.

206 Lastly, because so little is known about the factors contributing to seed-dispersal  
207 mutualism distributions we performed classifications and regression trees (CART) after  
208 our initial analysis to better understand the structure of the data and identify factors that  
209 warrant future investigation. For this data exploration, we used R library, rpart (Therneau  
210 *et al.* 2015) using the ANOVA method. All analysis was performed in program R (R  
211 Development Core Team 2017).

212

## 213 RESULTS

214 *Distribution of seed dispersing animals*

215 We identified 183 animal species in North America that have a seed dispersing  
216 mutualism with plants either via frugivory or scatter-hoarding. Seed dispersing animals  
217 were most speciose in the southwestern portions of North America from the southern  
218 portion of the Colorado Plateau desert region and further north, east of the Rocky  
219 Mountains, to the southern Rocky Mountain-prairie border (Fig. 1). There was no

220 relationship between the richness of all mutualist animals and the plants they disperse;  
221 instead richness of all animal mutualists decreases with an increase in latitude ( $F_{1,195} =$   
222 207,  $p < 0.001$ , Fig. 2). Results from the regression models and the Monte Carlo  
223 simulations can be found in Table 1. The primary split in the CART model for all  
224 mutualists was at ~50°N latitude. At latitudes  $\geq 50^{\circ}\text{N}$ , the richness of animal mutualists is  
225 correlated with plant richness ( $F_{1,15} = 25.27$ ,  $p < 0.001$ ), but not at latitudes  $< 50^{\circ}\text{N}$  ( $F_{1,177}$   
226 = 2.47,  $p = 0.12$ ).

227 A total of 88 animal species were determined to participate in a frugivorous seed-  
228 dispersal mutualism, 65 species of birds and 23 species of mammals (Table S2).  
229 Frugivore richness is highest in the southwestern portions of North America, specifically  
230 in the Colorado Plateau semi-desert region, east to the Southwest plateau and dry steppe  
231 region (Fig. 1). Richness is relatively low in the Great Basin and Mojave deserts, with the  
232 lowest richness in in the far north tundra; richness of frugivorous animals decreases with  
233 increasing latitude ( $F_{1,195} = 262.6$ ,  $p < 0.001$ , Fig. 2). There is no relationship with  
234 frugivorous animal richness and the richness of the plants they disperse (Table 1). CART  
235 models again showed a primary split at ~50°N latitude, and when the data was divided at  
236 that point, there were similar relationships between richness as we found for all  
237 mutualists. At latitudes  $\geq 50^{\circ}\text{N}$ , frugivore richness and the richness of the plants they  
238 dispersed are correlated ( $F_{1,15} = 18.88$ ,  $p < 0.001$ ). However, at latitudes  $< 50^{\circ}\text{N}$ , this  
239 relationship disappears ( $F_{1,177} = 1.71$ ,  $p = 0.19$ ). Frugivorous bird and frugivorous  
240 mammal richness are similarly correlated negatively with latitude but not correlated with  
241 plant richness (Table 1).

242 Lastly, we identified a total of 102 animal species as scatter-hoarders involved in  
243 seed dispersal mutualisms; 10 species of birds and 92 species of rodents (Table S3). As  
244 with frugivorous animals, scatter-hoarder richness is concentrated in the southwestern  
245 North America. Scatter-hoarder richness is highest in Chihuahuan desert region, with  
246 richness hotspots in the Great Basin and Mojave deserts. The Sonoran Desert has a  
247 surprisingly low scatter-hoarder richness (Fig. 1). Richness is lower in eastern North  
248 America with the lowest regions being in the Adirondacks and northern tundra. Richness  
249 decreases with an increase in latitude ( $F_{1,195} = 39.01, p < 0.001$ ), but is not correlated with  
250 plant richness (Table 1, Fig. 2). CART models do not show a ~50°N latitude split (in fact,  
251 latitude is not a primary split in the data at all), instead the primary split occurs at ~900 m  
252 elevation. Further exploratory analysis of the data did not provide any relationships  
253 between scatter-hoarder richness and the plants they disperse between the high- and low-  
254 elevation groups. Scatter-hoarding rodents are similarly negatively correlated with  
255 latitude and are not correlated with plant richness. Conversely, scatter-hoarding birds are  
256 not correlated with plant richness nor latitude (Table 1)

257

258 *Seed dispersal mutualisms*

259 There was a clear mismatch of richness between seed dispersers and the plants  
260 that they disperse (Fig. 1) with the highest richness of plants dispersed by animals being  
261 in eastern North America, while the highest richness of animal dispersers being in  
262 western North America. The divide is approximately 100°W longitude for both guilds of  
263 seed dispersers, and the two guilds combined. Indeed, in all CART models, longitude is  
264 the second split in the data further suggesting its importance.

265 There was no relationship between the  $Z_{\text{diff}}$  of all mutualists and precipitation,  
266 AET, nor latitude (Table 2) However, there was a negative relationship with median  
267 elevation (Fig. 3) and the  $Z_{\text{diff}}$  of all mutualists. As elevation increases, there was a larger  
268 proportion of animal richness compared to plant richness. Monte Carlo simulations  
269 supported the observed relationship with elevation was different from random, and  
270 supported our findings of no relationships between other variables (Table 2). The sub-  
271 panels in Figure 3 show the results of the Monte Carlo simulations which were largely  
272 consistent with our regression models.

273 There was no relationship between  $Z_{\text{diff}}$  of frugivores and precipitation, AET, or  
274 latitude; but there was with median elevation (Table 2, Fig. 3). Similarly, there were no  
275 relationships between  $Z_{\text{diff}}$  of frugivorous birds and precipitation, AET, latitude, median  
276 elevation; nor between  $Z_{\text{diff}}$  of frugivorous mammals and precipitation, AET, latitude, nor  
277 median elevation (Table S4). Monte Carlo simulations largely supported our findings  
278 again (Fig. 3, sub-panels) but suggested that our data was different from random for  
279 elevation ( $\rho = -0.49$ ,  $\hat{p} = 0$ ), suggesting that we observed fewer frugivorous animals at  
280 higher elevations than plants dispersed by them.

281 The  $Z_{\text{diff}}$  of scatter-hoarding animals was also not correlated with latitude (Table  
282 2). However, there were relationships with AET, precipitation, and median elevation. As  
283 AET or precipitation increases there are proportionately more plants dispersed by scatter-  
284 hoarders than scatter-hoarders (Fig. 3). The proportion of scatter-hoarders increased  
285 compared to the plants they disperse with an increase in median elevation (Fig. 3). The  
286  $Z_{\text{diff}}$  of scatter-hoarding birds follows the same pattern as the whole guild. There was no  
287 relationship between the  $Z_{\text{diff}}$  of scatter-hoarding birds and latitude, but there were

288 relationships with precipitation, AET, and median elevation (Table S4). There was an  
289 increase in the proportion of scatter-hoarders as AET decreased or elevation increased.  
290 The  $Z_{\text{diff}}$  of scatter-hoarding rodents also was correlated with precipitation, AET, median  
291 elevation (Table S4). The proportion of scatter-hoarding rodents increased with a  
292 decrease in precipitation, a decrease in AET, or an increase in elevations. The  $Z_{\text{diff}}$  of  
293 scatter-hoarding rodents was not correlated with latitude. Monte Carlo simulations again  
294 largely corroborated our findings, with the only contradicting result involving  
295 precipitation. Simulations suggest there was a relationship with precipitation for all  
296 scatter-hoarders, with more scatter-hoarders being found in areas of less precipitation ( $\rho$   
297  $= -0.04$ ,  $\hat{p} = 0.04$ , Fig. 3 sub-panels).

298

## 299 **DISCUSSION**

300 There was an apparent mismatch between the richness of seed dispersing animals  
301 and the plants that they disperse across North America. We hypothesized that because of  
302 the increased fitness between two species or guilds of mutualists that we would expect  
303 positive relationships of species richness between both sides of the mutualism, depending  
304 on the degree of co-dependency (i.e., facultative-to-obligate). Although we found positive  
305 relationships between all subguilds of seed dispersing animals and seed-dispersed plants,  
306 the richness of both plants and animals were better explained by environmental variables  
307 than by the richness of each other. This result was surprising and suggests that diversity  
308 of mutualistic partners do not necessarily beget diversity of one another.

309 Species richness of frugivores, scatter-hoarders, and all seed dispersing animals  
310 combined decreased with an increase in latitude (Fig. 2). This pattern matches the pattern

311 observed for the plants that they disperse (Vander Wall *et al.* submitted; Vander Wall &  
312 Moore 2016). The increase of species richness with decreasing latitude was not a  
313 surprising result as the generality of the latitudinal diversity gradient has been found to be  
314 robust (Hillebrand & Thomas 2004). However, when hoarding birds are considered  
315 alone, they did not show a significant latitudinal gradient ( $F_{1,194} = 3.08, p = 0.08$ ). This  
316 result was likely because the data are limited to one small, generalist family of birds  
317 (Corvidae) that have their center of diversity in the north temperate zone.

318 As with previous studies (Karr 1976; Hawkins *et al.* 2003b; Kissling *et al.* 2009),  
319 animal species richness was correlated with environmental variables (data not shown).  
320 Surprisingly, the difference in relative abundance of animals and plants in seed dispersal  
321 mutualisms was not strongly correlated with environmental variables. One exception was  
322 that the proportion of plants dispersed by scatter-hoarding animals increased with AET  
323 (Fig. 5), a variable often found important for predicting species richness at large scales.  
324 Seed disperser mutualisms appear to be more frequent (i.e., more plants dependent on  
325 scatter-hoarders) in more productive environments. Our Monte Carlo simulations also  
326 suggested that scatter-hoarding mutualism should be correlated with precipitation (which  
327 is correlated with AET) and we found that richness of scatter-hoarding rodents was  
328 correlated with precipitation. These results are congruent with the predictions made by  
329 Vander Wall & Jenkins (2011) on why western species of chipmunks (*Tamias*) have  
330 adapted scatter-hoarding in arid and semi-arid western North America, but not in the  
331 mesic eastern North America. However, the proportion of scatter-hoarders was positively  
332 correlated with median elevation (Fig. 3) and does not follow the global pattern; a  
333 decrease in richness with an increase in elevation (Rahbek 1995). Richness is believed to

334 decrease at higher elevations partially due to a decrease in productivity, smaller land area,  
335 and harsher climates leading to higher extinction and lower dispersal due to greater  
336 distances between suitable habitat (Rahbek 1995; Rowe 2009; Wu *et al.* 2013). The  
337 relationship with elevation may be due to the fact that in southwestern North America,  
338 where the majority of seed-disperser richness was found, net productivity actually  
339 increases with elevation into the montane forests before decreasing again above tree line  
340 (Whittaker & Niering 1975). Since plants are positively correlated with AET, this may  
341 influence the relationship with elevation.

342 The distribution of animal species richness contrasts with the richness distribution  
343 of the plant species being dispersed by those animals (Figs. 3, 4). Plants dispersed by  
344 frugivores and scatter-hoarding animals have their highest richness around the Great  
345 Lake regions and southeastern parts of North America in general. This mismatch of  
346 species richness between plants and the animals that disperse them is clearly seen in Fig.  
347 1 with animal richness being greater in southwestern North America and plant richness  
348 being greater in southeastern North America. A possible explanation for this enigma is  
349 that seed dispersing animals might be far more numerous in the southeastern United  
350 States, where there are relatively few species, compared to the southwestern part of the  
351 continent where abundance may be lower, but species richness is higher.

352 The strength of coevolution between individual plant and vertebrate disperser  
353 species has been suggested to be diffuse (Thompson 1982; Wheelwright & Orians 1982;  
354 Herrera 1985). In particular seed dispersal communities of plant and animal species have  
355 found that species interactions are often asymmetrical, variable in time and space, and  
356 non-obligate (Janzen 1980; Wheelwright 1988; Bascompte & Jordano 2007). This is

357 particularly driven by generalists animal species, which interact with multiple plant  
358 species causing high complementarity and trait convergence (Guimaraes Jr. *et al.*, 2011).  
359 Most, if not all, of the animal species in North America that we considered seed disperser  
360 mutualists would fall under this definition of generalists as they have wide diet breadths.  
361 The plants dispersed by animals in North America are also generalists as fruits and seeds  
362 have evolved to attract a variety of dispersers and not any one species in particular.  
363 Diffuse interactions inhibit strong directional coevolution and lead to the diffuse patterns  
364 we witness.

365 The current distribution of plants and animals in North America has changed over  
366 the last 18,000 years (Ray & Adams 2001). The last glacial maximum dramatically  
367 altered species distributions across North America, and it may be that there has not been  
368 enough time since the last glacial maximum for coevolutionary selection pressures to  
369 form or be strong enough to be detected at coarse spatial scales. It is also probable that  
370 animals have migrated faster than the plants they disperse because of the diffuse  
371 relationship between animals and plants, in addition to the short period since the last  
372 glacial maximum. Davis *et al.* (1986) and Woods & Davis (1989) have shown that some  
373 animal-dispersed plants have not reached their potential distributions since the last glacial  
374 maximum, despite their dispersers being common across the plant's potential geographic  
375 range.

376 Two major limitations of the study were (i) the assumption that abundance is  
377 uniform across a species range and (ii) a mismatch of scale between occurrence and  
378 environmental data. First, assumptions of studies using species range data are that the  
379 abundance of a species is uniform across its range, that all species have equal

380 abundances, and that abundances are high enough throughout the range for the species to  
381 be an effective part of the community. This latter point, in this case, means that each  
382 species is an effective disperser of plants wherever it occurs. These assumptions are  
383 rarely met (Hurlbert & Jetz 2007), but occurrence maps are typically the only data on  
384 species occurrence available at large spatial scales, and if maps are constructed in a  
385 similar way, they can provide insights into the richness of species in a region (Rocchini *et*  
386 *al.* 2011).

387 Secondly, Hurlbert & Jetz (2007) also suggested that a mismatch of scale between  
388 occurrence data and environmental variables can lead to erroneous results. Instances of  
389 mismatch often occur when species occurrence data (generally course resolution) is  
390 overlaid onto climatic variables (generally finer resolution). We believe the concerns of  
391 mismatch are minimal for this study as the overarching aim was to identify the  
392 distribution of animals in comparison to the plants that they disperse. Analyses with  
393 climatic variables were chosen based on previous findings and hypotheses and the data  
394 were taken at the coarsest scale available to match occurrence data as best as possible. As  
395 with similar studies, the purpose of these analyses is to identify broad patterns of  
396 distribution with the goal of providing focal points for finer scale studies and not to  
397 suggest detailed patterns.

398 This study is the first to compare the collective distribution of animals involved in  
399 seed dispersal mutualisms to the distribution of the plants they disperse. The distribution  
400 of plants nor animals accounts for the distribution of either group. In fact, there is an  
401 apparent mismatch of richness between plants and the animals that disperse their seeds  
402 (Figs. 1, 2). As with animal-dispersed plants (Vander Wall & Moore 2016)

403 environmental variables, particularly latitude, better describes the richness distribution of  
404 animal mutualists. In the case of seed dispersal mutualisms, median elevation was  
405 correlated with all mutualists and scatter-hoarding, additionally, scatter-hoarding was  
406 correlated with AET suggesting that environmental factors, such as productivity may play  
407 a key role in the distribution of the mutualism. Further work is sorely needed to better  
408 understand the effect of climate on distributions of seed dispersing animals. However,  
409 with this data of seed dispersing animal distributions, we can now identify locations that  
410 warrant further study either to understand better seed-dispersal mutualisms or the factors  
411 that influence the distribution of the plants and animals involved in these mutualisms.  
412 The biggest challenge to further understanding many of these observed patterns has been  
413 the lack of appropriate data (Hawkins & Pausas 2004), and we hope this study will serve  
414 as a stepping stone to further discoveries.

415

#### 416 **Acknowledgements**

417 We'd like to thank M. Matocq, C. Feldman, W. Longland, and S. Mensing for providing  
418 comments on a previous draft of the manuscript. We'd also like to thank Bioclim, Global-  
419 AET, Natural Earth, Bird Life International, NatureServe, IUCN and the for the data used  
420 in this study

421   **Literature Cited**

422   1.

424   Almeida-Neto, M., Campassi, F., Galetti, M., Jordano, P. & Oliveira-Filho, A. (2008).  
425   Vertebrate dispersal syndromes along the Atlantic forest: broad-scale patterns and  
426   macroecological correlates. *Glob. Ecol. Biogeogr.*, 17, 503–513

427

428   2.

429   Bascompte, J. & Jordano, P. (2007). Plant-Animal Mutualistic Networks: The  
430   Architecture of Biodiversity. *Annu. Rev. Ecol. Evol. Syst.*, 38, 567–593

431

432   3.

433   BirdLife International and NaturServe. (2014). *Bird species distribution maps of the*  
434   world. BirdLife International, Cambridge, UK and NatureServe, Arlington, USA.  
435   NatureServe (Version 3.0) is in collaboration with Robert Ridgely, James Zook, The  
436   Nature Conservancy – Migratory Bird Program, Conservation International – Center  
437   for Applied Biodiversity Science, World Wildlife Fund – U.S. and Environment  
438   Canada – WILDSpace

439

440   4.

441   Bowyer, R.T., Van Ballenberghe, V. & Kie, J.G. (1997). The role of moose in landscape  
442   processes: effects of biogeography, population dynamics, and predation. In: *Wildlife*  
443   and *Landscape Ecology*. Springer, pp. 265–287

444

445   5.

446   Bronstein, J.L. (2015). *Mutualism*. Oxford University Press, USA

447

448   6.

449   Davis, M.B., Woods, K.D., Webb, S.L. & Futyma, R.P. (1986). Dispersal versus climate:  
450   expansion of *Fagus* and *Tsuga* into the Upper Great Lakes region. *Vegetatio*, 67, 93–  
451   103

452

453   7.

454   Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., et al.  
455   (2007). Methods to account for spatial autocorrelation in the analysis of species  
456   distributional data: a review. *Ecography*, 30, 609–628

457

458   8.

459   Guimaraes Jr., P.R., Jordano, P. & Thompson, J.N. (2011). Evolution and coevolution  
460   in mutualistic networks. *Ecol. Lett.*, 14, 877–885

461

462   9.

463   Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufman, D.M., et al.  
464   (2003a). Energy, water, and broad-scale geographic patterns of species richness.  
465   *Ecology*, 84, 3105–3117

- 466  
467 10.  
468 Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufman, D.M., *et al.*  
469 (2003b). Energy, Water, and Broad-Scale Geographic Patterns of Species Richness.  
470 *Ecology*, 84, 3105–3117  
471  
472 11.  
473 Hawkins, B.A. & Pausas, J.G. (2004). Does plant richness influence animal richness?:  
474 the mammals of Catalonia (NE Spain). *Divers. Distrib.*, 10, 247–252  
475  
476 12.  
477 Herrera, C.M. (1985). Determinants of plant-animal coevolution: the case of  
478 mutualistic dispersal of seeds by vertebrates. *Oikos*, 44, 132–141  
479  
480 13.  
481 Hiemstra, P.H., Pebesma, E.J., Twenhöfel, C.J. & Heuvelink, G.B. (2009). Real-time  
482 automatic interpolation of ambient gamma dose rates from the Dutch radioactivity  
483 monitoring network. *Comput. Geosci.*, 35, 1711–1721  
484  
485 14.  
486 Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005). Very high  
487 resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.*, 25,  
488 1965–1978  
489  
490 15.  
491 Hillebrand, H. & Thomas, A.E.C.D. (2004). On the Generality of the Latitudinal  
492 Diversity Gradient. *Am. Nat.*, 163, 192–211  
493  
494 16.  
495 Howe, H.F. & Smallwood, P.D. (1982). Ecology of seed dispersal. *Annu. Rev. Ecol.*  
496 *Syst.*, 13, 201–228  
497  
498 17.  
499 Hurlbert, A.H. & Jetz, W. (2007). Species richness, hotspots, and the scale  
500 dependence of range maps in ecology and conservation. *Proc. Natl. Acad. Sci.*, 104,  
501 13384–13389  
502  
503 18.  
504 IUCN. (2012). *IUCN Red List of Threatened Species Version 2012.1*. Available at:  
505 <http://www.iucnredlist.org>. Last accessed 15 August 2014  
506  
507 19.  
508 Janzen, D.H. (1980). When is it coevolution? *Evolution*, 34, 611–612  
509  
510

- 511 20.
- 512 Jetz, W. & Rahbek, C. (2002). Geographic range size and determinants of avian  
513 species richness. *Science*, 297, 1548–1551
- 514
- 515 21.
- 516 Karr, J.R. (1976). Seasonality, resource availability, and community diversity in  
517 tropical bird communities. *Am. Nat.*, 973–994
- 518
- 519 22.
- 520 Kissling, W.D., Böhning-Gaese, K. & Jetz, W. (2009). The global distribution of  
521 frugivory in birds. *Glob. Ecol. Biogeogr.*, 18, 150–162
- 522
- 523 23.
- 524 Kissling, W.D., Rahbek, C. & Böhning-Gaese, K. (2007). Food plant diversity as broad-  
525 scale determinant of avian frugivore richness. *Proc. R. Soc. Lond. B Biol. Sci.*, 274,  
526 799–808
- 527
- 528 24.
- 529 Knops, J.M., Tilman, D., Haddad, d N., Naeem, S., Mitchell, C.E., Haarstad, J., *et al.*  
530 (1999). Effects of plant species richness on invasion dynamics, disease outbreaks,  
531 insect abundances and diversity. *Ecol. Lett.*, 2, 286–293
- 532
- 533 25.
- 534 Kreft, H. & Jetz, W. (2007). Global patterns and determinants of vascular plant  
535 diversity. *Proc. Natl. Acad. Sci.*, 104, 5925–5930
- 536
- 537 26.
- 538 MacArthur, R.H. (1972). *Geographical ecology: patterns in the distribution of species*.  
539 Princeton University Press
- 540
- 541 27.
- 542 Mackey, R.L. & Currie, D.J. (2001). The Diversity-Disturbance Relationship: Is It  
543 Generally Strong and Peaked? *Ecology*, 82, 3479–3492
- 544
- 545 28.
- 546 Natural Earth. (2017). *Gray earth with shaded relief, hypsography, and flat water*
- 547
- 548 29.
- 549 Oberdorff, T., Guégan, J.-F. & Hugueny, B. (1995). Global scale patterns of fish species  
550 richness in rivers. *Ecography*, 18, 345–352
- 551
- 552 30.
- 553 Pearson, R.G. & Dawson, T.P. (2003). Predicting the impacts of climate change on the  
554 distribution of species: are bioclimate envelope models useful? *Glob. Ecol. Biogeogr.*,  
555 12, 361–371
- 556

- 557 31.
- 558 R Development Core Team. (2017). *R: A language and environment for statistical*  
559 *computing*. R Foundation for Statistical Computing, Vienna, Austria
- 560
- 561 32.
- 562 Rahbek, C. (1995). The Elevational Gradient of Species Richness: A Uniform Pattern?  
563 *Ecography*, 18, 200–205
- 564
- 565 33.
- 566 Rahbek, C., Gotelli, N.J., Colwell, R.K., Entsminger, G.L., Rangel, T.F.L. & Graves, G.R.  
567 (2007). Predicting continental-scale patterns of bird species richness with spatially  
568 explicit models. *Proc. R. Soc. Lond. B Biol. Sci.*, 274, 165–174
- 569
- 570 34.
- 571 Rahbek, C. & Graves, G.R. (2001). Multiscale assessment of patterns of avian species  
572 richness. *Proc. Natl. Acad. Sci.*, 98, 4534–4539
- 573
- 574 35.
- 575 Ray, N. & Adams, J. (2001). A GIS-based vegetation map of the world at the last  
576 glacial maximum (25,000–15,000 BP). *Internet Archaeol.*, 11
- 577
- 578 36.
- 579 Ridgley, R.S., Allnutt, T.F., Brooks, T., McNicol, D.K., Mehlman, D.W., Young, B.E., et al.  
580 (2007). *Digital distribution maps of the birds of the Western Hemisphere*.  
581 NatureServe, Arlington, Virginia, USA
- 582
- 583 37.
- 584 Rocchini, D., Hortal, J., Lengyel, S., Lobo, J.M., Jimenez-Valverde, A., Ricotta, C., et al.  
585 (2011). Accounting for uncertainty when mapping species distributions: the need  
586 for maps of ignorance. *Prog. Phys. Geogr.*, 35, 211–226
- 587
- 588 38.
- 589 Rowe, R.J. (2009). Environmental and geometric drivers of small mammal diversity  
590 along elevational gradients in Utah. *Ecography*, 32, 411–422
- 591
- 592 39.
- 593 Scheiner, S.M. & Willig, M.R. (2008). A general theory of ecology. *Theor. Ecol.*, 1, 21–  
594 28
- 595
- 596 40.
- 597 Schlather, M., Malinowski, A., Menck, P.J., Oesting, M., Strokorb, K. & others. (2015).  
598 Analysis, simulation and prediction of multivariate random fields with package  
599 Random Fields. *J. Stat. Softw.*, 63, 1–25
- 600
- 601

- 602 41.
- 603 Schlather, M., Menck, P., Singleton, R. & Team, R.C. (2013). Random Fields:  
604 simulation and analysis of random fields. *R Package Version*, 2, 66
- 605
- 606 42.
- 607 Siefert, A., Ravenscroft, C., Weiser, M.D. & Swenson, N.G. (2013). Functional beta-  
608 diversity patterns reveal deterministic community assembly processes in eastern  
609 North American trees. *Glob. Ecol. Biogeogr.*, 22, 682–691
- 610
- 611 43.
- 612 Somero, G.N. (2005). Linking biogeography to physiology: evolutionary and  
613 acclamatory adjustments of thermal limits. *Front. Zool.*, 2, 1
- 614
- 615 44.
- 616 Svenning, J.-C., Gravel, D., Holt, R.D., Schurr, F.M., Thuiller, W., Münkemüller, T., *et al.*  
617 (2014). The influence of interspecific interactions on species range expansion rates.  
618 *Ecography*, 37, 1198–1209
- 619
- 620 45.
- 621 Terborgh, J. (1990). Seed and fruit dispersal—commentary. *Reprod. Ecol. Trop. For.*  
622 *Plants*, 181–190
- 623
- 624 46.
- 625 Therneau, T., Atkinson, B. & port), B.R. (author of initial R. (2015). *rpart: Recursive*  
626 *Partitioning and Regression Trees*
- 627
- 628 47.
- 629 Thompson, J.N. (1982). *Interaction and Coevolution*. John Wiley and Sons, New York
- 630
- 631 48.
- 632 Trabucco, A. & Zomer, R.J. (2010). Global soil water balance geospatial database.  
633 *CGIAR Consort. Spat. Inf. Publ. Online Available CGIAR-CSI GeoPortal*  
634 *Http://www.Cgiar-Csi.Org*
- 635
- 636 49.
- 637 Vander Wall, S.B. (1990). *Food hoarding in animals*. University or Chicago Press,  
638 Chicago
- 639
- 640 50.
- 641 Vander Wall, S.B., Barga, S.C. & Seaman, A. (submitted). Geographic distribution of  
642 seed-dispersal mutualisms in North America. *J. Ecol.*
- 643
- 644 51.
- 645 Vander Wall, S.B. & Jenkins, S.H. (2011). Plant-animal interactions and climate: Why  
646 do yellow pine chipmunks (*Tamias amoenus*) and eastern chipmunks (*Tamias*  
647 *striatus*) have such different effects on plants? *Ecoscience*, 18, 130–137

- 648 52.
- 649 Vander Wall, S.B. & Moore, C., M. (2016). Interaction diversity of North American  
650 seed-dispersal mutualisms. *Glob. Ecol. Biogeogr.*
- 651
- 652 53.
- 653 Wheelwright, N.T. (1988). Fruit-eating birds and bird-dispersed plants in the tropics  
654 and temperate zone. *Trends Ecol. Evol.*, 3, 270–274
- 655
- 656 54.
- 657 Wheelwright, N.T. & Orians, G.H. (1982). Seed dispersal by animals: contrasts with  
658 pollen dispersal, problems of terminology, and constraints on coevolution. *Am. Nat.*,  
659 119, 402–413
- 660
- 661 55.
- 662 Whittaker, R.H. & Niering, W.A. (1975). Vegetation of the Santa Catalina Mountains,  
663 Arizona. V. Biomass, production, and diversity along the elevation gradient. *Ecology*,  
664 56, 771–790
- 665
- 666 56.
- 667 Willson, M.F., Rice, B.L. & Westoby, M. (1990). Seed Dispersal Spectra: A Comparison  
668 of Temperate Plant Communities. *J. Veg. Sci.*, 1, 547–562
- 669
- 670 57.
- 671 Woods, K.D. & Davis, M.B. (1989). Paleoecology of range limits: beech in the upper  
672 peninsula of Michigan. *Ecology*, 70, 681–696
- 673
- 674 58.
- 675 Wu, Y., Yang, Q., Wen, Z., Xia, L., Zhang, Q. & Zhou, H. (2013). What drives the species  
676 richness patterns of non-volant small mammals along a subtropical elevational  
677 gradient? *Ecography*, 36, 185–196
- 678

679 **Table 1:** Statistical results of regression models and Monte Carlo simulations for  
680 subguild richness (dependent variable) and the richness of the plants they disperse  
681 (independent variable). For the regression models, the table includes the  $F$ -statistic,  $p$ -  
682 value, effect size ( $\beta$ ), and  $R^2$  for each model. Monte Carlo simulations include the  
683 predicted  $p$ -value ( $\hat{p}$ ) and Spearman's correlation coefficient ( $\rho^*$ ).

684

685 **Table 2:** Statistical results of GLS models and Monte Carlo simulations for mutualisms  
686 ( $Z_{\text{diff}}$ ; dependent variable) and environmental variables (independent variables). For  
687 spatial regression models, the table includes whether there was a spatial correlation in the  
688 data, how it was corrected for,  $F$ -statistic,  $p$ -value, effect size ( $\beta$ ), and  $R^2$  for each model.  
689 Monte Carlo simulations include the predicted  $p$ -value ( $\hat{p}$ ) and Spearman's correlation  
690 coefficient ( $\rho^*$ ). A dagger ( $\dagger$ ) signifies that the effect size is in units per 100 mm/yr AET  
691 and a double dagger ( $\ddagger$ ) signifies that the effect size is in units per 100 m elevation.

692

693 **Figure 1:** Distribution of seed dispersal mutualism richness. The left panels are the  
694 distribution of plants involved in each guild of seed dispersal mutualism after (Vander  
695 Wall *et al.* submitted). The middle panel is the richness distribution of animals involved  
696 in each guild of seed dispersal mutualisms, and the right panel is the difference between  
697 plant and animal richness ( $Z_{\text{diff}}$ ) involved in guild of mutualisms. In the left and middle  
698 panels, the legend represents the number of plants or animals at any given locations.  
699 While in the right panel the legend represents the relative difference in richness between  
700 plants and animals.

701 **Figure 2:** The richness of animals involved in seed dispersing mutualisms as a function  
702 of the plants they disperse (left column) and latitude (right column). Each plot has the  
703 Spearman correlation coefficient ( $\rho^*$ ) and  $p$ -value of the linear model; red lettering  
704 signifies a significant linear model. The only significant interactions were between the  
705 richness of all mutualists and frugivores with latitude (all mutualists:  $F_{1,195} = 207$ ,  $p <$   
706 0.001, frugivores:  $F_{1,195} = 262.6$ ,  $p < 0.001$ ). The red line is the LOWESS smoothing  
707 curve to reveal the internal structure of the distribution of data points.

708

709 **Figure 3:** The relationships between environmental variables (rows) and differences in  
710 the richness of plant and animal mutualists ( $Z_{\text{diff}}$ ; columns). All statistics and  
711 relationships can be found in Table 2. The scatterplots show the environmental variable  
712 on the  $x$  axis and the difference in plant and animal mutualist richness on the  $y$  axis.  
713 From left to right, the environmental variables represent AET (mm/yr), elevation (m),  
714 precipitation (log(mm/yr)), and latitude. An asterisk (\*) next to the variable implies that  
715 the values are in the hundreds. Each scatterplot is colored according to greater plant  
716 richness (green), equal plant and animal richness (white), or greater animal richness  
717 (brown). We further included subplots of the spatially-structured randomizations to show  
718 how extreme the observed correlation (Spearman's  $\rho^*$ ; vertical red line) was compared  
719 with 1,000 randomizations (density plot). The subplots have ticks for values for  
720 correlation values  $\rho^* = -1$ , 0, and 1.

Table 1:

Dependent variable	Independent variable	Regression models			Monte Carlo simulations	
		F-statistic	p-value	Effect size ( $\beta$ )	$R^2$	$\hat{p}$
All mutualists	All plant mutualists	0.39	0.534	0.33	0.00	0.02
	Plants dispersed by frugivores					0.66
All frugivores		3.79	0.053	0.71	0.01	0.01
	Plants dispersed by frugivorous birds					0.67
Frugivorous birds		1.05	0.306	0.37	0.00	0.01
	Plants dispersed by frugivorous mammals					0.62
Frugivorous mammals		1.24	0.327	0.24	0.00	0.04
	Plants dispersed by scatter-hoarders					0.44
All scatter-hoarders		0.03	0.873	-0.02	-0.01	0.03
	Plants dispersed by scatter-hoarding birds					0.59
Scatter-hoarding birds		0.33	0.566	-0.04	0.00	0.03
	Plants dispersed by scatter-hoarding rodents					0.47
Scatter-hoarding rodents		0.34	0.561	0.05	0.00	0.04
						0.58

Table 2:

Independent variable	Dependent variable	Spatial regression models				Monte Carlo simulations	
		Spatial correlation	F-statistic	p-value	Effect size ( $\beta$ )	$R^2$	$\hat{p}$
AET	All mutualists	Gaussian	3.57	0.06	0.08 <sup>†</sup>	0.03	0.07
	All frugivores	Gaussian	2.07	0.15	0.06 <sup>†</sup>	-0.02	0.18
	All scatter-hoarders	Gaussian	247.53	0.00	0.34 <sup>†</sup>	0.23	0.00
Elevation	All mutualists	Gaussian	160.42	0.00	-0.09 <sup>††</sup>	0.08	0.00
	All frugivores	Gaussian	84.45	0.00	-0.07 <sup>††</sup>	-0.02	0.00
	All scatter-hoarders	Gaussian	224.85	0.00	-0.18 <sup>††</sup>	0.19	0.00
Latitude	All mutualists	Gaussian	1.63	0.20	0.02	0.07	0.34
	All frugivores	Gaussian	12.41	0.00	0.04	0.20	0.22
	All scatter-hoarders	Gaussian	0.62	0.43	0.01	-0.01	0.29
Precipitation	All mutualists	Gaussian	0.32	0.57	0.11	0.01	0.13
	All frugivores	Gaussian	46.33	0.00	0.70	0.02	0.22
	All scatter-hoarders	Gaussian	109.06	0.00	1.19	0.00	0.04

Figure 1:

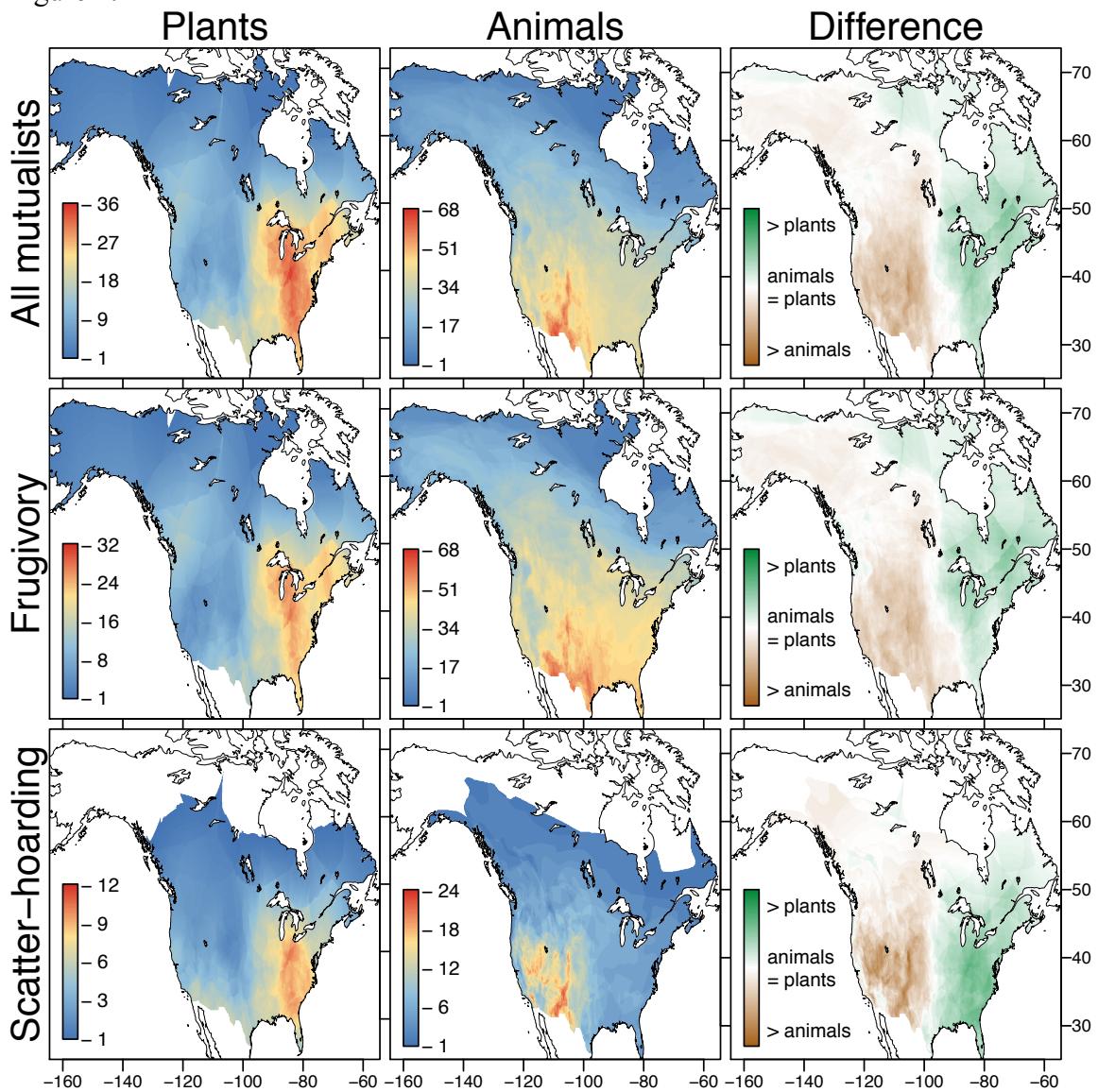


Figure 2:

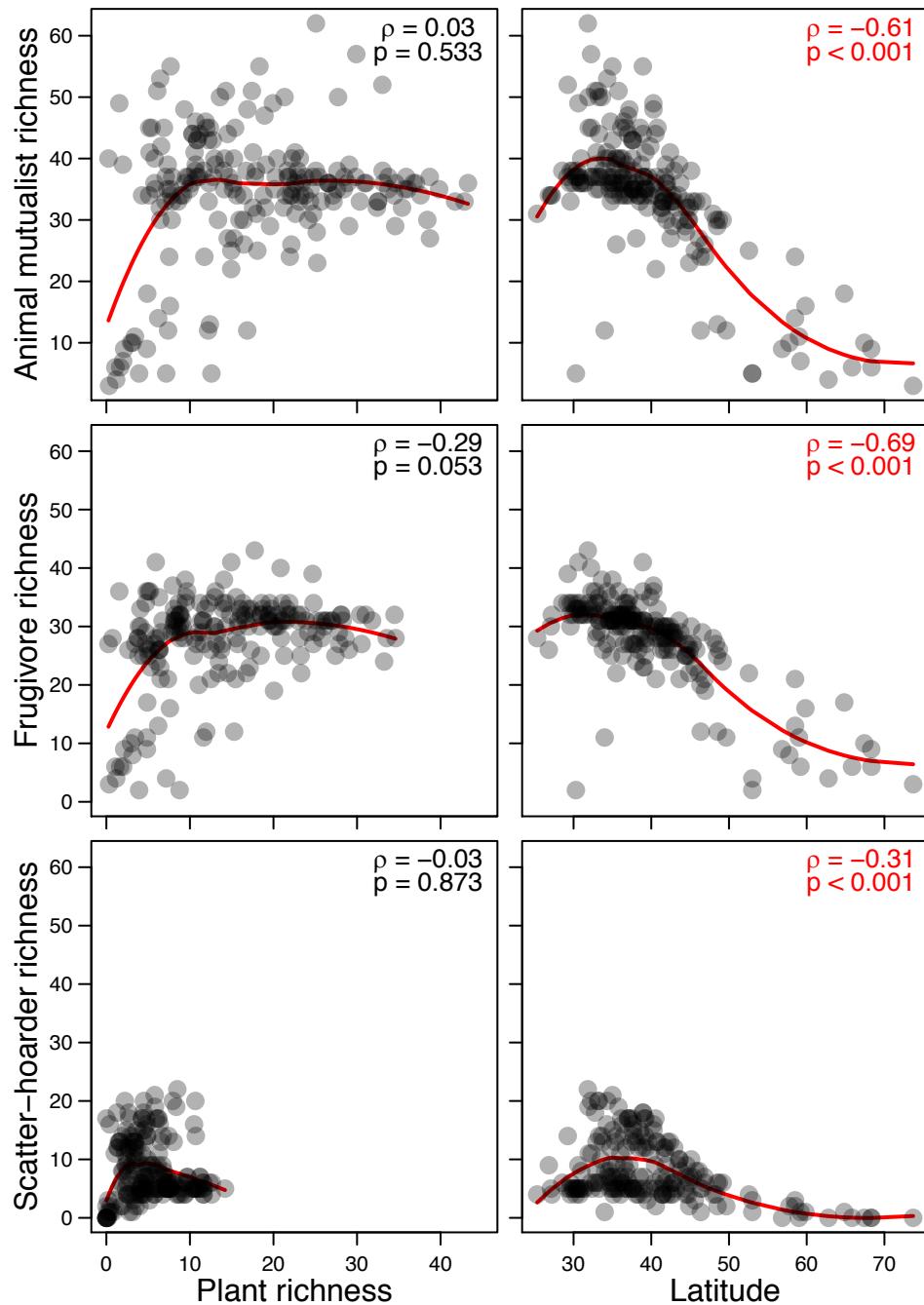
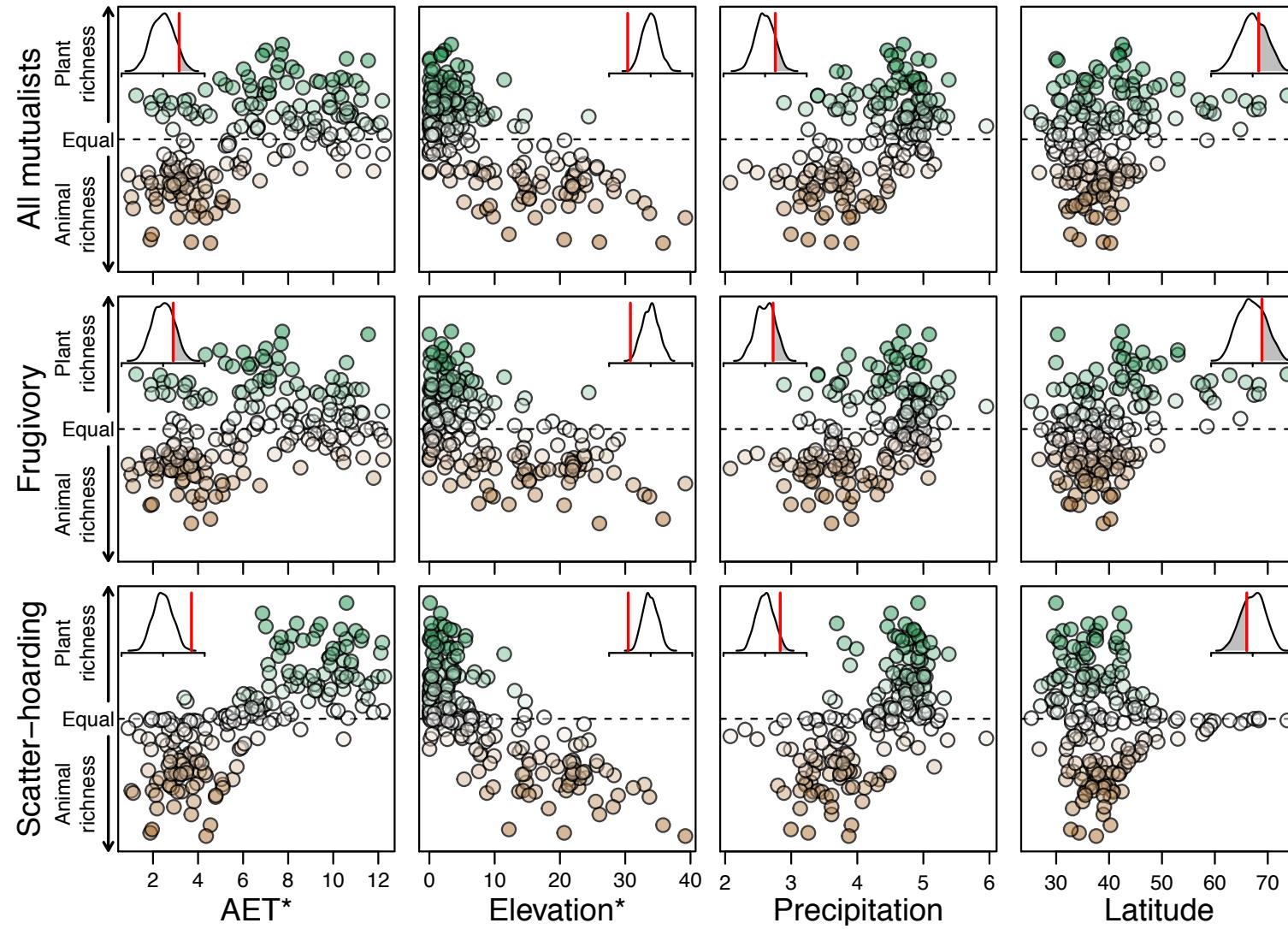


Figure 3:



## Appendix S1

### a) Full description of species assignment to seed-dispersing guilds

To determine how the distribution of vertebrate seed dispersers compares to the plants that they disperse, we first assigned the birds and mammals of North America (north of Mexico) to two seed-dispersing guilds: frugivorous and scatter-hoarding seed dispersers. Animals were considered frugivorous seed dispersers if they consume fruits containing seeds as a significant portion of their diet, and the seeds remain viable after being either regurgitated or passed through the digestive tract. We excluded animals that eat lots of fleshy fruit but that do not disperse seeds, like the northern cardinals (*Cardinalis cardinalis*) and ruffed grouse (*Bonasa umbellus*), which eat fruit, but possess gizzards that destroy seeds by grinding them up. Additionally, animals that disperse seeds but do so infrequently (e.g. most members of the family Vireonidae), were excluded, as they are unlikely to influence plant-disperser coevolution in a significant way. Scatter-hoarding of seeds, which frequently results in a mutualism with plants, is limited to the bird family Corvidae and the mammal order Rodentia in North America (Vander Wall 1990). A species was considered a scatter-hoarder if seeds are a significant portion of its diet, it scatter-hoards them in soil, and there is a reasonable expectation that some of those seeds germinate.

Animals were identified to be frugivorous or scatter-hoarders through a combination of personal knowledge and the literature. For species that we suspected of being seed dispersers, we consulted the literature. This included Bird species accounts (American Ornithologist Union), Bent's Life History of Birds series (Bent, 1919-1968), and Mammalian species accounts (American Society of Mammalogists). In some cases we surveyed the primary literature. If no source provided evidence for frugivory or scatter-hoarding of seeds, we excluded the species from the list. The taxonomy of all species is based on current species lists published for birds and

mammals of North America (American Ornithologists' Union 1998; Wilson & Reeder 2005).

Our list of seed-dispersing vertebrates is intended to be comprehensive but the inclusion or exclusion of certain species is debatable. But we maintain that the inclusion or exclusion of a few species is unlikely to change our results in any meaningful way.

### *b) Raster Creation*

All of the rasters were then masked to our geographic range of interest (North America, north of Mexico) using major land areas (largely excluding islands) from CIA World DataBank II (<https://www.evl.uic.edu/pape/data/WDB/>) in R library, mapdata (Brownrigg 2016). The master raster has a resolution of  $1221 \times 1077$  longitude by latitude (573933 terrestrial cells evaluated), and an extent of  $164.4167^{\circ}\text{W}$ – $54.41667^{\circ}\text{W}$  and  $25.06667^{\circ}\text{N}$  –  $73.56667^{\circ}\text{N}$ . Data were rasterized, overlaid, and projected using Program R (R Core Team 2014) with R libraries, maptools (Lewin-Koh *et al.* 2011), raster (Hijmans 2014), sp (Pebesma & Bivand 2005; Bivand *et al.* 2008), and rgdal (Keitt *et al.* 2014). Composite distribution maps were made for all mutualists (frugivores + scatter-hoarders), all frugivorous animals, frugivorous birds, frugivorous mammals, all scatter-hoarding animals, scatter-hoarding birds, and scatter-hoarding mammals.

For initial data analysis, we extracted the animal mutualist richness from the 197 sites used in Vander Wall & Moore (2016). To obtain richness, we used the extract function from the R library, Raster (Hijmans 2014). This function works by extracting specified data from a raster at given points. The latitude and longitude of the center (mean latitude and longitude) of each site was used as x, y coordinates for data extraction. The center of each site was deemed acceptable because the range maps of the included animals are not detailed enough to show significant differences within a given study site. Furthermore, we reviewed the species list for

both frugivorous and scatter-hoarding animals at each site to eliminate species that were supposedly present according to their range maps but were unlikely actually present due to elevational or ecological limitations.

**Table S2:** List of frugivorous animals broken up into frugivorous birds (top) and frugivorous mammals (bottom). Species are listed alphabetically by family then genus, order of species does not insinuate a species ability to disperse seeds via frugivory.

**Table S3:** List of scatter-hoarding animals broken up into scatter-hoarding birds (top) and scatter-hoarding rodents (bottom). For both scatter-hoarding birds and mammals only one family possesses scatter-hoarding behavior (Corvidae and Rodentia respectively), therefore species are listed alphabetically by genus. Order of species does not insinuate a species ability to disperse seeds via scatter-hoarding

**Table S4:** Statistical results of GLS models and Monte Carlo simulations for mutualisms ( $Z_{\text{diff}}$ ) and environmental variables. An asterisk (\*) signifies that the effect size is in units per 100 mm/yr AET and a double asterisk (\*\*) signifies that the effect size is in units per 100 m elevation. Arrows signify if the relating ship is negative (downward arrow) or positive (upward arrow).

Table S2:

Frugivorous Birds of North America		
Genus Species	Family	Common Name
<i>Bombycilla cedrorum</i>	Bombycillidae	Cedar Waxwing
<i>Bombycilla garrulus</i>	Bombycillidae	Bohemian Waxwing
<i>Patagioenas fasciata</i>	Columbidae	Band-tailed Pigeon
<i>Patagioenas flavirostris</i>	Columbidae	Red-billed Pigeon
<i>Patagioenas leucocephala</i>	Columbidae	White-crowned Pigeon
<i>Zenaida asiatica</i>	Columbidae	White-winged Dove
<i>Aphelocoma californica</i>	Corvidae	Scrub Jay
<i>Aphelocoma coerulescens</i>	Corvidae	Florida Scrub Jay
<i>Aphelocoma insularis</i>	Corvidae	Island Scrub Jay
<i>Corvus ossifragus</i>	Corvidae	Fish Crow
<i>Corvus brachyrhynchos</i>	Corvidae	American Crow
<i>Corvus caurinus</i>	Corvidae	Northwestern Crow
<i>Cyanocitta cristata</i>	Corvidae	Blue Jay
<i>Cyanocitta stelleri</i>	Corvidae	Steller's Jay
<i>Gymnorhinus cyanocephalus</i>	Corvidae	Piñon Jay
<i>Perisoreus canadensis</i>	Corvidae	Gray Jay
<i>Pica hudsonia</i>	Corvidae	Black-billed Magpie
<i>Pica nutalli</i>	Corvidae	Yellow-billed Magpie
<i>Psilorhinus morio</i>	Corvidae	Brown Jay
<i>Crotophaga sulcirostris</i>	Cuculidae	Groove-billed Ani
<i>Crotophaga ani</i>	Cuculidae	Smooth-billed Ani
<i>Icterus bullockii</i>	Icteridae	Bullock's Oriole
<i>Icterus cucullatus</i>	Icteridae	Hooded Oriole
<i>Icterus galbula</i>	Icteridae	Baltimore Oriole
<i>Icterus gularis</i>	Icteridae	Altamira Oriole
<i>Icterus parisorum</i>	Icteridae	Scott's Oriole
<i>Icterus spurius</i>	Icteridae	Orchard Oriole
<i>Quiscalus major</i>	Icteridae	Boat-tailed Grackle
<i>Quiscalus mexicanus</i>	Icteridae	Great-tailed Grackle
<i>Quiscalus quiscula</i>	Icteridae	Common Grackle
<i>Dumetella carolinensis</i>	Mimidae	Gray Catbird
<i>Mimus polyglottos</i>	Mimidae	Norther Mockingbird
<i>Oreoscoptes montanus</i>	Mimidae	Sage Thrasher
<i>Toxostoma bendirei</i>	Mimidae	Bendire's Thrasher
<i>Toxostoma crissale</i>	Mimidae	Crissal Thrasher
<i>Toxostoma curvirostre</i>	Mimidae	Curve-billed Thrasher
<i>Toxostoma redivivum</i>	Mimidae	California Thrasher
<i>Toxostoma rufum</i>	Mimidae	Brown Thrasher
<i>Dendroica coronata</i>	Parulidae	Yellow-rumped Warbler
<i>Icteria virens</i>	Parulidae	Yellow-breasted Chat
<i>Melanerpes aurifrons</i>	Picidae	Golden-fronted Woodpecker
<i>Melanerpes carolinus</i>	Picidae	Red-bellied Woodpecker
<i>Melanerpes erythrocephalus</i>	Picidae	Red-headed Woodpecker
<i>Melanerpes lewis</i>	Picidae	Lewis' Woodpecker
<i>Melanerpes uropygialis</i>	Picidae	Gila Woodpecker
<i>Conuropsis carolinensis</i>	Psittacidae	Carolina Parakeet
<i>Phainopepla nitens</i>	Ptilogonatidae	Phainopepla
<i>Piranga flava</i>	Thraupidae	Hepatic Tanager
<i>Piranga ludoviciana</i>	Thraupidae	Western Tanager

<i>Piranga olivacea</i>	Thraupidae	Scarlet Tanager
<i>Piranga rubra</i>	Thraupidae	Summer Tanager
<i>Chamaea fasciata</i>	Timalidae	Wren-tit
<i>Trogon elegans</i>	Trogonidae	Elegant Trogon
<i>Catharus bicknelli</i>	Turdidae	Bicknell's Thrush
<i>Catharus fuscescens</i>	Turdidae	Veery
<i>Catharus guttatus</i>	Turdidae	Hermit Thrush
<i>Catharus minimus</i>	Turdidae	Gray-cheeked Thrush
<i>Catharus ustulatus</i>	Turdidae	Swainson's Thrush
<i>Hylocichla mustelina</i>	Turdidae	Wood Thrush
<i>Ixoreus naevius</i>	Turdidae	Varied Thrush
<i>Myadestes townsendi</i>	Turdidae	Townsend's Solitaire
<i>Sialia currucoides</i>	Turdidae	Mountain Bluebird
<i>Sialia mexicana</i>	Turdidae	Western Bluebird
<i>Sialia sialis</i>	Turdidae	Eastern Bluebird
<i>Turdus migratorius</i>	Turdidae	American Robin

**Fruigivorous Mammals of North America**

Genus Species	Family	Common Name
<i>Canis latrans</i>	Canidae	Coyote
<i>Canis lupus</i>	Canidae	Gray Wolf
<i>Urocyon cinereoargenteus</i>	Canidae	Gray Fox
<i>Vulpes macrotis</i>	Canidae	Kit Fox
<i>Vulpes velox</i>	Canidae	Swift Fox
<i>Vulpes vulpes</i>	Canidae	Red Fox
<i>Odocoileus virginianus</i>	Cervidae	White-tailed Deer
<i>Dasyurus novemcinctus</i>	Dasylopodidae	Armadillo
<i>Didelphis virginiana</i>	Didelphidae	Opossum
<i>Conepatus leuconotus</i>	Mephitidae	North American Hog-nosed Skunk
<i>Mephitis macroura</i>	Mephitidae	Hooded Skunk
<i>Mephitis mephitis</i>	Mephitidae	Striped Skunk
<i>Spilogale gracilis</i>	Mephitidae	Western Spotted Skunk
<i>Spilogale putorius</i>	Mephitidae	Eastern Spotted Skunk
<i>Gulo gulo</i>	Mustelidae	Wolverine
<i>Martes americana</i>	Mustelidae	American Marten
<i>Martes pennanti</i>	Mustelidae	Fisher
<i>Bassaris astutus</i>	Procyonidae	Ringtail
<i>Nasua narica</i>	Procyonidae	Coatis
<i>Procyon lotor</i>	Procyonidae	Raccoon
<i>Pecari tajacu</i>	Tayassuidae	Collared Peccary
<i>Ursus americanus</i>	Ursidae	Black Bear
<i>Ursus arctos</i>	Ursidae	Brown Bear

Table S3:

Frugivorous Birds of North America		
Genus Species	Family	Common Name
<i>Bombycilla cedrorum</i>	Bombycillidae	Cedar Waxwing
<i>Bombycilla garrulus</i>	Bombycillidae	Bohemian Waxwing
<i>Patagioenas fasciata</i>	Columbidae	Band-tailed Pigeon
<i>Patagioenas flavirostris</i>	Columbidae	Red-billed Pigeon
<i>Patagioenas leucocephala</i>	Columbidae	White-crowned Pigeon
<i>Zenaida asiatica</i>	Columbidae	White-winged Dove
<i>Aphelocoma californica</i>	Corvidae	Scrub Jay
<i>Aphelocoma coerulescens</i>	Corvidae	Florida Scrub Jay
<i>Aphelocoma insularis</i>	Corvidae	Island Scrub Jay
<i>Corvus ossifragus</i>	Corvidae	Fish Crow
<i>Corvus brachyrhynchos</i>	Corvidae	American Crow
<i>Corvus caurinus</i>	Corvidae	Northwestern Crow
<i>Cyanocitta cristata</i>	Corvidae	Blue Jay
<i>Cyanocitta stelleri</i>	Corvidae	Stellar's Jay
<i>Gymnorhinus cyanocephalus</i>	Corvidae	Piñon Jay
<i>Perisoreus canadensis</i>	Corvidae	Gray Jay
<i>Pica hudsonia</i>	Corvidae	Black-billed Magpie
<i>Pica nutalli</i>	Corvidae	Yellow-billed Magpie
<i>Psilorhinus morio</i>	Corvidae	Brown Jay
<i>Crotophaga sulcirostris</i>	Cuculidae	Groove-billed Ani
<i>Crotophaga ani</i>	Cuculidae	Smooth-billed Ani
<i>Icterus bullockii</i>	Icteridae	Bullock's Oriole
<i>Icterus cucullatus</i>	Icteridae	Hooded Oriole
<i>Icterus galbula</i>	Icteridae	Baltimore Oriole
<i>Icterus gularis</i>	Icteridae	Altamira Oriole
<i>Icterus parisorum</i>	Icteridae	Scott's Oriole
<i>Icterus spurius</i>	Icteridae	Orchard Oriole
<i>Quiscalus major</i>	Icteridae	Boat-tailed Grackle
<i>Quiscalus mexicanus</i>	Icteridae	Great-tailed Grackle
<i>Quiscalus quiscula</i>	Icteridae	Common Grackle
<i>Dumetella carolinensis</i>	Mimidae	Gray Catbird
<i>Mimus polyglottos</i>	Mimidae	Norther Mockingbird
<i>Oreoscoptes montanus</i>	Mimidae	Sage Thrasher
<i>Toxostoma bendirei</i>	Mimidae	Bendire's Thrasher
<i>Toxostoma crissale</i>	Mimidae	Crissal Thrasher
<i>Toxostoma curvirostre</i>	Mimidae	Curve-billed Thrasher
<i>Toxostoma redivivum</i>	Mimidae	California Thrasher
<i>Toxostoma rufum</i>	Mimidae	Brown Thrasher
<i>Dendroica coronata</i>	Parulidae	Yellow-rumped Warbler
<i>Icteria virens</i>	Parulidae	Yellow-breasted Chat
<i>Melanerpes aurifrons</i>	Picidae	Golden-fronted Woodpecker
<i>Melanerpes carolinus</i>	Picidae	Red-bellied Woodpecker
<i>Melanerpes erythrocephalus</i>	Picidae	Red-headed Woodpecker
<i>Melanerpes lewis</i>	Picidae	Lewis' Woodpecker

<i>Melanerpes uropygialis</i>	Picidae	Gila Woodpecker
<i>Conuropsis carolinensis</i>	Psittacidae	Carolina Parakeet
<i>Phainopepla nitens</i>	Ptilogonatidae	Phainopepla
<i>Piranga flava</i>	Thraupidae	Hepatic Tanager
<i>Piranga ludoviciana</i>	Thraupidae	Western Tanager
<i>Piranga olivacea</i>	Thraupidae	Scarlet Tanager
<i>Piranga rubra</i>	Thraupidae	Summer Tanager
<i>Chamaea fasciata</i>	Timalidae	Wren-tit
<i>Trogon elegans</i>	Trogonidae	Elegant Trogon
<i>Catharus bicknelli</i>	Turdidae	Bicknell's Thrush
<i>Catharus fuscescens</i>	Turdidae	Veery
<i>Catharus guttatus</i>	Turdidae	Hermit Thrush
<i>Catharus minimus</i>	Turdidae	Gray-cheeked Thrush
<i>Catharus ustulatus</i>	Turdidae	Swainson's Thrush
<i>Hylocichla mustelina</i>	Turdidae	Wood Thrush
<i>Ixoreus naevius</i>	Turdidae	Varied Thrush
<i>Myadestes townsendi</i>	Turdidae	Townsend's Solitaire
<i>Sialia currucoides</i>	Turdidae	Mountain Bluebird
<i>Sialia mexicana</i>	Turdidae	Western Bluebird
<i>Sialia sialis</i>	Turdidae	Eastern Bluebird
<i>Turdus migratorius</i>	Turdidae	American Robin

**Fruigivorous Mammals of North America**

Genus	Species	Family	Common Name
<i>Canis latrans</i>	Canidae	Coyote	
<i>Canis lupus</i>	Canidae	Gray Wolf	
<i>Urocyon cinereoargenteus</i>	Canidae	Gray Fox	
<i>Vulpes macrotis</i>	Canidae	Kit Fox	
<i>Vulpes velox</i>	Canidae	Swift Fox	
<i>Vulpes vulpes</i>	Canidae	Red Fox	
<i>Odocoileus virginianus</i>	Cervidae	White-tailed Deer	
<i>Dasypus novemcinctus</i>	Dasyproctidae	Armadillo	
<i>Didelphis virginiana</i>	Didelphidae	Opossum	
<i>Conepatus leuconotus</i>	Mephitidae	North American Hog-nosed Skunk	
<i>Mephitis macroura</i>	Mephitidae	Hooded Skunk	
<i>Mephitis mephitis</i>	Mephitidae	Striped Skunk	
<i>Spilogale gracillis</i>	Mephitidae	Western Spotted Skunk	
<i>Spilogale putorius</i>	Mephitidae	Eastern Spotted Skunk	
<i>Gulo gulo</i>	Mustelidae	Wolverine	
<i>Martes americana</i>	Mustelidae	American Marten	
<i>Martes pennanti</i>	Mustelidae	Fisher	
<i>Bassariscus astutus</i>	Procyonidae	Ringtail	
<i>Nasua narica</i>	Procyonidae	Coatis	
<i>Procyon lotor</i>	Procyonidae	Raccoon	
<i>Pecari tajacu</i>	Tayassuidae	Collared Peccary	
<i>Ursus americanus</i>	Ursidae	Black Bear	
<i>Ursus arctos</i>	Ursidae	Brown Bear	

Table S4:

Independent Variable	Dependent Variable ( $Z_{\text{diff}}$ )	Regression Models						Monte Carlo Simulations		
		Spatially correlated?	Fit	F-statistic	p-value	Effect size	R <sup>2</sup>	Spatially correlated?	p-value (estimated)	rho
<b>Frugivory</b>										
Precipitation	Birds and plants	Yes	Gaussian	1.14	0.29	0.12	0.01	Yes	0.14	0.21
	Mammals and plants	Yes	Gaussian	0.81	0.37	0.12	0.04	Yes	0.25	0.17
	<b>Scatter-Hoarding</b>									
	Birds and plants	Yes	Gaussian	41.52	0.00	0.60 ↑	0.05	Yes	0.10	0.22
AET	Rodents and plants	Yes	Gaussian	124.20	0.00	1.21 ↑	0.39	Yes	0.02	0.41 ↑
	<b>Frugivory</b>									
	Birds and plants	Yes	Gaussian	1.61	0.21	0.08*	-0.08	Yes	0.21	0.21
	Mammals and plants	Yes	Gaussian	2.48	0.12	0.11*	0.13	Yes	0.07	0.37
	<b>Scatter-Hoarding</b>									
	Birds and plants	Yes	Gaussian	130.67	0.00	0.29* ↑	0.23	Yes	0.00	0.58 ↑
Elevation	Rodents and plants	Yes	Gaussian	252.95	0.00	.33* ↑	0.26	Yes	0.00	0.70 ↑
	<b>Frugivory</b>									
	Birds and plants	Yes	Gaussian	0.97	0.33	0.1**	-0.54	Yes	0.00	-0.45 ↓
	Mammals and plants	Yes	Gaussian	0.08	0.78	0.003**	0.01	Yes	0.07	0.37
	<b>Scatter-Hoarding</b>									
	Birds and plants	Yes	Gaussian	3.03	0.08	0.11**	0.09	Yes	0.00	-0.50 ↓
latitude	Rodents and plants	Yes	Gaussian	15.09	0.00	0.11** ↓	0.19	Yes	0.00	-0.52 ↓
	<b>Frugivory</b>									
	Birds and plants	Yes	Gaussian	23.37	0.00	0.06 ↑	0.31	Yes	0.15	0.30
	Mammals and plants	Yes	Gaussian	0.94	0.33	-0.16	-0.26	Yes	0.35	-0.14
	<b>Scatter-Hoarding</b>									
	Birds and plants	Yes	Gaussian	3.54	0.06	0.02	0.00	Yes	0.15	-0.23
	Rodents and plants	Yes	Gaussian	1.15	0.22	0.01	-0.01	Yes	0.29	-0.15

## SUPPLEMENTARY INFORMATION—SPATIAL RANDOMIZATIONS

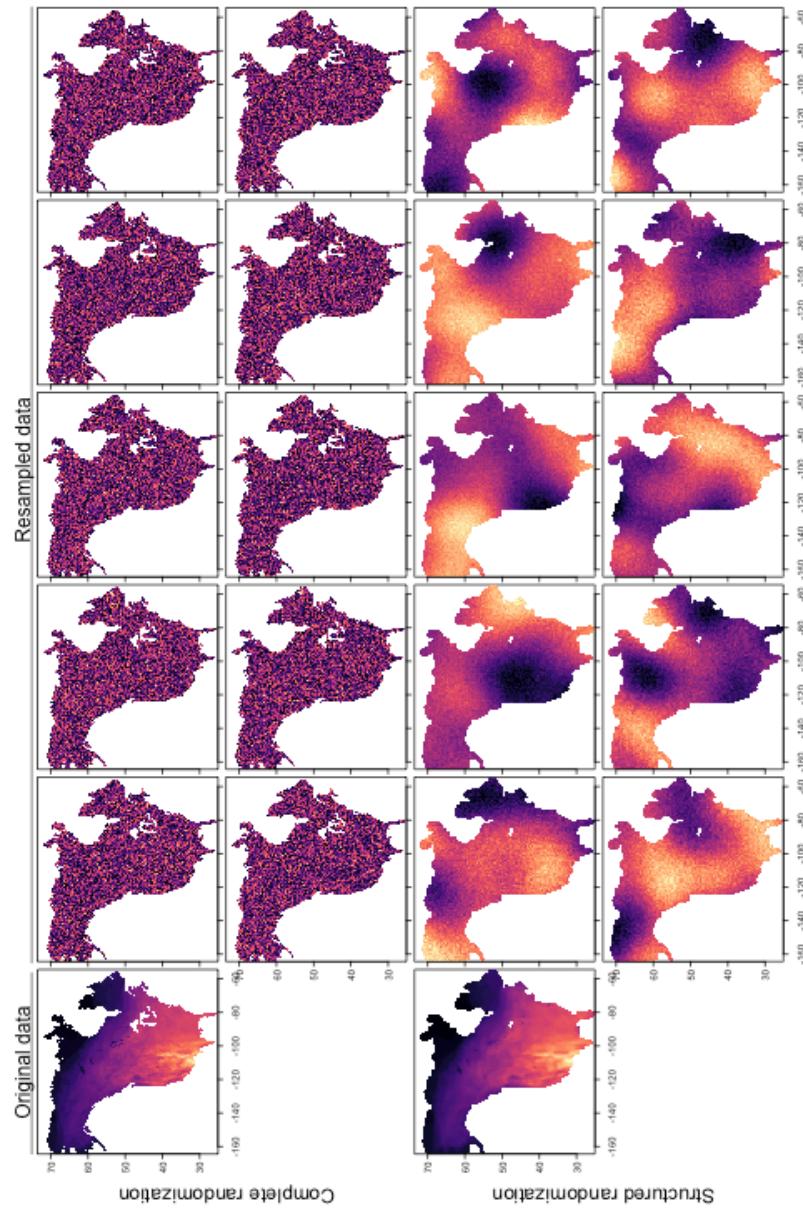
Included in this document are the results from the complete (S6–9) and structured (S10–13) spatial randomizations. The methods are described in *Materials and Methods, §Data Analysis* of the paper, and the code to recreate the analysis and figures can be found at <https://github.com/dispersing/SpatialRandomizations>.

Figure S5 shows an example of an observed pattern (column 1) and 10 complete randomizations (rows 1 and 2) and 10 structured randomizations (rows 3 and 4). Figures S6–9 show the results for the complete randomizations of the correlations between animal and environmental variables (S5), the animal and plant variables (S7), the difference in richness and environmental variables (S8), and the plant and environmental variables (S9). Figures S10–13 show the results for the structured randomizations of the correlations between animal and environmental variables (S10), the animal and plant variables (S11), the difference in richness and environmental variables (S12), and the plant and environmental variables (S13).

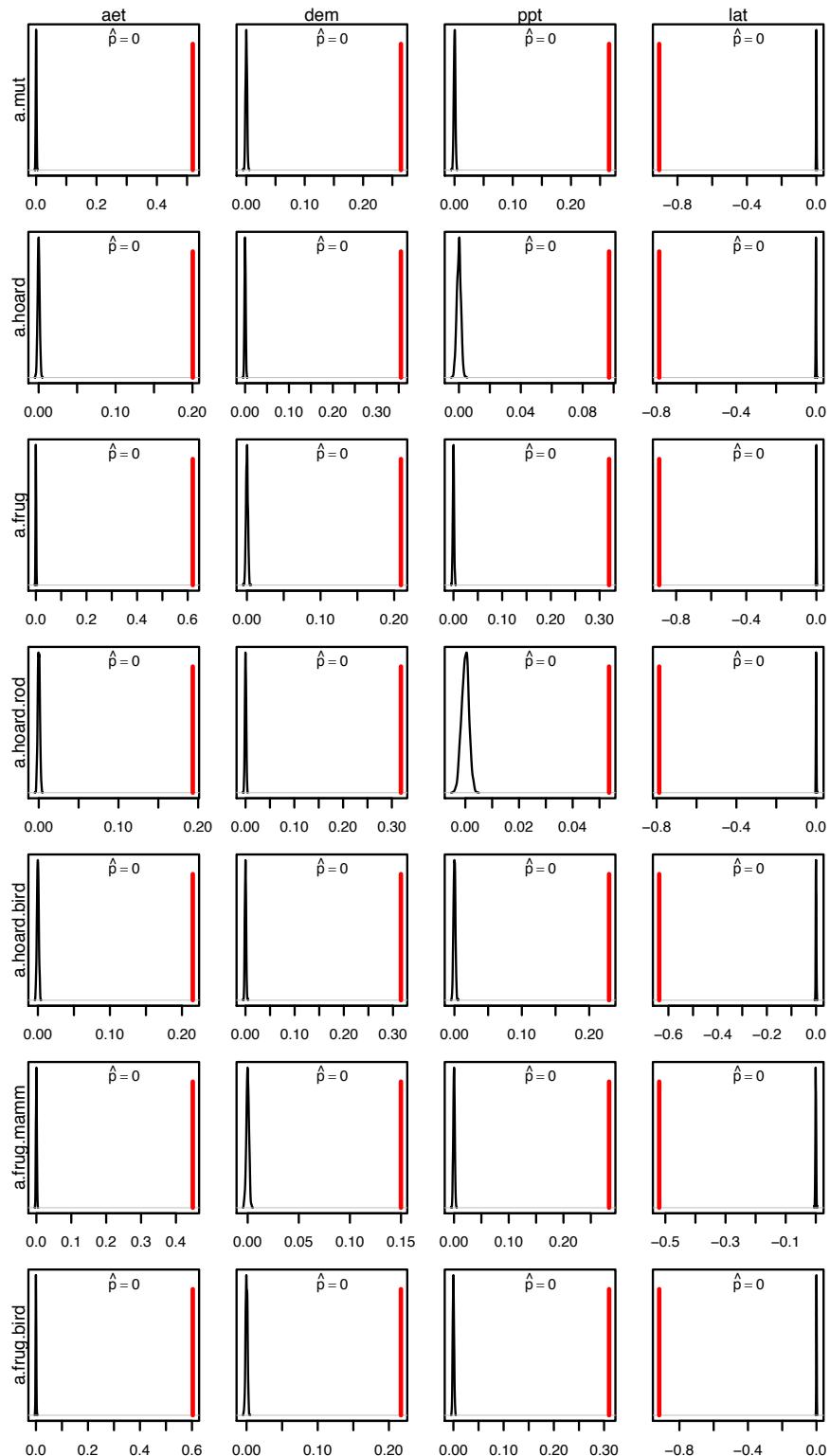
Variables names translate:

- I. Environmental variables
  - a. aet: actual evapotranspiration
  - b. dem: elevation
  - c. ppt: precipitation
  - d. lat: latitude
- II. Animal variables
  - a. a.mut: all mutualist animals
  - b. a.hoard: hoarding animal guild
  - c. a.frug: frugivorous animal guild
  - d. a.hoard.rod: hoarding rodent subguild
  - e. a.hoard.bird: hoarding bird subguild
  - f. a.frug.mamm: frugivorous mammal subguild
  - g. a.frug.bird: frugivorous bird subguild
- III. Plant variables
  - a. p.mut: all mutualist plants
  - b. p.hoard: hoarded plant guild
  - c. p.frug: frugivory plant guild
  - d. p.hoard.rod: rodent-hoarded plant subguild
  - e. p.hoard.bird: bird-hoarded plant subguild
  - f. p.frug.mamm: mammal frugivory plant subguild
  - g. p.frug.bird: bird frugivory plant subguild
- IV. Richness difference
  - a. d.mut: difference in richness of all mutualists
  - b. d.hoard: difference in richness of the hoarding guild
  - c. d.frug: difference in richness of the frugivory guild
  - d. d.hoard.rod: difference in richness of the rodent hoarding subguild
  - e. d.hoard.bird: difference in richness of the bird hoarding subguild
  - f. d.frug.mamm: difference in richness of the mammal frugivory subguild
  - g. d.frug.bird: difference in richness of the bird frugivory subguild

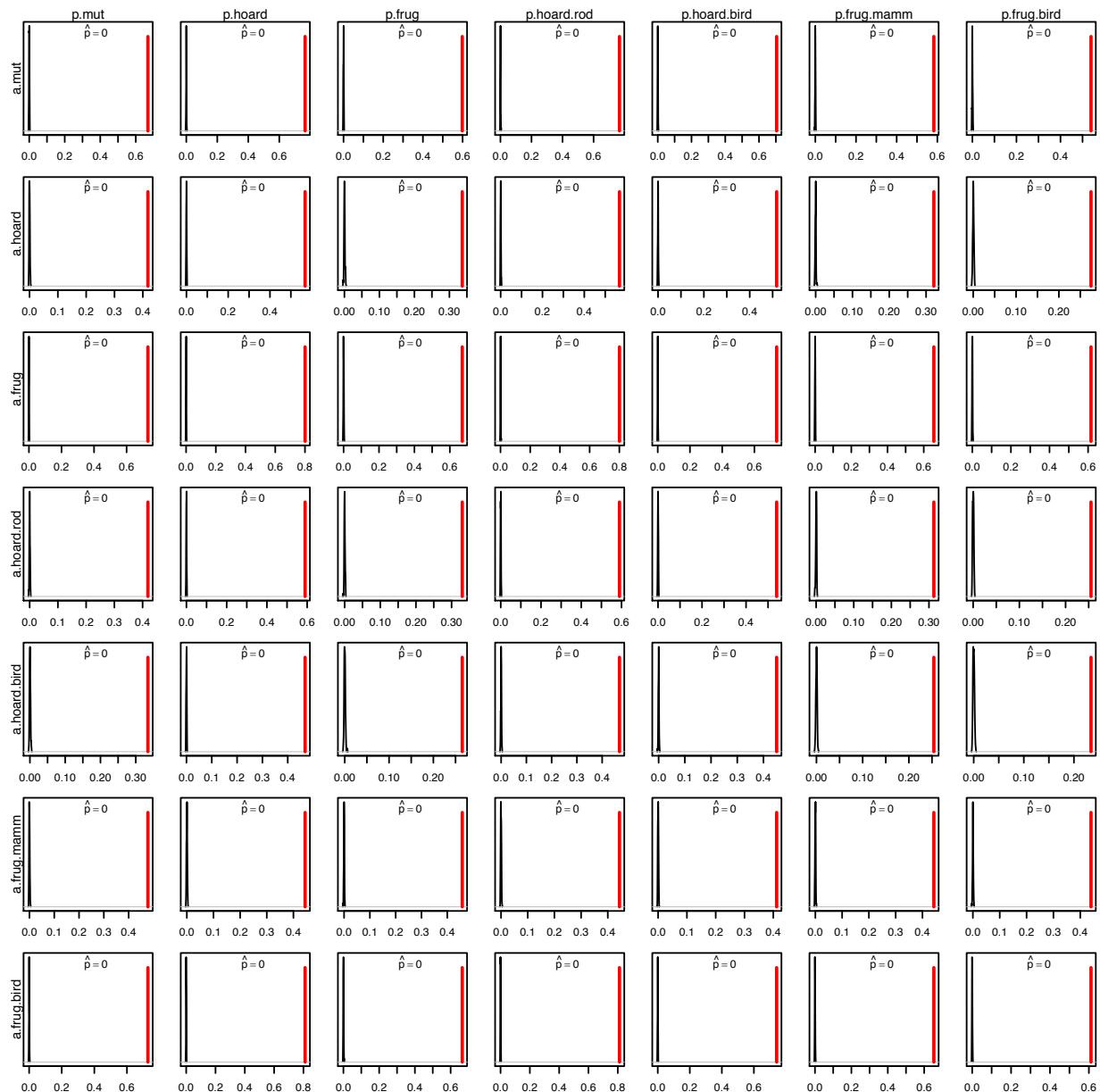
**Figure S5.** An example of an observed pattern (column 1, "Original data") and 10 complete randomizations (rows 1 and 2) and 10 structured randomizations (rows 3 and 4). This example is to visually demonstrate to the reader the difference between the two tests. The latter preserves the spatial autocorrealtive structure and is therefore a more rigorous statistical test.



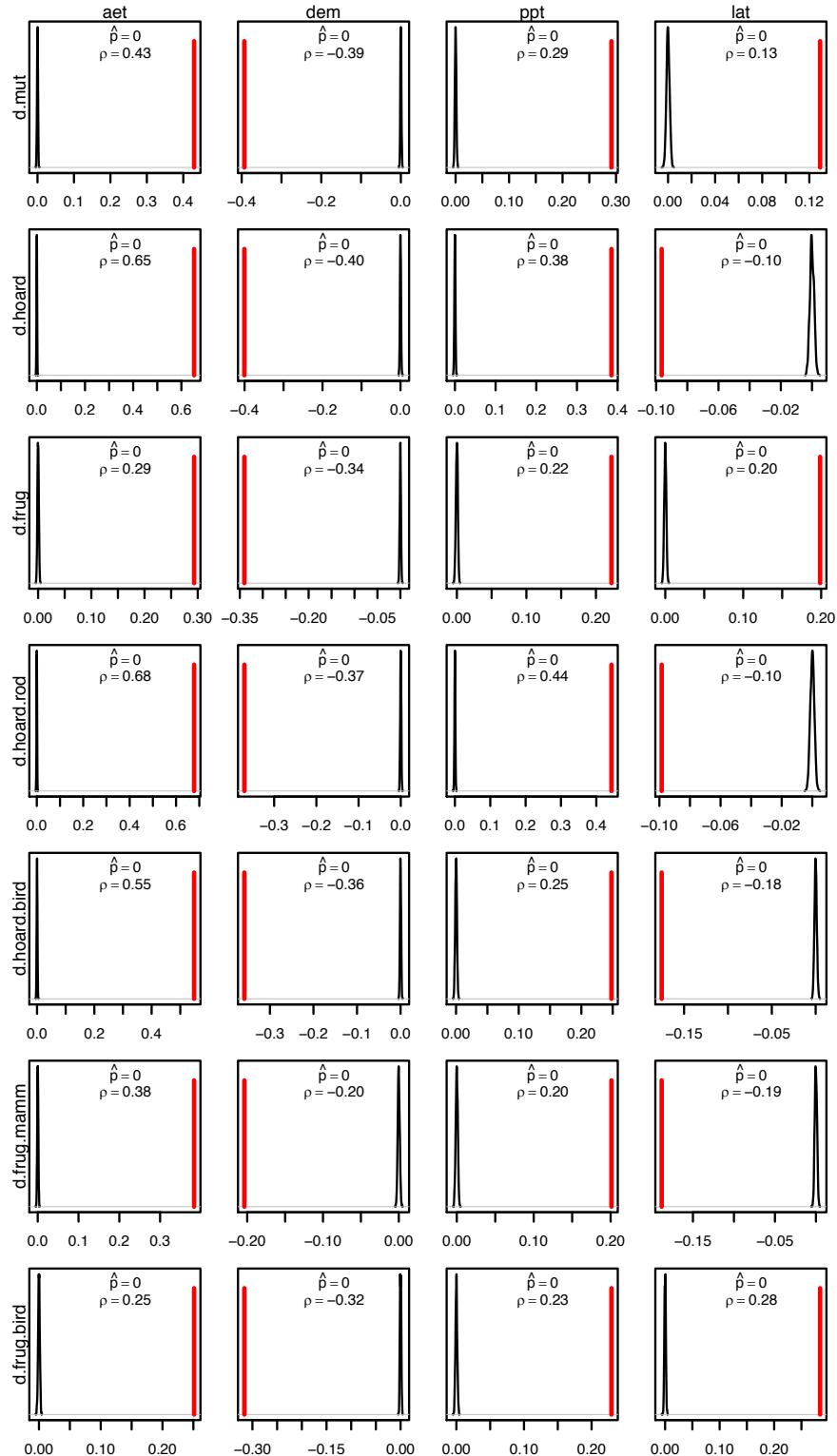
**Figure S6.** Results for the complete randomizations of the correlations between animal and environmental variables. Every randomization in each comparison had an observed value more extreme than all of randomizations, meaning all had an estimated  $p$ -value,  $\hat{p} = 0$ .



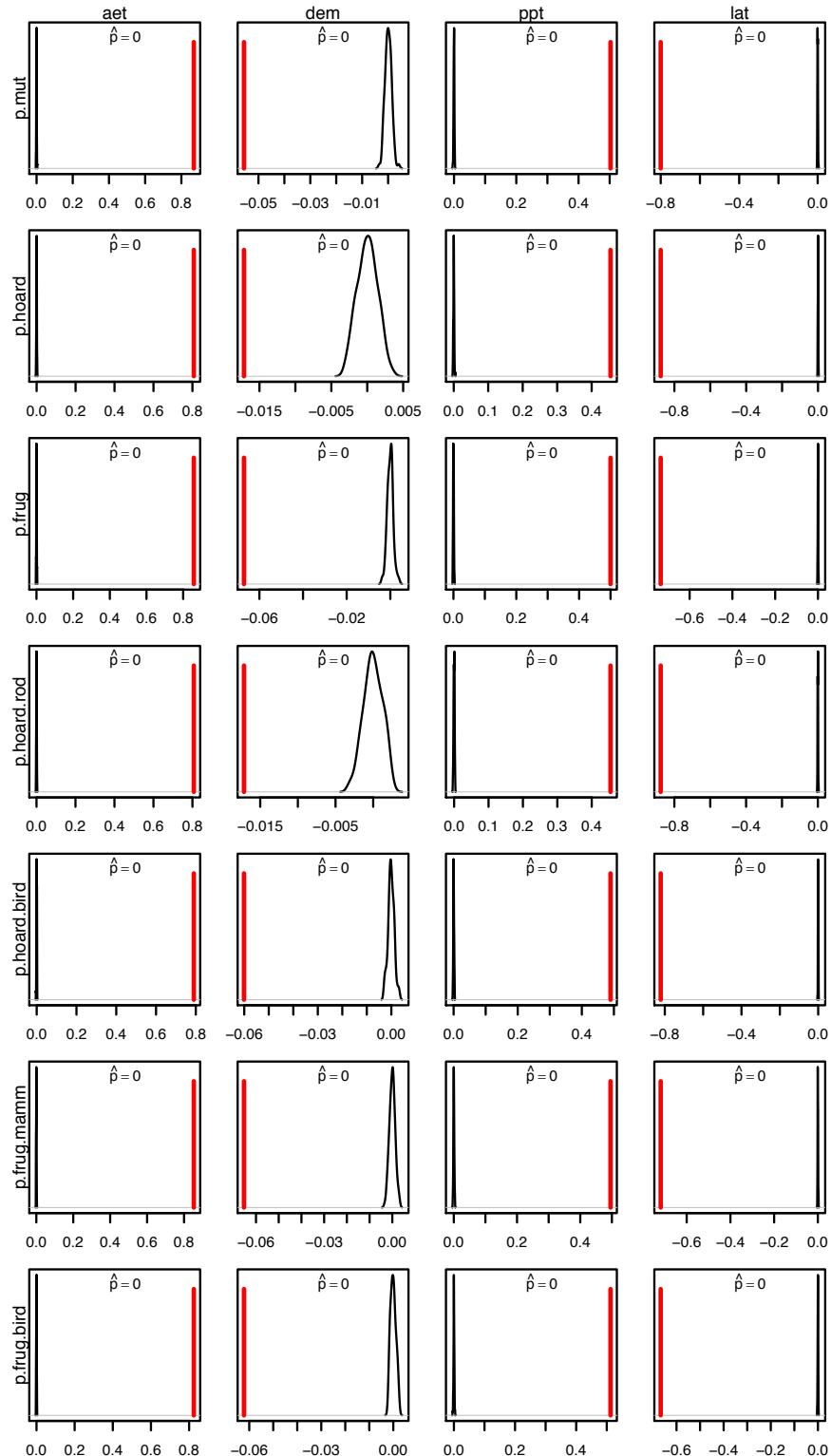
**Figure S7.** Results for the complete randomizations of the correlations between animal and plant variables. Every randomization in each comparison had an observed value more extreme than all of randomizations, meaning all had an estimated  $p$ -value,  $\hat{p} = 0$ .



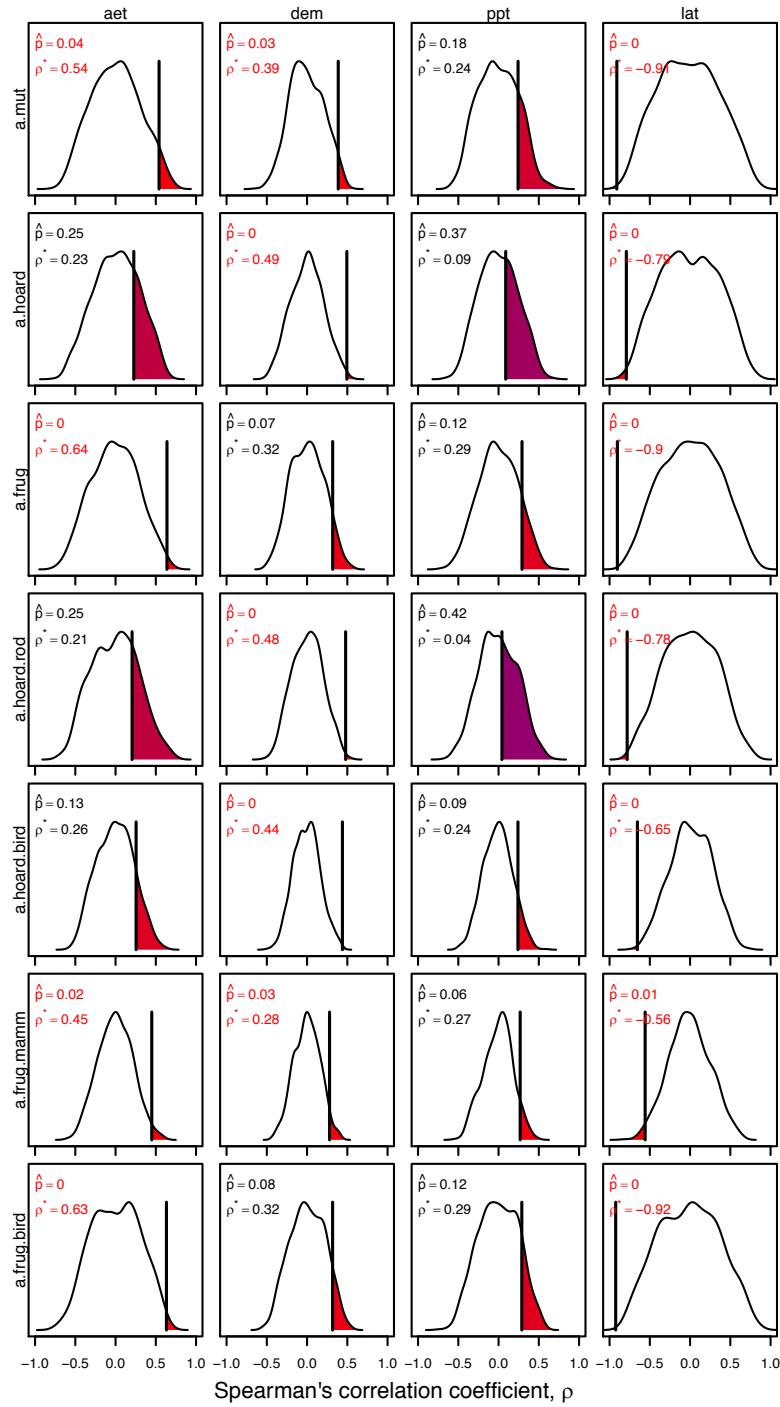
**Figure S8.** Results for the complete randomizations of the correlations between difference in richness and environmental variables. Every randomization in each comparison had an observed value more extreme than all of randomizations, meaning all had an estimated  $p$ -value,  $\hat{p} = 0$ .



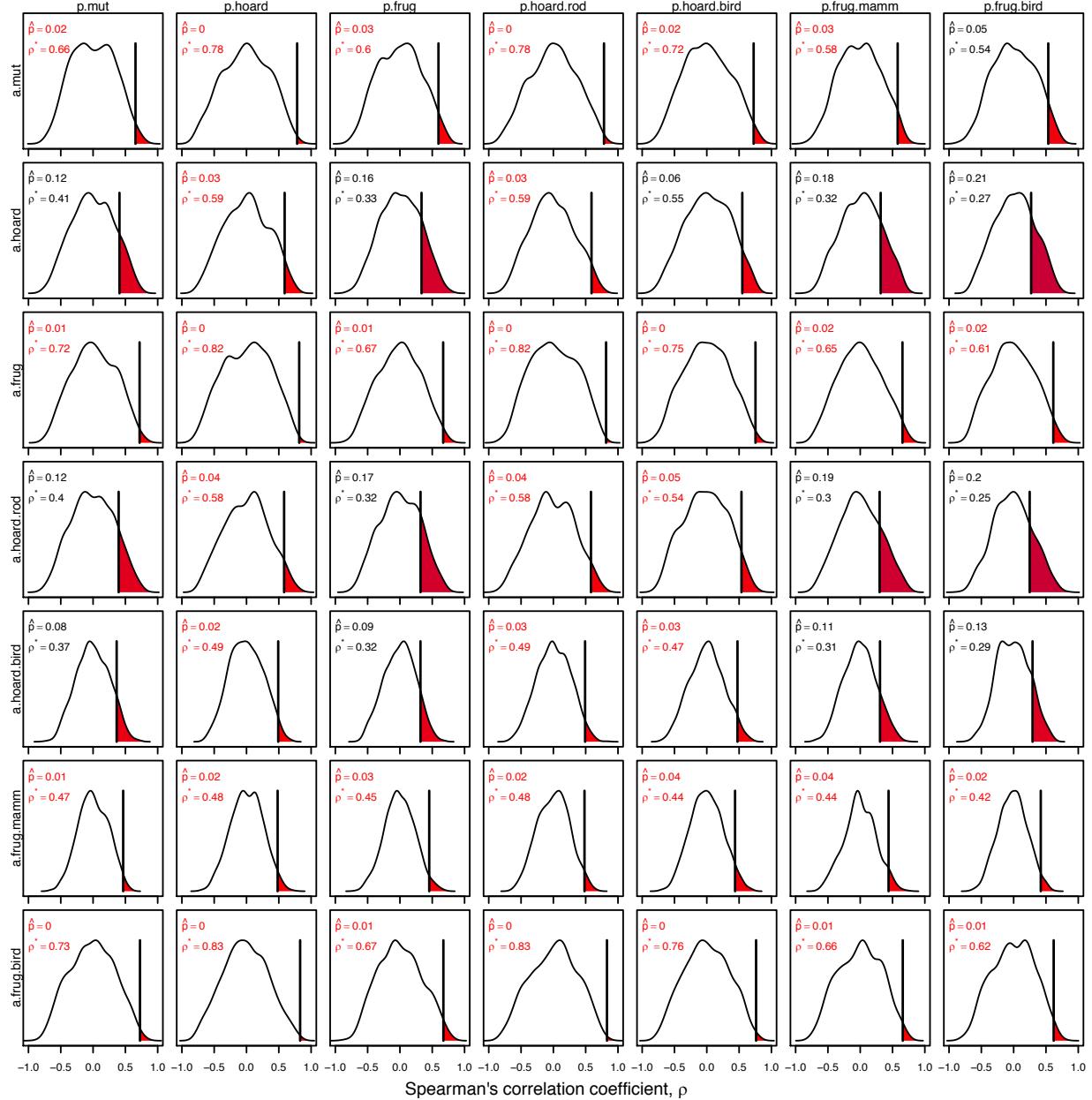
**Figure S9.** Results for the complete randomizations of the correlations between plant and environmental variables. Every randomization in each comparison had an observed value more extreme than all of randomizations, meaning all had an estimated  $p$ -value,  $\hat{p} = 0$ .



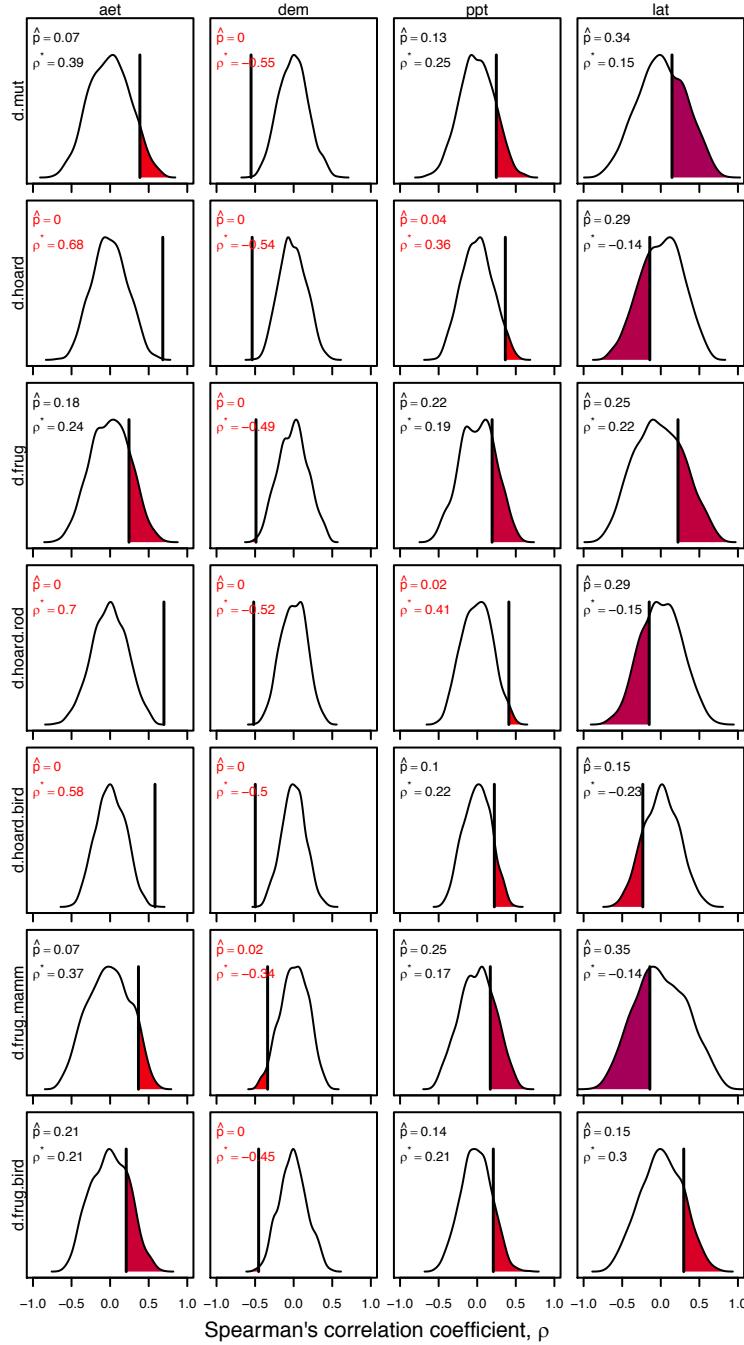
**Figure S10.** Results for the structured randomizations of the correlations between animal and environmental variables. Within each panel, the distribution represents the randomized Spearman's correlation coefficient,  $\rho$ ; vertical black lines represent the observed Spearman's correlation coefficient,  $\rho^*$ ; shaded areas represent parts of the distribution that were more extreme than  $\rho^*$ ; the  $\hat{\rho}$  is the randomizations  $\geq \rho^*$ ; and if  $\leq 5\%$  of the randomizations were more extreme than  $\rho^*$  then we interpret that as statistically significant and color the statistical font red rather than black.



**Figure S11.** Results for the structured randomizations of the correlations between animal and plant variables. Within each panel, the distribution represents the randomized Spearman's correlation coefficient,  $\rho$ ; vertical black lines represent the observed Spearman's correlation coefficient,  $\rho^*$ ; shaded areas represent parts of the distribution that were more extreme than  $\rho^*$ ; the  $\hat{p}$  is the randomizations  $\geq \rho^*$ ; and if  $\leq 5\%$  of the randomizations were more extreme than  $\rho^*$  then we interpret that as statistically significant and color the statistical font red rather than black.



**Figure S12.** Results for the structured randomizations of the correlations between the difference in richness and environmental variables. Within each panel, the distribution represents the randomized Spearman's correlation coefficient,  $\rho$ ; vertical black lines represent the observed Spearman's correlation coefficient,  $\rho^*$ ; shaded areas represent parts of the distribution that were more extreme than  $\rho^*$ ; the  $\hat{\rho}$  is the randomizations  $\geq \rho^*$ ; and if  $\leq 5\%$  of the randomizations were more extreme than  $\rho^*$  then we interpret that as statistically significant and color the statistical font red rather than black.



**Figure S13.** Results for the structured randomizations of the correlations between the plant and environmental variables. Within each panel, the distribution represents the randomized Spearman's correlation coefficient,  $\rho$ ; vertical black lines represent the observed Spearman's correlation coefficient,  $\rho^*$ ; shaded areas represent parts of the distribution that were more extreme than  $\rho^*$ ; the  $\hat{\rho}$  is the randomizations  $\geq \rho^*$ ; and if  $\leq 5\%$  of the randomizations were more extreme than  $\rho^*$  then we interpret that as statistically significant and color the statistical font red rather than black.

