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The mismatch in distributions of vertebrates and the plants that they disperse

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Little is known about how mutualistic interactions affect the distribution of species richness on broad geographic scales. Because mutualism positively affects the fitness of all species involved in the interaction, one hypothesis is that the richness of species involved should be positively correlated across their range, especially for obligate relationships. Alternatively, if mutualisms involve multiple mutualistic partners, the distribution of mutualists should not necessarily be related, and patterns in species distributions might be more strongly correlated with environmental factors. In this study, we compared the distributions of plants and vertebrate animals involved in seed-dispersal mutualisms across the United States and Canada. We compiled geographic distributions of plants dispersed by frugivores and scatter-hoarding animals, and compared their distribution of richness to the distribution in disperser richness. We found that the distribution of animal dispersers shows a negative relationship to the distribution of the plants that they disperse, and this is true whether the plants dispersed by frugivores or scatter-hoarders are considered separately or combined. In fact, the mismatch in species richness between plants and the animals that disperse their seeds is dramatic, with plants species richness greatest in the in the eastern United States and the animal species richness greatest in the southwest United States. Environmental factors were corelated with the difference in the distribution of plants and their animal mutualists and likely are more important in the distribution of both plants and animals. This study is the first to describe the broad-scale distribution of seed-dispersing vertebrates and compare the distributions to the plants they disperse. With these data, we can now identify locations that warrant further study to understand the factors that influence the distribution of the plants and animals involved in these mutualisms.

Keywords: seed dispersal, mutualism, species distributions

Introduction

A central problem in ecology is to understand the patterns and processes shaping the distribution of species. There is a preponderance of studies of species richness at broad geographic scales (Hawkins et al. 2003, Rahbek et al. 2007, Stein et al. 2014, Rabosky and Hurlbert 2015) that has facilitated our understanding of why species are found

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where they are, a central tenet within the domain of ecology (Scheiner and Willig 2008). Most commonly, these studies find species distributions to be correlated with resource availability and use environmental variables (e.g. temperature and productivity; Rabosky and Hurlbert 2015) to explain putative determinants of the distributions. Environmental variables are only one determinant of species' distributions. Another, species interaction, is a key and understudied determinant of species' distributions (Cazelles et al. 2016). In fact, in some cases species interactions may be more important for determining distribution than environmental variables (Fleming 2005).

When species interact, we expect their geographic distributions to be correlated – either positively or negatively – depending on the effect (or sign of the interaction) of one species on the other (Case et al. 2005). For pairwise interactions, where one species benefits from another species, a positive relationship is expected between the distribution and abundance due to the increase in the average fitness of the benefitting species where they overlap (Svenning et al. 2014). Furthermore, most species interactions are not simply pairwise, but diffuse, consisting of multiple interacting species, here referred to as guilds (with guilds referring to species that use the same resource). It therefore follows that where one guild benefits from another guild, a positive relationship is expected between the distribution and richness of the guilds. This should be true in the case of mutualisms, where both sides of the interaction share an increase in average fitness from being together (Bronstein 2015), and there is some evidence for correlated geographic distributions of mutualists in the New World (Fleming 2005). One example of a mutualism where both sides of the interaction have a fitness advantage in each other's presence is animal-mediated seed dispersal. Because both interacting species and guilds in seed dispersal mutualism benefit from the relationship we would predict that the richness of animal-dispersed plants ought to be correlated with the richness of their animal dispersers and vice versa. To our knowledge, this prediction has never been tested on a large geographic scale.

Seed dispersal mutualisms have been a major evolutionary innovation in plants (Tiffney and Mazer 1995, Eriksson et al. 2000, Tiffney 2004), allowing them to take advantage of dispersal vectors that deliver seeds to suitable microsites more regularly and predictably (Howe and Smallwood 1982). Most seed dispersal mutualisms occur between guilds of plants that are dependent on guilds of animals. Of those plants that are dispersed by animal mutualists, the mutualistic interactions are usually presumed to be asymmetrical – plants are obligate mutualists dependent on guilds of dispersing animals, whereas animals are facultative mutualists partially depending on the plants they disperse (Donatti et al. 2011). Many studies have described the richness of animal species (Jetz and Rahbek 2002, Kissling et al. 2007, 2009) and plant species (Kreft and Jetz 2007, Vander Wall and Moore 2016, Vander Wall et al. 2017) at broad geographic scales and their relationship with various environmental variables. In these studies, distributions are often most correlated with environmental

variables associated with productivity (e.g. precipitation and evapotranspiration). With these data, we should be able to ask questions about whether or not the distribution of plant species is determined by interactions with their dispersers and how much is determined by environmental variables. Similarly, we can ask the same questions about the animal dispersers and the mutualism as a whole.

One factor limiting the testing of hypotheses of seed-dispersal mutualism diversity, and the effects of plant diversity on animal diversity in general and vice versa, has been the lack of data on the distributions and diversity of plant species that are engaged in seed dispersal mutualisms (Hawkins and Pausas 2004). Recently, Vander Wall and Moore (2016) described the distribution of plants dispersed by animal mutualists in North America. They found that the distribution of plants with seed-dispersal mutualists are more correlated to environmental conditions than plants dispersed non-mutualistically but it is unknown whether the species richness of animal dispersers contributes to this pattern. In this study, we build upon Vander Wall and Moore (2016) to determine whether the diversity of seed-dispersing animals correlates with the diversity of animal-dispersed plants or whether richness of animal seed-dispersal mutualists are better described by environmental variables.

Given our theoretical predictions that species involved in mutualisms should be positively associated across their geographic distribution, we investigated the composite distribution of terrestrial bird and mammal seed dispersers across the United States and Canada. The ultimate goal of this study was to determine how the richness of seed-dispersing animals varies across the United States and Canada and how that composite distribution matches up with the composite distribution of the plants that they disperse. To do so, we investigated whether the richness of seed-dispersing animals is correlated with broad ecological and environmental variables, including the richness of the plants that they disperse. We hypothesize that if plants are closely dependent (i.e. mutualisms are obligate) on their seed dispersers, then the richness distribution of the plants would show a strong correlation with seed dispersers compared with environmental variables and vice versa. Alternatively, if the mutualisms between plants and seed-dispersing animals is facultative, as is presumed between the animals that disperse the plants, then we expect a stronger relationship between the richness distribution of animals and environmental variables compared with the plants.

Material and methods

Assignment of species 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 the United States and Canada 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 at least seasonally, and the seeds remain viable after being either regurgitated or passed through the digestive tract (Fleming et al. 1987). 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). For this study, 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 an expectation that some of those seeds are found in suitable sites for establishment. Hereafter, we use the terms frugivore and scatter-hoarder to mean species that are mutualist seed dispersers. Full details of species assignment can be found in the Supplementary material Appendix 1.

Data acquisition and preparation

We prepared for our analyses by first creating comparable datasets. We had four groups of data: animal mutualist richness, environmental variables, plant mutualist richness, and the difference between animal and plant mutualist richness. The animal mutualists consisted of seven sub-guilds: all animal mutualists, all frugivores, frugivorous mammals, frugivorous birds, all scatter-hoarders, scatter-hoarding rodents, and scatter-hoarding birds. Animal distribution data came in the form of polygons which were clipped to the boundaries of the United States and Canada if it exceeded those boundaries, then the polygons overlaid, richness was summed, and the resulting file was rasterized to generate animal mutualist species richness at each grid cell of a master raster. All geographic data manipulation was done in R (R Development Core Team). Bird distribution data provided by NatureServe in collaboration with Robert Ridgely, James Zook, The Nature Conservancy – Migratory Bird Program, Conservation International – Center for Applied Biodiversity Science, World Wildlife Fund – US, and Environment Canada – WILDSPACE <http://datazone.birdlife.org/species/request-dis> (Ridgley et al. 2007). Mammal data available from the International Union for Conservation of Nature Red List <www.iucnredlist.org/technical-documents/spatial-data/> (IUCN 2016).

Environmental variables were chosen because they have been found to be important predictors of species distributions in previous studies (Pearson and Dawson 2003). The environmental variables consisted of four datasets: mean actual evapotranspiration (mm yr^{-1}; hereafter AET), elevation (m), mean precipitation (mm yr^{-1}; hereafter precipitation) and latitude (degrees). AET is a proxy for terrestrial productivity (Mackey and Currie 2001) and has been found to be associated with bird and plant distributions (Karr 1976, Hawkins et al. 2003, Kissling et al. 2009). Precipitation is has been found to be correlated with the diversity of plants dispersed by frugivores and scatter-hoarders (Vander Wall and Moore 2016). Lastly, we included elevation because there are large elevational gradients in western North America and species richness generally decreases with an increase in elevation (Rahbek 1995). Each environmental variable was obtained

as a raster and bilinear interpolation was used to conform the extent and resolution of the original raster to our master raster (see Supplementary material Appendix 1 for details). AET data is available from the Global-AET Database <www.cgiar-csi.org> (Zomer et al. 2007, 2008). Elevation data is available from Natural Earth <www.naturalearthdata.com> (2016). Precipitation data is available from Bioclim <www.worldclim.org> (Hijmans et al. 2005).

The plant mutualists consisted of seven datasets: all plant mutualists, all plants in frugivory mutualisms, plants in frugivory mutualisms with mammals, plants in frugivory mutualisms with birds, all plants in scatter-hoarding mutualism, plants in scatter-hoarding mutualism with rodents, and plants in scatter-hoarding mutualism with birds. Each plant dataset was obtained from a previous study that identified plants in dispersal mutualisms at 197 sites across North America, north of Mexico. For this study, we used the plant species richness per site that are dispersed by frugivores or scatter hoarders. Sites were generally characterized as floras > 1000 ha in area, separated by > 50 km, and presumed to have completeness of vegetation sampling. See Vander Wall et al. (2017) for complete descriptions of the sites and Vander Wall and Moore (2016) for methods of dispersal mode determination. We interpreted the point values of plant richness and estimated values across our geographic range of interest. Specifically, we used ordinary kriging to interpolate values to our master raster using R library, automap (Hiemstra et al. 2009). The extrapolated maps created from Vander Wall et al. (2017) and used for this study can be seen in Fig. 1a, d, g. The differences between animal and plant mutualist richness were calculated for the same seven modes listed above. Because the means and variances were very different between animal and plant mutualists, we calculated z-scores (Eq. 1) between them and subtracted the z-score of plant from animal mutualists at each point to create a value (Z_{diff}) used in data analysis described below, yielding a range of values where Z_{diff} is > 0 there are relatively greater plant mutualist richness and where Z_{diff} < 0 there are relatively greater animal mutualist richness.

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

Where $\bar{X}$ is the mean richness, X_{obs} is the richness at the specific point, and $\sigma(X)$ is the standard deviation of the richness of either animal or plant mutualists. Further explanation on how the rasters for the Z_{diff} were created, including details of extent can be found in Supplementary material Appendix 1.2.

Data analysis

Data analysis was broken into three major categories: all seed dispersing mutualists, frugivorous animals, and scatter-hoarding animals. Within each major category, we had two general comparisons: 1) animal mutualists and plant mutualists and 2) Z_{diff} and environmental variables. Due to heteroscedasticity in the plant richness, data-weighted least squares
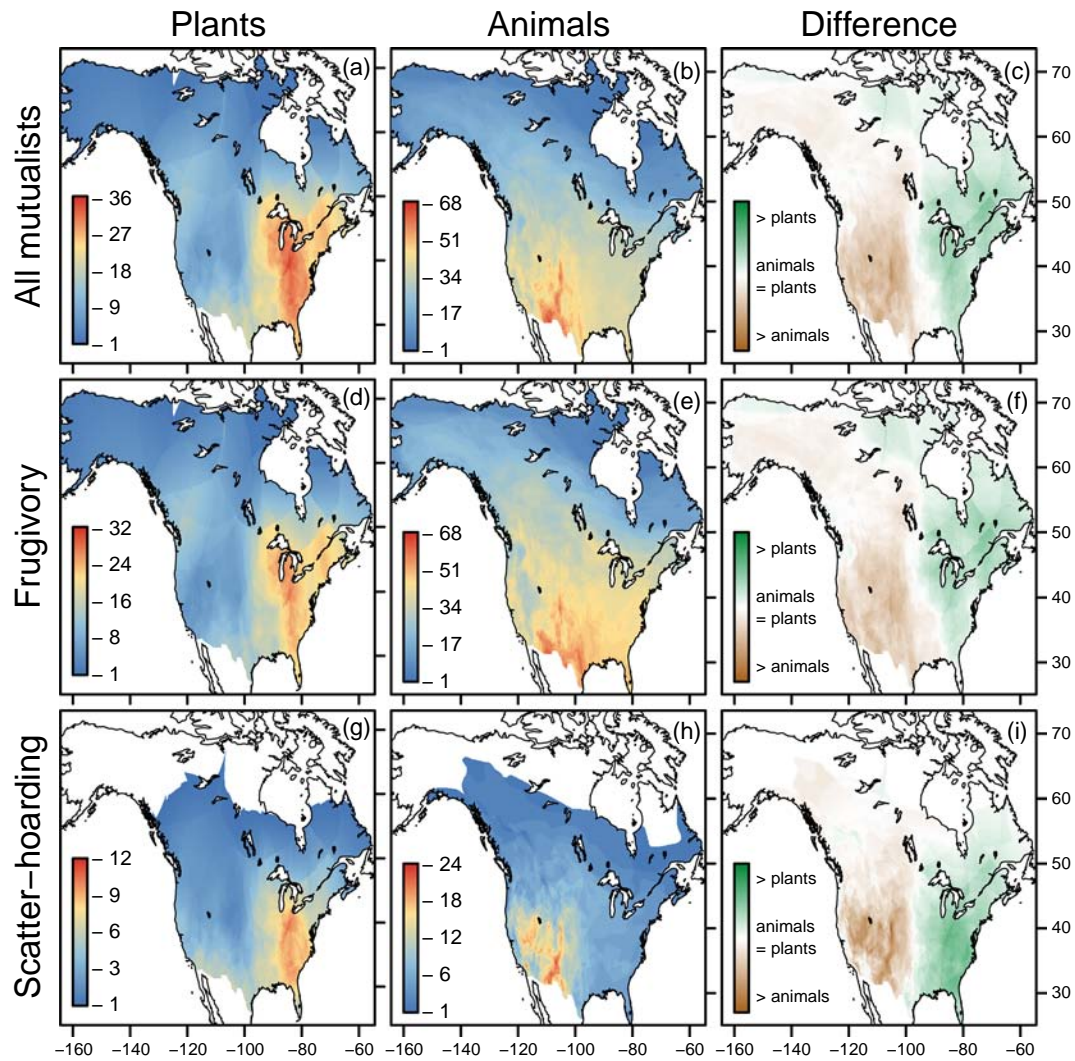
Figure 1. Richness of seed-dispersal mutualism. The left panels (a, d, g) are the distribution of plants involved in each category of seed dispersal mutualism after Vander Wall et al. (2017). The middle panels (b, e, h) are the richness distributions of animals involved in each category of seed dispersal mutualisms, and the right panels (c, f, i) are the differences between plant and animal richness (Z_{diff}) involved in each category of mutualisms. In the left and middle panels, the legend represents the number of plants or animals at any given locations. While in the right panel the legend represents the relative difference in richness between plants and animals.

regression models were created using the squared residuals of area adjusted plant richness as weights. Despite richness being count data, a Poisson distribution was not necessary because the data did not deviate from a normal distribution. Spatial autocorrelation is a common occurrence in range map and atlas survey data (Dormann et al. 2007) and was present in the environmental variables, but none of the richness of either plants or animals. To adjust for spatial autocorrelation, generalized least squares models (GLS) were built for each comparison using a Gaussian spatial correlation. Data were transformed with a natural log when necessary.

We then conducted two types of Monte Carlo simulations to test the statistical hypothesis that there is no relationship between groups of variables: a complete randomization and a spatially-structured randomization (i.e. restricted randomization, sensu Fortin and Jacquez 2000). The complete

randomization permuted grid cells across the continent, which allowed us to test the hypothesis that observations are random. The structured randomization statistically fit a spatial autocorrelation model (variogram), and then generated a random field (Lantuéjoul 2013) with the same degree of spatial autocorrelation using the Random Fields package in R (Schlather et al. 2013, 2015). Given that we know that geographic data are spatially autocorrelated, this allowed us to test the hypothesis that, given our observed levels of spatial autocorrelation, the observed data are random. We calculated Spearman's correlation coefficient, ρ, for each of 1000 iterations for the complete and structured randomizations. We then calculated the proportion of the complete or structured randomizations that were more extreme than the observed correlation, ρ^* as an estimated p-value, $\hat{p}$. R code used to conduct the analyses can be found at the following

Every complete randomization failed to detect a random distribution; thus, rendering the analysis uninformative. (Supplementary material Appendix 1 Fig. A6–A9 shows the full results of the complete randomizations.) Therefore, every Monte Carlo simulation reference henceforth is specific to the spatially-structured tests.

Lastly, because so little is known about the factors contributing to the distribution of seed-dispersal mutualisms we performed classifications and regression trees (CART) after our initial analysis to better understand the structure of the data and identify factors that warrant future investigation. For this data exploration, we used R library, rpart (Therneau et al. 2015) using the ANOVA method. All analyses were performed using the R language and environment (R Development Core Team).

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.cp39t21> (Dittel et al. 2018).

Results

Distribution of seed dispersing animals

We identified 183 animal species in North America that have a seed dispersing mutualism with plants either via frugivory or scatter-hoarding. Seed dispersing animals are most speciose in the southwestern portions of North America from the southern portion of the Colorado Plateau desert region and further north, east of the Rocky Mountains, to the southern Rocky Mountain-prairie border (Fig. 1). There was no significant correlation between the richness of all mutualist animals and the plants that they disperse ($F_{1,195} = 0.39$, $p = 0.53$); instead richness of all animal mutualists decreased with increasing in latitude ($F_{1,195} = 207$, $p < 0.001$, Fig. 2). Monte Carlo simulations, however, did suggest there were correlations between animal and plant richness. Results from the regression models and the Monte Carlo simulations can be found in Table 1. The primary split in the CART model for all mutualists was at ~50°N latitude. At latitudes ≥ 50°N, there is a relationship between the richness of animal mutualists and plant richness ($F_{1,15} = 25.27$, $p < 0.001$), but not at latitudes < 50°N ($F_{1,177} = 2.47$, $p = 0.12$).

A total of 88 animal species were determined to participate in a frugivorous seed-dispersal mutualism, 65 species of birds and 23 species of mammals (Supplementary material Appendix 1 Table A2). Frugivore richness is highest in the southwestern portions of North America, specifically in the Colorado Plateau semi-desert region, east to the Southwest plateau and dry steppe region (Fig. 1). Richness is relatively low in the Great Basin and Mojave deserts, with the lowest richness in in the far north tundra; richness of frugivorous animals decreases with increasing latitude ($F_{1,195} = 262.6$, $p < 0.001$, Fig. 2). There is no relationship with frugivorous
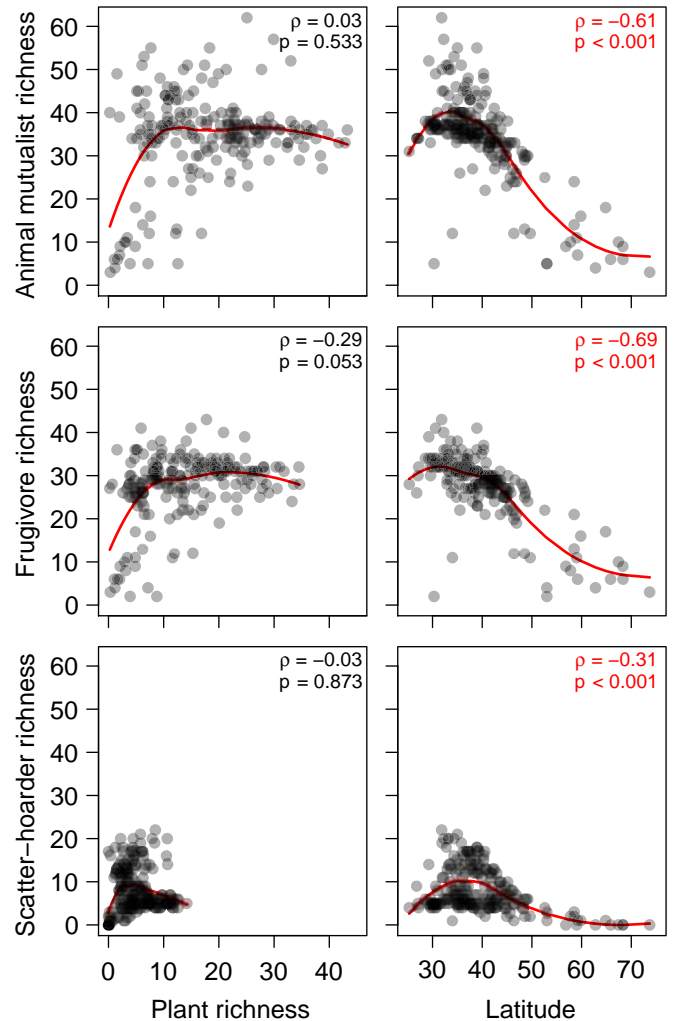

Figure 2. The richness of animals involved in seed dispersing mutualisms as a function of the plants they disperse (left column) and latitude (right column). Each plot has the Spearman correlation coefficient (ρ^*) and p-value of the linear model; red lettering signifies a significant linear model. The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

animal richness and the richness of the plants they disperse (Table 1). CART models again showed a primary split at ~50°N latitude. At latitudes ≥ 50°N, frugivore richness and the richness of the plants that they dispersed are correlated ($F_{1,15} = 18.88$, $p < 0.001$). However, at latitudes < 50°N, this relationship disappears ($F_{1,177} = 1.71$, $p = 0.19$). Frugivorous bird and frugivorous mammal richness are similarly correlated negatively with latitude but not correlated with plant richness (Table 1).

We identified a total of 102 animal species as scatter-hoarders involved in seed dispersal mutualisms; 10 species of birds and 92 species of rodents (Supplementary material

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

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

Appendix 1 Table A3). Scatter-hoarder richness decreased with increasing latitude ($F_{1,195} = 39.01$, p < 0.001), and is concentrated in the southwestern United States. Scatter-hoarder richness is highest in the Chihuahua Desert region, with richness hotspots in the Great Basin and Mojave Deserts. The Sonoran Desert has low scatter-hoarder richness (Fig. 1). Richness is lower in eastern North America with the low-est regions being in the Adirondacks and northern tundra. Scatter-hoarder richness is not correlated with plant richness (Table 1, Fig. 2). CART models do not show a ~50°N lati-tude split, instead the primary split occurs at ~900 m eleva-tion. Further exploratory analysis of the data did not reveal any relationships between scatter-hoarder richness and the plants that they disperse between the high- and low-elevation groups. Scatter-hoarding rodents are negatively correlated with latitude and are not correlated with plant richness. Conversely, scatter-hoarding birds are not correlated with plant richness nor latitude (Table 1).

Seed dispersal mutualism

There was a clear mismatch of richness between seed dispers-ers and the plants that they disperse (Fig. 1), with the highest

richness of plants dispersed by animals in southeastern North America, whereas the highest richness of animal dispersers is in southwestern North America. The divide is approximately 100°W longitude through the Great Plains for both guilds of seed dispersers. Indeed, in all CART models, longitude is the second split in the data, confirming its importance.

There was no relationship between the Z_{diff} of all mutu-alists and precipitation, AET, nor latitude (Table 2). However, there was a negative relationship with median elevation (Fig. 3). As elevation increased, there was a larger proportion of animal richness compared to plant richness. Monte Carlo simulations supported the conclusion that the observed relationship with elevation was different from ran-dom and supported our findings of no relationships between other variables (Table 2). The sub-panels in Fig. 3 show the results of the Monte Carlo simulations, which were largely consistent with our regression models (e.g. 10 of 12 corre-lations of Table 2 were consistent in determining statistical significance).

Z_{diff} of frugivores was not correlated with AET, but it was correlated with median elevation, latitude, and precipita-tion in our regression analysis (Table 2, Fig. 3). However, Monte Carlo simulations did not find significant correlations

Table 2. Statistical results of GLS models and Monte Caro simulations for mutualisms (Z_{diff}; dependent variable) and environmental variables (independent variables). For spatial regression models, the table includes (F-statistic, p-value, effect size (β), and R^2 for each model. All spatial models included a Gaussian correlation structure to correct for spatial autocorrelation. Monte Carlo simulations include the predicted p-value ($\hat{p}$) and Spearman's correlation coefficient (ρ^*). A dagger (†) signifies that the effect size is in units per 100 mm yr^{-1} AET and a double dagger (††) signifies that the effect size is in units per 100 m elevation.

| Independent variable	Dependent variable	Spatial regression models				Monte Carlo simulations	
		F-statistic	p-value	Effect size (β)	R^2	ρ^*	$\hat{p}$
AET	All mutualists	3.57	0.06	0.08†	0.03	0.39	0.07
	All frugivores	2.07	0.15	0.06†	–0.02	0.24	0.18
	All scatter-hoarders	247.53	0.00	0.34†	0.23	0.68	0.00
Elevation	All mutualists	160.42	0.00	–0.09††	0.08	–0.55	0.00
	All frugivores	84.45	0.00	–0.07††	–0.02	–0.49	0.00
	All scatter-hoarders	224.85	0.00	–0.18††	0.19	–0.54	0.00
Precipitation	All mutualists	0.32	0.57	0.11	0.01	0.25	0.13
	All frugivores	46.33	0.00	0.70	0.02	0.19	0.22
	All scatter-hoarders	109.06	0.00	1.19	0.00	0.36	0.04
Latitude	All mutualists	1.63	0.20	0.02	0.07	0.15	0.34
	All frugivores	12.41	0.00	0.04	0.20	0.22	0.25
	All scatter-hoarders	0.62	0.43	0.01	–0.01	–0.14	0.29
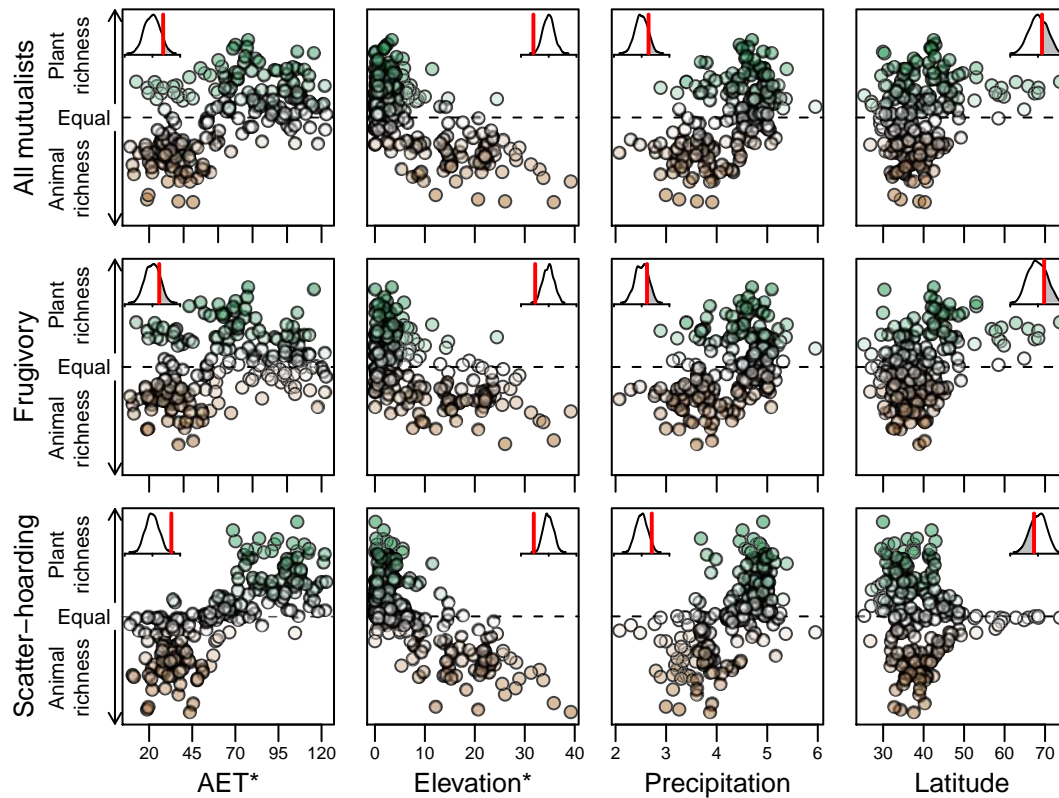
Figure 3. The relationships between environmental variables (rows) and differences in the richness of plant and animal mutualists (Z_{diff}; columns). All statistics and relationships can be found in Table 2. The scatterplots show the environmental variable on the *x* axis and the difference in plant and animal mutualist richness of on the y axis. From left to right, the environmental variables represent AET (mm yr^{-1}), elevation (m), precipitation (log(mm yr^{-1})), and latitude. An asterisk (*) next to the variable means that the x-axis was scaled; AET values are ×10 while elevation is ×100. Each scatterplot is colored according to greater plant richness (green), equal plant and animal richness (white), or greater animal richness (brown). Subplots are the spatially-structured randomizations to show how extreme the observed correlation (Spearman's ρ^*; vertical red line) was compared with 1000 randomizations (density plot). The subplots have ticks on the x-axis for values for correlation values $\rho^* = -1$, 0, and 1.

with the Z_{diff} of frugivores (i.e. $\hat{p} > 0.05$) for latitude or precipitation and should be considered when interpreting the results. The Z_{diff} of frugivorous birds and frugivorous mammals did not correlate with AET, latitude, or median elevation (Supplementary material Appendix 1 Table A4). Monte Carlo simulations confirm our findings (Fig. 3, subpanels) that our data was different from random for elevation ($\rho^* = -0.49$, $\hat{p} = 0$); we observed fewer frugivorous animals at higher elevations than plants dispersed by them.

The Z_{diff} of scatter-hoarding animals was also not correlated with latitude (Table 2). However, there were significant relationships between Z_{diff} and AET, precipitation, and median elevation. As AET or precipitation increases, there are proportionately fewer scatter-hoarding animals than plants dispersed by scatter-hoarders (Fig. 3). Simulations further support a relationship with AET and precipitation for all scatter-hoarders, with more scatter-hoarders being found in areas of lower AET and less precipitation (Table 2, Fig. 3 subpanels). The proportion of scatter-hoarders increased compared to the plants they disperse with an increase in median elevation (Fig. 3). The Z_{diff} of scatter-hoarding birds follows

the same pattern as the whole scatter-hoarder guild. The Z_{diff} of scatter hoarding birds follows the same pattern as the whole guild (Supplementary material Appendix 1 Table A4). The Z_{diff} of scatter-hoarding rodents increased with a decrease in precipitation, a decrease in AET, or an increase in elevations (Supplementary material Appendix 1 Table A4). There was no relationship between the Z_{diff} of scatter-hoarding rodents and latitude. Monte Carlo simulations again largely corroborated our findings, with the exception of precipitation, where simulations found a correlation (Table 2).

Discussion

We hypothesized, that if partnering species are obligately dependent then the richness distribution of the plants would show a strong relationship with the seed dispersers. Alternatively, if the mutualism is facultative we expected to see stronger relationships between the richness of animal dispersers and the environment than the plants they were dispersing. Although species richness of plant and animal

mutualists follow typical patterns with environmental variables, we surprisingly found a mismatch between the richness of seed-dispersing animals and the plants that they disperse across North America. This surprising result supports the idea that environmental factors have a greater effect on richness of species than do mutualistic, biotic interactions. Additionally, we found no spatial match between the richness of the guild of seed-dispersing animals and seed-dispersed plants; the richness of both plants and animals were better explained by environmental variables than by the richness of each other. These results are congruent with hypotheses, suggesting that seed-dispersing mutualism are facultative and diffuse. The diversity of one mutualistic partner does not necessarily beget diversity in the other.

The distribution of animal species richness contrasts with the richness distribution of the plant species being dispersed by those animals (Fig. 1, Supplementary material Appendix 1 Fig. A5, A6). Plants dispersed by frugivores and scatter-hoarding animals have their highest richness around the Great Lakes region and southeastern parts of North America (eastern United States) in general. Interestingly, at their most diverse locations the richness of animals is greater than the richness of plants at a ratio of about two to one. The mismatch of species richness between plants and the animals that disperse them can be seen in Fig. 1 with animal richness being greater in southwestern North America and plant richness being greater in southeastern North America. CART models supported these observations showing a divide in the data at 100°W longitude which roughly corresponds with the Great Plains of North America. A possible explanation for this enigma is that seed-dispersing animals might be far more abundant in the southeastern United States, where there are relatively few species, compared to the southwestern part of the continent where abundance for many species might be lower, but species richness is higher. To our knowledge, data to test this hypothesis does not exist.

Species richness of frugivores, scatter-hoarders, and all seed dispersing animals combined decreased with an increase in latitude (Fig. 2). This pattern matches the pattern observed for the plants that they disperse (Vander Wall and Moore 2016, Vander Wall et al. 2017). The increase of species richness with decreasing latitude was not a surprising result as the generality of the latitudinal diversity gradient has been found to be robust (Hillebrand and Thomas 2004). However, when hoarding birds are considered alone, they did not show a significant latitudinal gradient ($F_{1,194} = 3.08$, p = 0.08). This finding may be a result of the data being limited to one small, generalist family of birds (Corvidae) that have their center of diversity in the north temperate zone in North America.

As with previous studies (Karr 1976, Hawkins et al. 2003, Kissling et al. 2009), animal species richness was correlated with environmental variables. However, the difference in relative richness (Z_{diff}) of animals and plants in seed dispersal mutualisms showed no relationship with environmental variables. One exception was that the Z_{diff} increased (i.e. more plants) with AET (Fig. 3), a variable often found

important for predicting species richness at large scales. Seed disperser mutualisms appear to be more frequent (i.e. more plants dependent on scatter-hoarders) in more productive environments. Our Monte Carlo simulations also suggested that scatter-hoarding mutualism should be correlated with precipitation (which is correlated with AET) and we found that richness of scatter-hoarding rodents was correlated with precipitation. However, Z_{diff} decreased (i.e. more rodents) with an increase in median elevation (Fig. 3), which does not follow the global pattern: a decrease in richness with an increase in elevation (Rahbek 1995). Richness is believed to decrease at higher elevations partially due to a decrease in productivity, smaller land area, and harsher climates leading to higher extinction and lower dispersal due to greater distances between suitable habitat (Rahbek 1995, Rowe 2009, Wu et al. 2013). The relationship with elevation may be due to the fact that in southwestern North America, where the majority of seed-disperser richness was found, net productivity actually increases with elevation into the montane forests before decreasing again above tree line (Whittaker and Niering 1975). Since plants are positively correlated with AET, this may influence the relationship with elevation. An additional, and not necessarily mutually exclusive, explanation for the observed scatter-hoarder richness is the varying topography in southwestern North America. Varying topography creates greater opportunities for speciation and isolation of populations (Davis et al. 1986) Specifically, topography-driven isolation increases speciation rates in mountainous areas (Steinbauer et al. 2016). In fact, the three families of rodents that scatter-hoard (i.e. cricetids, heteromyids, and sciurids) have twice the species richness in the tectonically active southwestern North America than the tectonically less active eastern North America (Badgley 2010).

The coevolution between individual plant and vertebrate disperser species has been suggested to be diffuse, with many species of both sides of the mutualism adapting to multiple species on the other side (Thompson 1982, Wheelwright and Orians 1982, Herrera 1985). This is largely due to particular species interactions often being asymmetrical, variable in time and space, and non-obligate (Janzen 1980, Wheelwright 1988, Bascompte and Jordano 2007) and particularly driven by generalist animal species which interact with multiple plant species causing high complementarity and trait convergence (Guimaraes Jr et al. 2011) or indirect coevolutionary pressures (Guimaraes Jr et al. 2017). Most, if not all, of the animal species in North America that we considered seed-disperser mutualists would fall under this definition of generalists as they have wide diet breadths. The plants dispersed by animals in North America are also generalists as fruits and seeds have evolved to attract a variety of dispersers and not any one species in particular. Diffuse interactions inhibit strong directional coevolution and may lead to the diffuse patterns we witness.

The distribution of plants and animals in North America have changed over the last 18 000 yr since the last glacial

maximum (Ray and Adams 2001). The resulting contemporary patterns observed in this study have likely been influenced by this fact through limited time for dispersal, influence by indigenous Americans, and through disruption of coevolution. Davis et al. (1986) and Woods and Davis (1989) have shown that some animal-dispersed plants have not reached their potential distributions since the last glacial maximum, despite their dispersers being common across the plant's potential geographic range. If not all plants or animals have reached their potential distributions, with a negative bias towards more northern latitudes that are the farthest away from their distributions during the last glacial maximum, that may explain our finding that the richness of plants and their animal dispersers are correlated at latitudes > 50°. Because we are only seeing a small proportion of the potential mutualisms, our analyses may be more sensitive to detecting real or spurious correlations. Additionally, more recent and substantive changes to the North American communities from the settlement of the continent by indigenous peoples to present (Whitney 1996, Barnosky et al. 2004) may have disrupted historical mutualisms. Particularly, the extinction of megafauna in the late quaternary and subsequent introduction of domesticated livestock (not considered in this study) has likely changed (or negated) coevolutionary selection pressures (Pires et al. 2014).

Two major limitations of the study were 1) the assumption that abundance is uniform across a species range, and 2) a mismatch of scale between occurrence and environmental data. First, assumptions of studies using species range data are that the abundance of a species is uniform across its range, that all species have equal abundances, and that abundances are high enough throughout the range for the species to be an effective part of the community. This latter point, in this case, means that each species is an effective disperser of plants wherever it occurs. These assumptions are rarely met (Hurlbert and Jetz 2007), but occurrence maps are typically the only data on species occurrence available at large spatial scales, and if maps are constructed in a similar way, they can provide insights into the richness of species in a region (Rocchini et al. 2011).

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

This study compared the collective distribution of animals involved in seed-dispersal mutualisms to the distribution of the plants that they disperse. The distribution of animals does not account for the distribution of the plants. In fact, there is an apparent mismatch of richness between plants and the animals that disperse their seeds (Fig. 1, 2). As with animal-dispersed plants (Vander Wall and Moore 2016), environmental variables, particularly latitude, are more related to the richness distribution of animal mutualists. In the case of seed dispersal mutualisms, median elevation was correlated with all mutualists and scatter-hoarding, additionally, scatter-hoarding was correlated with AET suggesting that environmental factors, such as productivity may play a key role in the distribution of the mutualism. Further work is sorely needed to better understand the effect of climate on distributions of seed-dispersing animals. However, with these data on the distributions of seed-dispersing animal, we can now identify locations that warrant further study either to understand better seed-dispersal mutualisms or the factors that influence the distribution of the plants and animals involved in these mutualisms. The biggest challenge to understanding better many of these observed patterns has been the lack of appropriate data (Hawkins and Pausas 2004), and we hope this study will serve as a stepping stone to further discoveries.

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Supplementary material (Appendix ECOG-03876 at <www.ecography.org/appendix/ecog-03876>). Appendix 1.