RESEARCH PAPER

Interaction diversity of North American seed-dispersal mutualisms

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ABSTRACT

Aim We determine the prevalence of mutualistic seed-dispersal interactions across the North American landscape and then test the hypothesis that patterns in interaction diversity are correlated with latitude, longitude, precipitation, midpoint elevation and the elevational range of sites.

Location North America north of the Mexican border.

Methods We used regional plant lists to determine the diversity of animal seed-dispersal interactions across North America (over more than 48° of latitude). For each plant list ($n = 197$ sites, 12,424 terrestrial plant species and 123,519 plant records), we assigned plant species to one of four seed-dispersal modes (i.e. frugivory, scatter hoarding, myrmecochory or non-mutualist) and to an animal vector (e.g. bird, carnivorous mammal, rodent, ant).

Results We identified 14 types of animal-mediated seed dispersal. Plants with seed-dispersal mutualists are most diverse in the south-eastern portion of the continent. Dispersal by frugivores and scatter hoarders is strongly negatively correlated with latitude but myrmecochory is not. The diversity of interaction types is significantly correlated with precipitation and elevational range and negatively correlated with latitude, longitude and midpoint elevation.

Main conclusions The diversity of seed-dispersal mutualisms varies dramatically across the continent, suggesting that the co-evolutionary processes that produce these interactions are stronger in certain regions and vegetation types and weaker in others. Elucidation of these patterns and their causes will help us to better understand the co-evolutionary processes that shape communities.

Keywords
Biogeography, elaiosome, frugivory, fruit, geographical patterns, latitudinal gradient, longitude, myrmecochory, nuts, scatter-hoarding, seed caching.

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INTRODUCTION

Ecological communities consist of sets of interacting species. Early studies attempted to characterize communities by measuring and comparing the diversity of species (Willig *et al.*, 2003). More recently, attention has focused on the diversity of the interactions within communities (e.g. Albrecht *et al.*, 2007; Dyer *et al.*, 2007; Mougi & Kondoh, 2012). While measures of species diversity provide some useful information on the richness of species in a community, interaction diversity provides far more information on how a community is organized, its complexity and how it functions. The absence of an interaction type from a community, for example, reveals that certain processes are not occurring in that community. Communities with a great diversity of interaction types are much more complex, with more interrelationships among members of the community; this could lead to greater stability and the maintenance of greater biodiversity (Bascompte *et al.*, 2006). Dyer *et al.* (2010) have argued that the diversity of interactions is a more intuitive measure for understanding the mechanistic relationships within a community, and that it is easier to understand the consequences of loss of interactions than it is to understand the loss of species.

There is a large amount of variation in the prevalence of different kinds of species interactions across the landscape (Ollerton & Cranmer, 2002; Dyer *et al.*, 2007; Schemske *et al.*, 2009), suggesting that the environment selects for certain types of species interactions. A pressing question in ecology is what causes the distribution of species interactions. We are just beginning to answer this question. In many cases we have yet to document the geographical patterns of species interactions. A number of hypotheses have been proposed, and many revolve around the idea that co-evolution in benign, tropical environments increases the rate of adaptation, specialization, speciation and persistence in a community leading to an accumulation of species (Willig *et al.*, 2003; Schemske *et al.*, 2009; Brown, 2014). At higher latitudes and elevations, species adapt more to their abiotic environment and co-evolutionary forces are weaker. Plants involved in mutualistic interactions with animals often exchange resources (nutrients) for a service (movement of propagules or genes). Novel resources resulting from co-evolutionary interactions create opportunities in a community for more species. For example, a mutualism where the rewards offered by plants (e.g. nectar, fruit pulp or large, poorly defended seeds) to entice animals to perform a service (i.e. pollination or seed dispersal) creates opportunities for competitors and antagonists, such as seed-eating insects, birds that eat pulp without dispersing seeds and nectar thieves that don't pollinate flowers, to exploit the mutualism. These animals act as parasites on the mutualism and add to interaction diversity, causing greater species diversity. Because of the resources that are typically involved in mutualisms, these kinds of interactions have a greater capacity to foster increased species diversity than antagonistic interactions (e.g. competition, predation). To date, attempts to measure the interaction diversity of plant–animal mutualisms at large (e.g. continental or global) scales have focused mostly on plant–pollinator interactions (Olesen & Jordano, 2002; Ollerton & Cranmer, 2002; Trøjelsgaard & Olesen, 2013). Studies of regional patterns of seed dispersal have been much more limited (e.g. Almeida-Neto *et al.*, 2008).

Examination of ecological patterns at large spatial scales has important advantages. It allows one to infer about processes that are difficult to distinguish at the local scales on which most ecological research is conducted (e.g. Turner, 1989; Levin, 1992; Willig *et al.*, 2003). Local stochasticity can be reduced by scaling up, which averages out local heterogeneities (Chesson, 1998), revealing more clearly the identity, direction and strength of the processes that shape observed patterns.

Here we determined the frequency of seed-dispersal mutualisms for 197 sites scattered across North America north of Mexico. We recognized three modes of animal-mediated seed dispersal: frugivory, scatter hoarding and myrmecochory. Plants dispersed by some other mode were grouped as non-mutualists. We eliminated non-native plants and aquatic plants from our data sets. Within each of the three modes we categorized dispersers into one or more vectors (e.g. birds, rodents, carnivorous mammals, ants) and also distinguished between primary dispersal (from the plant) and secondary dispersal or dispersal by a mutualist following some other form of dispersal (e.g. wind dispersal followed by scatter hoarding or ballistic dispersal followed by ant dispersal), for a total of 14 different types of animal-mediated seed dispersal. Then we developed a series of measures (see Materials and Methods) to compare the diversity of seed-dispersal types across sites and compared those diversity measures with a set of environmental response variables.

We used these data to test several non-mutually exclusive hypotheses.

1. Interaction diversity increases with decreasing latitude, a pattern found with many other measures of diversity (e.g. Brown, 2014).

2. Interaction diversity increases with greater mean annual precipitation. Frugivory, for example, is thought to be less frequent in arid ecosystems because lack of water limits the formation of fleshy fruits (Bronstein *et al.*, 2007; Beck and Vander Wall, 2010).

3. Interaction diversity increases with decreasing longitude, because in southern North America, at least, longitude is a proxy for aridity.

4. Interaction diversity increases with increasing elevational range, because sites that span a greater range of elevations (e.g. mountains) have a greater variety of habitats, leading to more species and hence a greater opportunity for species interactions.

5. Interaction diversity increases with decreasing midpoint elevation of a site, for reasons related to those that drive the latitudinal gradient in interaction diversity.

Availability of potential animal mutualists might also influence the richness and distribution of plant–animal seed-dispersal mutualisms (Hughes *et al.*, 1994; Eriksson *et al.*, 2000), but we consider that possibility elsewhere (Dittel *et al.*, in preparation).

MATERIALS AND METHODS

Data acquisition

We searched the literature and the internet for regional floras that appeared complete and accurate for defined areas across North America (for more details see Vander Wall *et al.*, in press). We found 197 sites that met our criteria. Most sites were larger than 1000 ha (11 sites were smaller) and more than 50 km apart except when closer sites sampled very different vegetation types (seven pairs of sites were closer than 50 km). We compiled lists of species, excluding non-native, non-seed and aquatic plants. For each of the 12,424 plant species in our study, we assessed seed-dispersal mode and vector, including possible secondary dispersal. For many plant groups (e.g. *Quercus*, *Rubus*, *Viola*), the mode of primary dispersal and the likelihood of secondary dispersal are well established. When the vector or mode of dispersal was uncertain, we searched published literature for investigations of seed dispersal. If empirical studies were not available, we consulted botanical works (e.g. the *Flora of North America*) and searched for photographs of fruits and seeds. We assigned each

Figure 1 Fourteen dispersal pathways for plants with seed-dispersal mutualisms in North America. The numbers are the records of plant mutualists in our dataset (of 20,426 total records) and the width of the arrows is proportional to the number of records of mutualists. Different modes are in different coloured/shaded boxes and vectors are italicized under the mode type.
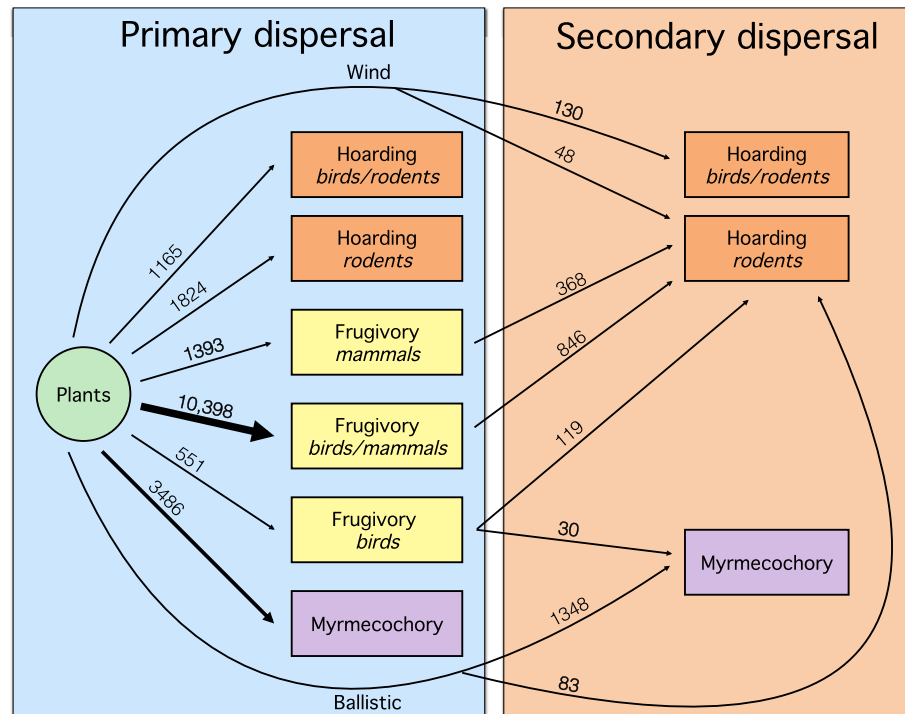
species to one of seven combinations of dispersal modes and vectors: (1) frugivory by birds and mammals – small, colourful fruits that are adapted for dispersal by birds, but which are commonly eaten by carnivorous mammals such as raccoons and bears (although most fleshy fruits appear to be adapted for dispersal by birds, many of these are commonly eaten by carnivorous mammals as well so we classify them as being dispersed by both birds and mammals); (2) frugivory by birds – small, brightly coloured fruits eaten by birds but rarely eaten by mammals; (3) frugivory by mammals – large, yellow, brown or green edible fruits that are too large for birds to ingest intact; (4) scatter hoarding by birds and rodents – relatively small seeds and nuts that are eaten and stored by both birds and rodents; (5) scatter-hoarding by rodents – large nuts that are too large or too hard for birds to handle, but which are commonly stored by rodents; (6) myrmecochory – seeds with an elaiosome or similar structure that attract ants, which transport the seeds back to their nest where they eventually discard the seed in a situation where it can germinate; (7) non-mutualistic plants – not dispersed by an animal mutualist (e.g. abiotic, burs attached to hair or feathers). Where relevant, we also assigned secondary dispersal when the second mode of dispersal was distinctly different from the first mode, including cases of abiotic dispersal (wind, ballistic dispersal) when followed by dispersal by an animal. Since secondary dispersal is often inconspicuous, poorly studied and not evident from fruit morphology (e.g. scatter hoarding of seeds taken from animal faeces), our quantification of these pathways might be underestimated.

Ancillary data were collected for each site, including mean annual precipitation, minimum and maximum elevation and area. We gathered data from the original publication or website when possible (about half of the sites). We obtained missing data from other sources. For precipitation, we used the closest site at a similar elevation using the US Climate Data website (http://www.usclimatedata.com/). We obtained mean latitude, mean longitude and minimum and maximum elevation from GoogleEarth. We calculated the elevational range and midpoint elevation (the midpoint between the minimum and maximum elevation). Elevational range was used as an indirect measure of habitat diversity at a site.

Because of the variation in the size of sites and presumed sampling effort, we chose to standardize our data by dividing the response variables by $\log_{10}$(area), transforming our data to relative densities. There are potential pitfalls with this method (Gotelli & Colwell, 2001, 2011), but they have little effect here because we are comparing across sites rather than generating a precise estimate of richness. Given the nature of our sampling scheme (site incidence data), we were unable to standardize taxon sampling curves but assumed that sampling effort was high enough in these comprehensive florulas that we were sampling from the asymptote of the species sampling curves. At least with regard to the plant species dispersed by mutualists, this assumption seems valid because most animal-dispersed plants are large with conspicuous flowers and fruits that would be unlikely to be overlooked in a comprehensive survey.

Spatial autocorrelation

Spatial interdependence was largely avoided by choosing sites that were >50 km apart unless they sampled different types of vegetation. We assessed independence of sample sites in two ways: (1) spatial autocorrelation, and (2) community similarity. With our response variables, we found no statistically significant spatial autocorrelation using Moran's *I*, confirming spatial
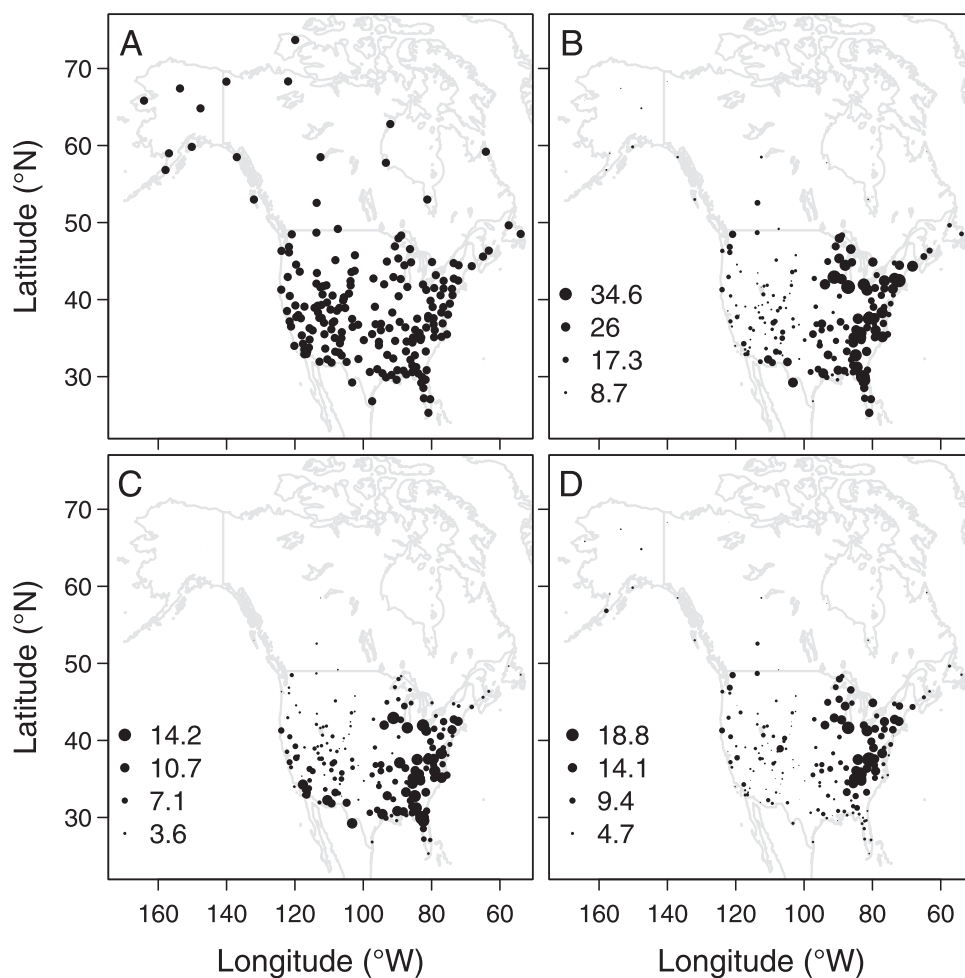
Figure 2 Geographical distribution of dispersal modes across North America: (a) the distribution of sampling sites ($n = 197$), (b) frugivores, (c) scatter hoarders, and (d) ants. Data in (b)–(d) are scaled relative densities (number of mutualist species/$\log_{10}$ area of the sampling site).

independence. Because of this, we chose not to include a spatial autocorrelation covariate in our statistical models. We did, however, analyse spatial similarity separately as a way to determine if there were differences between the spatial distributions of different kinds of mutualism. We assessed independence by calculating the Sørensen–Dice coefficient (β_{sor}, for incidence-type data) for all sites. No sites had an intersection of both a high β_{sor} and close proximity (Figure S1 in the Supporting Information), so we chose to keep all sites in the remaining analyses.

Analyses

We generated a set of four response variables to compare the number and types of interactions across sites, with the interaction type being one of the 14 dispersal pathways we identified above and the number of interactions being the number of species with an interaction type. Specifically, we calculated: (1) the number of interaction types present at a site, (2) the total number of interactions at a site (i.e. the number of plant species dispersed by animal mutualists), (3) the unbiased sample variance (Figure S2) in interaction types, a measure that is inversely proportional to interaction evenness, and (4) the abundance of the most abundant interaction at a site.

We included latitude, longitude, precipitation (cm $year^{-1}$), elevational range (m), and the midpoint of the elevation (m) as additive predictor variables in a linear multiple regression analysis of nine response variables. Precipitation, elevation and elevational range were $\log_{10}$ transformed to conform to the requirements of subsequent statistical analyses. None of the predictor variables were significantly correlated. The nine response variables included area-adjusted numbers of total species, mutualists (=total interactions), non-mutualists, three dispersal modes (frugivory, scatter-hoarding, myrmecochory) and the three other measures of interaction diversity (interaction type, interaction variance and abundance of the most abundant interaction). Interaction variance was the only predictor variable that was transformed to fit assumptions of normality for subsequent statistical analyses after adjusting for sample effort [$\log_{10}$(area)]. Finally, niche conservatism probably has an effect but we were unable to phylogenetically adjust for all 12,424 species in the study, so we chose to ignore it. Stepwise regression and Akaike information criterion (AIC) model selection were used to determine the best-fit models, and were congruent in all cases. Figures are presented as partial regressions of the residual variance of the best-fit models excluding the predictor variable of interest against that variable (latitude in Fig. 4).
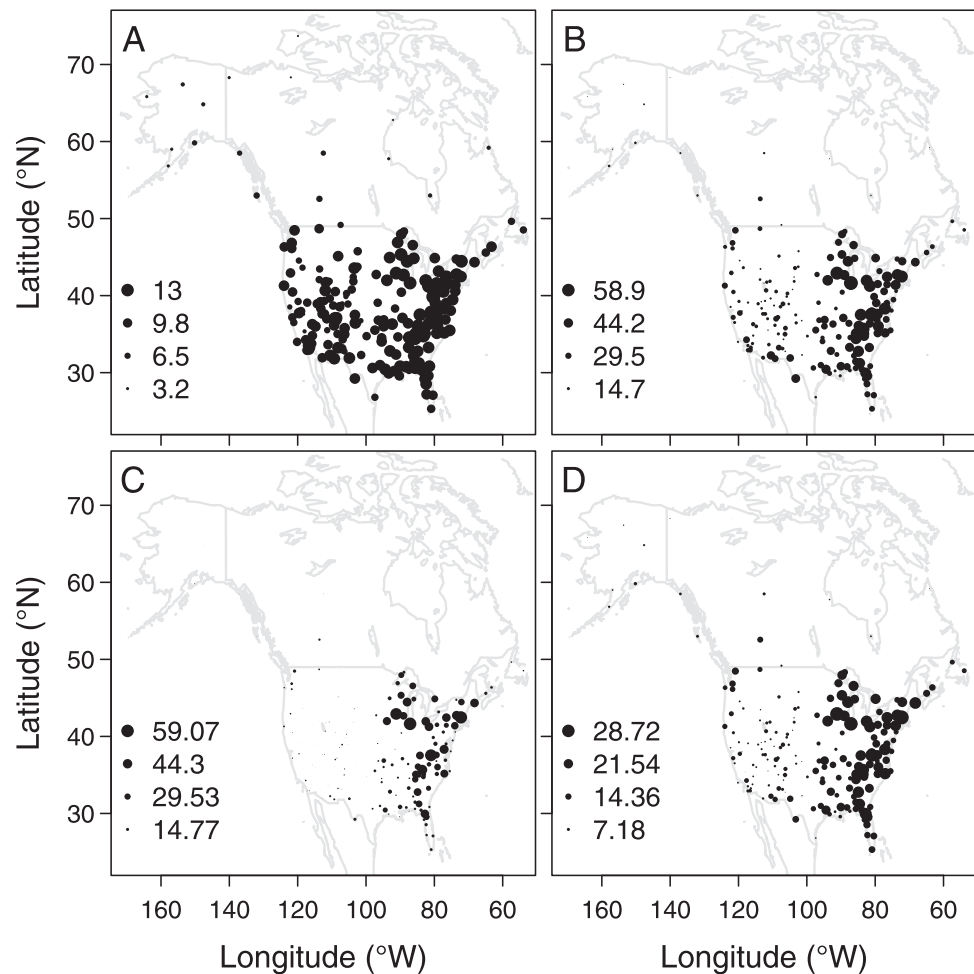
Figure 3 The geographical distribution of four measures of interaction diversity: (a) number of interaction types, (b) an index of interaction richness (number of mutualist species/$\log_{10}$ area of the sampling site), (c) variance in interaction types (a measure inversely proportional to evenness), and (d) $\log_{10}$ abundance of the most abundant type of interaction.

We also fitted general linear models against latitude to address: how (1) species and interaction diversity and (2) the diversity of plants with and without seed-dispersal mutualists covary. An analysis of covariance was used to assess the statistical significance of the differences of the slopes after standardizing scores to meet the assumption of homoscedasticity, which needed to be done in both cases.

RESULTS

Our dataset contained 123,519 records of native terrestrial plants, including 20,426 records with seed-dispersal mutualisms: 16.5% of the plants across North America have seed-dispersal mutualists. We identified 14 types of seed-dispersal interactions (Fig. 1). Dispersal by frugivorous birds and mammals is the most common type of interaction. Myrmecochory and scatter hoarding by rodents and jays are of roughly equal prevalence and less than half as common as frugivory. There are several forms of secondary dispersal: seed-caching rodents remove seeds from the faeces of birds and mammals or gather wind-dispersed seed, and ants gather ballistically dispersed seeds.

Seed-dispersal mutualisms are most common in the south-eastern portion of the continent, generally east of the Mississippi River Valley and south of Canada (Fig. 2b–d). This region is roughly coincident with the eastern deciduous forest (Greller, 1988). The distributions of frugivory and scatter-hoarding seed-dispersal syndromes are similar, but scatter hoarding is less common in the northern tier of states, Canada and southern Florida and relatively more common in the south-west than frugivory. Myrmecochory has a smaller centre of diversity in the Appalachian Mountains, Great Lakes states and the north-eastern United States.

The diversity of interactions (i.e. the set of interactions illustrated in Fig. 1) varied greatly across sites. Interaction richness (Fig. 3a) was strongly negatively correlated with latitude ($t = 8.742$, d.f. = 195, $P < 0.0001$; Fig. 4a). Northern regions lacked many of the interaction types, especially those involving scatter-hoarding animals. The number of interaction types is six or fewer north of 49° N latitude (Fig. 5), roughly coincident with the US–Canadian border in the western half of the continent. Between 30° and 49° N latitude, richness of interactions is highly variable across sites. Much of this variation is related to environmental conditions; interactions between plants and seed dispersers are less frequent in western dry habitats than eastern mesic forests. The total number of interactions (Fig. 3b) was greatest in the south-eastern portion of the continent and negatively correlated with latitude ($t = 3.612$, d.f. = 195, $P < 0.0001$; Fig. 4b). The variance in interaction types (Fig. 3c) was greatest in the
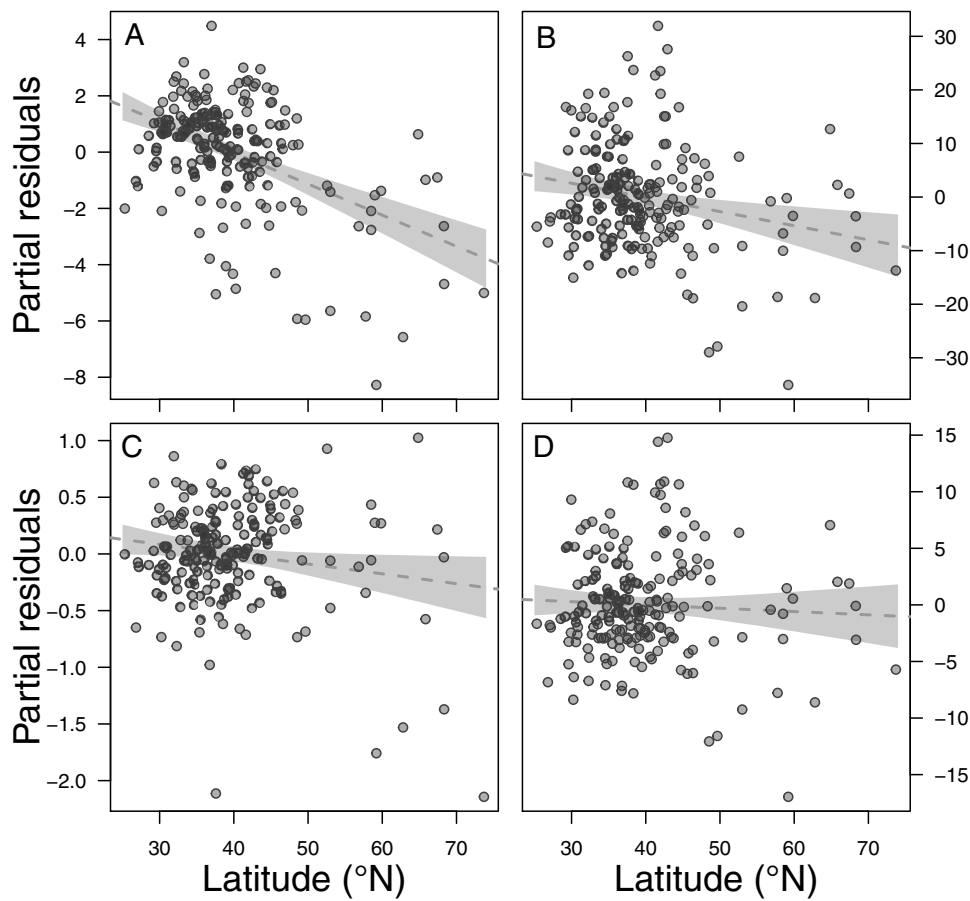
Figure 4 Partial regressions of measures of interaction diversity and latitude: (a) number of interaction types, (b) total number of interactions, (c) interaction variance, and (d) abundance of the most abundant interaction type. Points are sites and the shaded areas are 95% confidence intervals of the least squares estimates of the regressions. Regressions in A-C are statistically significant at alpha <0.05.

Figure 5 Number of interaction types and latitude. Above 49° N latitude, the number of interaction types decline sharply.

south-east and Great Lakes region, but lower in the Plains, the west and the north. Interaction variance was strongly, negatively correlated with latitude ($t = 3.670$, d.f. = 195, $P < 0.0001$; Fig. 4c). Abundance of the most frequent interaction type (Fig. 3d) was low in the interior arid west and northern Canada and Alaska. This measure was negatively correlated with longitude ($t = 7.992$, d.f. = 195, $P < 0.0001$; Fig. 3d). The most frequent interaction type was frugivory by birds and mammals at 186 of the 197 sites, so this measure resembles the pattern seen in frugivory (Fig. 2b).

We fitted multiple linear regressions to nine diversity responses using five environmental predictor variables (Table 1). Plant species with a seed-dispersal mutualist fit a model that included all variables and explained nearly half of the variation ($R^2 = 0.474$), whereas the model for non-mutualists included only latitude, elevational range and precipitation, and explained only one-fifth of the variation ($R^2 = 0.211$). The greatest amount of variation explained for a response variables was for richness of interaction types, with $R^2 = 0.543$, which was a model that included all predictor variables but most strongly correlated with latitude, longitude and elevational range. These data seem to suggest that plants with seed-dispersal mutualists are more sensitive to the environmental predictor variables that we measured, i.e. that plant seed-dispersal mutualists are favoured by specific types of environments.

We expected a strong relationship between latitude and seed-dispersal mutualisms (Willson et al., 1990; Ollerton et al., 2006; Moles et al., 2007), and latitude was significant in all regression models except for myrmecochory and the abundance of the most frequent interaction type (Table 1). There is a marginally significant difference between the slopes of total species richness and interaction richness (interaction
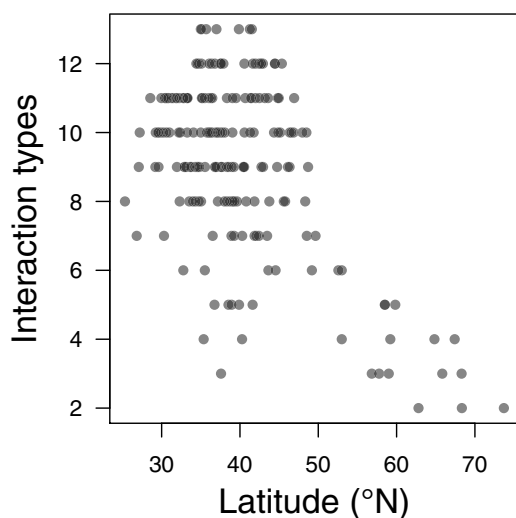
Table 1 Minimum adequate multiple regression models of nine response variables of seed-dispersal mutualisms across temperate North America regressed against five environmental predictor variables using stepwise removal of five predictor variables.

Response variable	Predictor variables	Standardized coefficient	Coefficient	t-value	F-value	Adjusted R^2
Species	Latitude	−0.388	−2.431	5.784	16.64	0.242
	Elevational range	0.282	18.25	3.946		
	Precipitation	0.195	33.35	2.733		
	Longitude	−0.161	−0.445	2.084		
Mutualists	Longitude	−0.400	−0.284	5.960	36.38	0.474
	Precipitation	0.281	12.39	4.574		
	Elevational range	0.287	4.770	4.027		
	Latitude	−0.214	−0.344	3.612		
	Elevation midpoint	−0.248	−0.004	3.238		
Non-mutualists	Latitude	−0.438	−2.254	6.672	18.45	0.211
	Elevational range	0.279	14.81	4.006		
	Precipitation	0.149	20.92	2.176		
Frugivory	Longitude	−0.418	−0.181	6.428	41.22	0.506
	Precipitation	0.280	7.552	4.699		
	Latitude	−0.182	−0.180	3.180		
	Elevation midpoint	−0.236	−0.002	3.175		
	Elevational range	0.202	2.057	2.928		
Hoarding	Latitude	−0.542	−0.210	8.892	39.42	0.440
	Elevation midpoint	−0.352	−0.001	4.622		
	Elevational range	0.252	1.009	3.425		
	Longitude	−0.214	−0.036	3.178		
Myrmecochory	Longitude	−0.435	−0.090	6.374	37.61	0.359
	Precipitation	0.377	4.849	5.758		
	Elevational range	0.339	1.648	5.185		
Interaction types	Latitude	−0.482	−0.144	8.742	47.48	0.543
	Longitude	−0.399	−0.052	6.369		
	Elevational range	0.340	1.051	5.127		
	Precipitation	0.161	1.315	2.804		
	Elevation midpoint	−0.163	−0.000	2.284		
Interaction variance ($\log_{10}$)	Precipitation	0.415	0.901	7.233	47.63	0.543
	Longitude	−0.346	−0.012	5.537		
	Elevational range	0.222	0.182	3.340		
	Latitude	−0.202	−0.016	3.670		
	Elevation midpoint	−0.196	−0.000	2.748		
Abundance of the most abundant interaction type	Longitude	−0.480	−0.174	7.992	54.23	0.521
	Precipitation	0.330	7.429	5.626		
	Elevation midpoint	−0.182	−0.001	2.633		
	Elevational range	0.170	1.445	2.586		

The incidence (presence and absence) of plants with mutualisms and measures of interaction diversity were better predicted by environmental variables than those of plant species that do not have their seeds dispersed by an animal mutualist. Unstandardized and standardized coefficients are reported. All models and predictor variables included had a $P < 0.05$.

term, new: $F_{3,390} = 41.1$, $P = 0.072$; Fig. 6a). These regression lines cross at $c.$ 40° N latitude; there are more types of mutualisms than expected at lower latitudes and fewer than expected at higher latitudes. Brown (2014) posited from a kinetic perspective that we would expect more diversity at lower latitudes owing to more and faster rates of biotic interactions and thus co-evolution. This is not a new perspective for those who study mutualisms, as guild co-evolution has often been evoked for explanations of angiosperm diversity (Tiffney, 2004; Lorts et al., 2008; but see Herrera, 1989). However, the effect of latitude did not have a different effect on mutualist and non-mutualist richness (interaction term,

new: $F_{3,390} = 19.83$, $P = 0.504$; Fig. 6b). This means that as one approaches the equator, the richness of interaction types increases faster than expected but the number of plant species with seed-dispersal mutualists does not.

Of the five predictor variables, elevational range was the only variable in all nine multiple regression models (Table 1). All of these relationships were positive. Elevational range is an indirect measure of habitat diversity, which should increase plant diversity at all levels. Midpoint elevation significantly predicted the number of mutualist plant species, the number of species dispersed by frugivores and scatter-hoarding animals and interaction richness at a given site, but
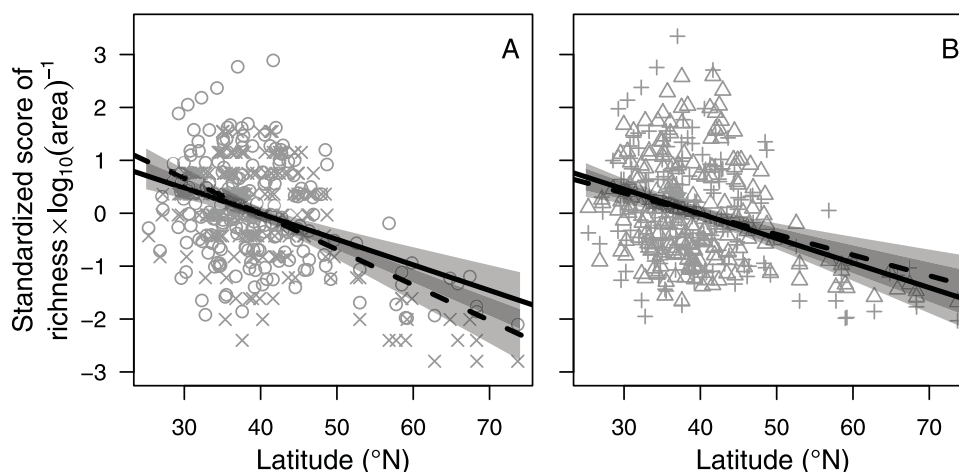
Figure 6 Change in interaction richness across 48° of latitude: (a) total species richness (circles; solid line) compared with interaction richness ('x'; dashed line), and (b) non-mutualist richness ('+'; solid line) compared with mutualist richness (triangles; dashed line). Data are scaled relative densities (number of species/$\log_{10}$ area) that have been standardized (z scores) because of heteroscedasticity between these groups (total species richness = 138.4 ± 53.1 and interaction richness 9.1 ± 2.5 per site; non-mutualists = 114.9 ± 43.6 and mutualist richness = 23.4 ± 13.7). The shaded areas are 95% confidence intervals of the least squares estimate of the slopes for 197 sites. An analysis of covariance detected a marginally significant difference between the slopes of total species richness versus interaction richness but not between mutualist richness versus non-mutualist richness.

midpoint elevation was not included in the model for non-mutualist species. All of these relationships for plant mutualists were negative, which supports the idea that at higher elevations environmental stochasticity may play a role in shaping communities by filtering out species that depend upon the presence of another species (as in a mutualistic interaction), much like high latitude appears to do.

We expected precipitation to have a strong effect on interaction diversity, and it was found to be significant in eight of the nine models (Table 1). The only response variable that was not significantly correlated to precipitation was scatter hoarding. Not finding a relationship with scatter hoarding is intuitive because scatter hoarding occurs not only in areas where primary productivity and precipitation are high (e.g. mesic forests) but also in areas where precipitation is low, like the semi-arid south-western United States where burial of large seeds is important in seedling establishment (e.g. Beck & Vander Wall, 2010).

Longitude was also included in eight of nine models, including everything except non-mutualists. All of the relationships were negative, reflecting a general decrease in all types of interactions on the western side of the continent relative to the east.

DISCUSSION

We found strong latitudinal gradients in two out of the three modes of seed dispersal (frugivory and scatter hoarding) within North America, but these patterns were complicated by the distribution of precipitation and the nature of the terrain. Interaction diversity is greatest in the mountainous, moist, south-eastern portion of the continent, and lower than expected (relative to regression lines, Fig. 4) in the dry plains and the arid and semi-arid south-western portion of the continent. We

interpret the significant negative relationship between longitude and interaction richness to reflect the increased aridity of the south-western versus south-eastern portions of the continent. And we attribute the significant negative relationship between midpoint elevation and interaction richness to processes similar to those that cause the latitudinal gradient in interaction richness. Despite these regional differences, we found support for the idea that interaction richness not only increases with decreasing latitude, but increases faster than one would predict based on total species richness (Fig. 6a).

Our study covered a wide variety of habitats and about 48.5° of latitude, but did not include any truly tropical sites (our southern-most site was Everglades National Park, FL, at 25.3° N). It is uncertain how the patterns that we report here might change as one approaches the equator because of a lack of comparable data on seed-dispersal mutualisms. One exception is the study by Almeida-Neto et al. (2008) that included 135 sites spanning 12.5° of latitude within the Atlantic forest of Brazil. This study had a narrower focus: frugivory by birds and mammals on woody plants. They found levels of frugivore-dispersed plants ranging from 45–91% of woody plants, considerably higher than most sites in this study, even when considering only woody plants. They did not detect a latitudinal gradient in this seed-dispersal mutualism, probably because the study was within a relatively homogeneous floristic assemblage near the equator, but their results are consistent with the prediction that the prevalence of frugivory should increase as one travels from the southern United States to tropical South America. The types of frugivory in tropical environments are also known to be much more diverse, including primates, bats, reptiles, fish and a much greater variety of birds (e.g. trogons, toucans, parrots), interactions that are rare or lacking north of the US–Mexican border.

The sites used in this study were not selected at random, and we had no way to standardize the size of sites or sampling effort. Variation in the sampling effort of the many botanists who prepared the plant species checklists could cause bias in the number of mutualistic interactions that we report. We took several steps to minimize this type of bias.

1. We were very selective in our inclusion of sites. Although florulas are never complete, we attempted to include only those that appeared comprehensive and accurate. Most of the checklists were prepared by professional botanists or botanical clubs that collected voucher specimens. In the process of selecting the sites, we discarded data from nearly 100 sites because the areas were too small or because the florulas appeared incomplete or the accuracy of the lists was uncertain.

2. The florulas were large, averaging 627 terrestrial, native, seed plant species per site. With such large samples and the fact that we treated all sites the same, the omission of a few species per site is unlikely to affect the richness of interactions in a biased manner.

3. Plants that are dispersed by animals are typically large shrubs and trees that produce large fruits and nuts or prominent perennial herbs with showy flowers that are dispersed by ants. Because of their conspicuousness, these are the types of plants that are most likely to be included in a comprehensive survey. Plants that are more likely to be overlooked are small, rare or with inconspicuous flowers with small seeds, plants that seed-dispersal mutualists often ignore because they offer no rewards. Consequently, the number of plants dispersed by mutualists at a site is not likely to be greatly underestimated, but because some species might not be counted, the percentage of plants with mutualists at a site might be slightly over estimated. We attempted to minimize this problem by dividing the number of plants by $\log_{10}$(area) to help adjust for variation in area (inversely proportional to sampling effort per unit area). In preliminary analyses, we found a significant species–area relationship for total plant species but not for species with seed-dispersal mutualisms (Vander Wall *et al.*, in press).

A great variety of hypotheses have been proposed to explain latitudinal gradients in species diversity. One hypothesis is that biotic interactions promote tropical species richness (Mittelbach *et al.*, 2007), the idea that in stable, benign tropical environments, organisms adapt more to each other, co-evolve and ultimately speciate at a faster rate relative to strongly seasonal and abiotically demanding temperate and polar environments (Schemske, 2002; Brown, 2014). Our results are consistent with this hypothesis, at least for dispersal by frugivores and scatter-hoarding animals. The idea that tropical diversity and species interactions are causally linked has been difficult to test because of the lack of data on the prevalence of species interactions at large geographical scales. More complete data on modes and vectors of animal-mediated seed dispersal that bridge the current gap between temperate and tropical regions are needed to test possible relationships between diversity gradients and the prevalence and strength of species interactions. The methodology that we present here represents a means of doing that on a global scale.

REFERENCES

Albrecht, M., Duelli, P., Schmid, B. & Müller, C.B. (2007) Interaction diversity within quantified insect food webs in restored and adjacent intensively managed meadows. *Journal of Animal Ecology*, **76**, 1015–1025.

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

Bascompte, J., Jordano, P. & Olesen, J.M. (2006) Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science*, **312**, 431–433.

Beck, M.J. & Vander Wall, S.B. (2010) Seed dispersal by scatter-hoarding rodents in arid environments. *Journal of Ecology*, **98**, 1300–1309.

Bronstein, J.L., Izhaki, I., Nathan, R., Tewksbury, J.J., Spiegel, O., Lotan, A. & Altstein, O. (2007) Fleshy-fruited plants and frugivores in desert ecosystems. *Seed dispersal: theory and its application in a changing world* (ed. by A.J. Dennis, E.W. Schupp, R. Green and D.A. Westcott), pp. 148–177. CAB International, Wallingford.

Brown, J.H. (2014) Why are there so many species in the tropics? *Journal of Biogeography*, **41**, 8–22.

Chesson, P. (1998) Making sense of spatial models in ecology. *Modeling spatiotemporal dynamics in ecology* (ed. by J. Bascompte and R.V. Solé), pp. 151–166. Springer, Berlin, Berlin.

Dyer, L.A., Singer, M.S., Lill, J.T., Stireman, J.O., Gentry, G.L., Marquis, R.J., Ricklefs, R.E., Greeney, H.F., Wagner, D.L., Morais, H.C., Diniz, I.R., Kursar, T.A. & Coley, P.D. (2007) Host specificity of Lepidoptera in tropical and temperate forests. *Nature*, **448**, 696–699.

Dyer, L.A., Walla, T.R., Greeney, H.F., Stireman, J.O. & Hazen, R.F. (2010) Diversity of interactions: a metric for studies of biodiversity. *Biotropica*, **42**, 281–289.

Eriksson, O., Friis, E.M. & Lofgren, P. (2000) Seed size, fruit size, and dispersal systems in angiosperms from the early Cretaceous to the late Tertiary. *The American Naturalist*, **156**, 47–58.

Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379–391.

Gotelli, N.J. & Colwell, R.K. (2011) Estimating species richness. *Biological diversity* (ed. by A.E. Magurran and B.J. McGill), pp. 39–54. Oxford University Press, New York.

Greller, A.M. (1988) Deciduous forest. *North American terrestrial vegetation* (ed. by M.G. Barbour and W.D. Billings), pp. 287–316. Cambridge University Press, Cambridge, Mass.

Herrera, C.M. (1989) Seed dispersal by animals – a role in angiosperm diversification. *The American Naturalist*, **133**, 309–322.

Hughes, L., Dunlop, M., French, K., Leishman, M.R., Rice, B., Rodgerson, L. & Westoby, M. (1994) Predicting dispersal spectra: a minimal set of hypotheses based on plant attributes. *Journal of Ecology*, **82**, 933–950.

Levin, S.A. (1992) The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. *Ecology*, **73**, 1943–1967.

Lorts, C.M., Briggeman, T. & Sang, T. (2008) Evolution of fruit types and seed dispersal: a phylogenetic and ecological snapshot. *Journal of Systematics and Evolution*, **46**, 396–404.

Mittelbach, G.G., Schemske, D.W., Cornell, H.V. *et al.* (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters*, **10**, 315–331.

Moles, A.T., Ackerly, D.D., Tweddle, J.C., Dickie, J.B., Smith, R., Leishman, M.R., Mayfield, M.M., Pitman, A., Wood, J.T. & Westoby, M. (2007) Global patterns in seed size. *Global Ecology and Biogeography*, **16**, 109–116.

Mougi, A. & Kondoh, M. (2012) Diversity of interaction types and ecological community stability. *Science*, **337**, 349–351.

Olesen, J.M. & Jordano, P. (2002) Geographic patterns in plant–pollinator mutualistic networks. *Ecology*, **83**, 2416–2424.

Ollerton, J. & Cranmer, L. (2002) Latitudinal trends in plant–pollinator interactions: are tropical plants more specialised? *Oikos*, **98**, 340–350.

Ollerton, J., Johnson, S.D. & Hingston, A.B. (2006) Geographical variation in diversity and specificity of pollination syndromes. *Plant–animal interaction: an evolutionary approach* (ed. by N.M. Waser and J. Ollerton), pp. 283–308. University of Chicago Press, Chicago, IL.

Schemske, D.W. (2002) Ecological and evolutionary perspectives on the origin of tropical diversity. *Foundations of tropical forest biology* (ed. by R.L. Chazdon and T.C. Whitmore), pp. 163–173. University of Chicago Press, Chicago, IL.

Schemske, D.W., Mittelbach, G.G., Cornell, H.V., Sobel, J.M. & Roy, K. (2009) Is there a latitudinal gradient in the importance of biotic interactions? *Annual Review of Ecology, Evolution, and Systematics*, **40**, 245–269.

Tiffney, B.H. (2004) Vertebrate dispersal of seed plants through time. *Annual Review of Ecology, Evolution, and Systematics*, **35**, 1–29.

Trøjelsgaard, K. & Olesen, J.M. (2013) Macroecology of pollination networks. *Global Ecology and Biogeography*, **22**, 149–162.

Turner, M.G. (1989) Landscape ecology: the effect of pattern on process. *Annual Review of Ecology, Evolution, and Systematics*, **20**, 171–197.

Vander Wall, S.B., Barga, S.C. & Seaman, A.E. The geographic distribution of seed dispersal mutualisms in North America. *Journal of Biogeography*, in press.

Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 273–309.

Willson, M.F., Rice, B.L. & Westoby, M. (1990) Seed dispersal spectra: a comparison of temperate plant communities. *Journal of Vegetation Science*, **1**, 547–562.

SUPPORTING INFORMATION

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Figure S1 Sites were selected to be widely spaced or in dissimilar environments. Comparing the pairwise distance between plots ($\log_{10}$ of distance in km) and Sørensen–Dice dissimilarity shows that there were no sites that were both close and similar in plant community composition, which would be points found in the lower left. With 197 sites, there were $(197^2 - 197)/2 = 19{,}306$ pairwise distances/dissimilarity indices calculated. Fifty-two of these sites are within 100 km of one another and one pair of sites (Rocky Mountains National Park and Rocky Mountains National Park Alpine) were very close but floristically dissimilar.

Figure S2 Formula used to calculate unbiased sample variance.

BIOSKETCHES

Stephen Vander Wall is a professor of biology who has over 45 years' experience of studying seed dispersal, primarily involving scatter-hoarding rodents and corvids. Other aspects of his research involve caching behaviour, caching pilfering and the roles of olfaction and spatial memory in cache recovery.

Christopher Moore is a post-doctoral research associate studying the population dynamics of mutualism. His interests include the ecology of positive species interactions and dispersal.

S.B.V. conceived the project, acquired the raw data, determined the modes and vectors of seed dispersal and prepared the manuscript. C.M.M. managed the data, prepared graphs and tables and conducted statistical analyses. The authors contributed equally to the project.

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