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Plant dispersal systems in Neotropical forests: availability of dispersal agents or availability of resources for constructing zoochorous fruits?

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ABSTRACT

Aim We used abiotic and biotic factors as predictors of the proportions of different dispersal systems in Neotropical forests, to test whether the geographical patterns in dispersal systems are mostly related to the availability of resources for constructing zoochorous fruits or to the availability of dispersal agents.

Location 101 one-hectare vegetation plots established in eight Holdridge life-zones in Colombian Neotropical forests.

Methods We assigned dispersal systems to 2262 species and 1210 morphospecies, using the relative frequency and relative abundance of endozoochory, synzoochory, anemochory and hydrochory per plot as response variables. We assessed the relationships between dispersal systems and ecological factors (elevation, climatic and edaphic variables, raw and weighted richness of potential frugivores, biomass of primates, wind speed, flooding regime and fragmentation), controlling for spatial autocorrelation and phylogenetic constraints.

Results Endozoochory was highly represented in all plots. High levels of rainfall and low precipitation seasonality were associated with high proportions of zoochory (endozoochory and synzoochory) and low proportions of anemochory. The biomass of primates was positively associated with the relative abundance of endozoochory, and the weighted richness of frugivores was positively associated with the relative frequency of endozoochory. Contrary to the resource-availability hypothesis, synzoochory (the most expensive dispersal system in terms of plant investment in fruit mass) was most common in soils with low carbon densities. Finally, the proportions of anemochory and hydrochory were highest in windy areas and flooded forests, respectively.

Main conclusions Although there is a relationship between rainfall, zoochory and anemochory, the absence of any positive relationships between zoochory, temperature, soil total nitrogen density and soil carbon density shows that the proportions of dispersal systems in Colombian Neotropical forests are mostly related to the availability of dispersal agents.

Keywords

Anemochory, climatic and edaphic variables, elevation, endozoochory, flooding regime, fragmentation, frugivores, hydrochory, synzoochory, wind speed.

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INTRODUCTION

The relationships between functional traits of plants and ecological variables are not fully understood, especially in the

complex tropical forests. Dispersal systems (Ridley, 1930; van der Pijl, 1972) reflect key functional traits (e.g. seed mass) that have been considered fundamental for understanding the functioning and diversity of ecosystems at local scales, as well as the

distribution of species along geographical gradients (McGill *et al.*, 2006; Westoby & Wright, 2006). Because seed dispersal processes determine the template for plant recruitment, dispersal systems can also help to explain the spatial patterns of plants and the mechanisms of forest regeneration (Howe & Smallwood, 1982; Nathan & Muller-Landau, 2000). Many studies have related the patterns of occurrence of dispersal systems to environmental variables but, to our knowledge, none have tested whether those patterns are mostly related to the availability of dispersal agents or to the availability of resources for constructing zoochorous fruits in tropical forests.

To date, several abiotic and biotic factors have been associated with different dispersal systems in tropical forests. For instance, it has been shown that the proportion of species with fleshy fruits and large seeds is higher in wet forests (Howe & Smallwood, 1982; Gentry, 1983; Willson *et al.*, 1989; Jordano, 2000; Tabarelli *et al.*, 2003; Butler *et al.*, 2007; Moles *et al.*, 2007; Almeida-Neto *et al.*, 2008). In contrast, the proportion of species dispersed by wind is higher in dry forests (Howe & Smallwood, 1982; Gentry, 1983; Tabarelli *et al.*, 2003). These patterns could be explained as a result of the high metabolic costs involved in constructing and maintaining fleshy fruits, which would lead to an increase in the proportion of fleshy-fruited species in areas with greater availability of resources (water and soil nutrients) (Willson *et al.*, 1989; Hughes *et al.*, 1993; Tabarelli *et al.*, 2003). Other studies have shown that the proportions of dispersal systems are related to the availability of dispersal agents: the presence of large-seeded species has been positively associated with the availability of large frugivores (Lord, 2004; Forget *et al.*, 2007; Terborgh *et al.*, 2008), the presence of rivers is related to an increase in the proportion of species dispersed by water (Kubitzki & Ziburski, 1994; Umaña *et al.*, 2011), and the proportion of species dispersed by wind has been found to be higher in windy areas (Griffiths & Lawes, 2006). Fragmentation and hunting pressures have also been related to changes in the proportions of dispersal systems, as a result of modifications in the assemblages and population density of frugivores (Wright *et al.*, 2007; Nuñez-Iturri *et al.*, 2008; Terborgh *et al.*, 2008; Stevenson, 2011).

In this study, we explore the relationships between several ecological factors and dispersal systems. We test two hypotheses using a large dataset of vegetation plots established in Colombian Neotropical forests. First, we test whether abiotic factors are related to the relative frequency and relative abundance of dispersal systems (proportion of species and individuals within a plot, respectively), as a result of the availability of resources for constructing zoochorous fruits (resource-availability hypothesis). These fruits tend to be larger and have higher nutrient contents than abiotically dispersed fruits (Fig. S1 in Supporting Information; Howe, 1986; Leishman *et al.*, 1995). Second, we test whether the relative frequencies and relative abundances of dispersal systems vary in relation to the availability of dispersal agents (disperser-availability hypothesis).

The first hypothesis predicts that the proportion of species and individuals with costly fleshy structures and large seeds (endozoochory and synzoochory), will be higher in areas with

greater resource availability – highly productive forests that are mostly found in humid lowlands with high temperatures and rich soils (Malhi *et al.*, 2004; Chave *et al.*, 2010; Cleveland *et al.*, 2011). The second hypothesis predicts that the proportion of endozoochory will be higher in locations with more seed-dispersers, the proportion of anemochory will be higher in places with stronger winds, and the proportion of hydrochory will be higher in flood-plains (assuming only a minor role for ichthyochory).

Finally, we assess whether fragmentation increases the proportion of anemochory, and alters the proportion of endozoochory and synzoochory. Our results will help in understanding the relationships that exist between the dispersal systems of plants and ecological variables in tropical forests, using a database of vegetation plots established in the north-western South American Neotropics, which is considered a very important area for global biodiversity conservation (Mittermeier *et al.*, 1997, 2004).

MATERIALS AND METHODS

Our analyses are based on a set of 101 one-hectare Neotropical vegetation plots established in mature Colombian forests (Vallejo-Joyas *et al.*, 2005; Correa-Gómez *et al.*, 2013). They contain individuals with diameters at breast height (d.b.h.) of at least 10 cm, allowing us to compare the same growth-forms between plots (i.e. trees, treelets, climbers and hemiepiphytes), and are found across the country in eight Holdridge life-zones: tropical dry forest, tropical moist forest, tropical wet forest, tropical rain forest, premontane moist forest, premontane wet forest, lower montane moist forest and lower montane wet forest (Fig. 1). We assigned dispersal systems (anemochory, endozoochory, synzoochory, hydrochory, explosive dehiscence, myrmecochory and unassisted) to each of 2262 species (Correa-Gómez *et al.*, 2013) using the criteria proposed by Ridley (1930) and van der Pijl (1972) for dispersal syndromes, the morphology of the diaspores (using the virtual herbaria CHIC, COAH, COL, K and NY), information found in scientific literature (Gentry, 1993; van Roosmalen, 1985; Pennington *et al.*, 2004; Stevenson *et al.*, 2000) and expert knowledge. We also assigned dispersal systems to morphospecies that were determined only to the genus or family level (1057 and 153, respectively), when there was no known variation within these taxonomic levels (i.e. all species of the genus share the same dispersal system, or all genera in the family share the same dispersal system). Dispersal systems were thus assigned to 95.6% of species and morphospecies and to 96.5% of individuals.

Diaspores with fleshy structures that can be swallowed by frugivores, mimetic seeds and diaspores that are reported to be ingested by frugivores were included in the endozoochory category. Synzoochory was assigned to fleshy or non-fleshy fruits with seeds wider than 2 cm, which are not commonly ingested by large frugivores in the Neotropics (Dew, 2005; Stevenson *et al.*, 2005) but can be transported externally by scatterhoarding rodents (Brocardo *et al.*, 2013). Anemochory corresponded to non-fleshy diaspores with particular structures that

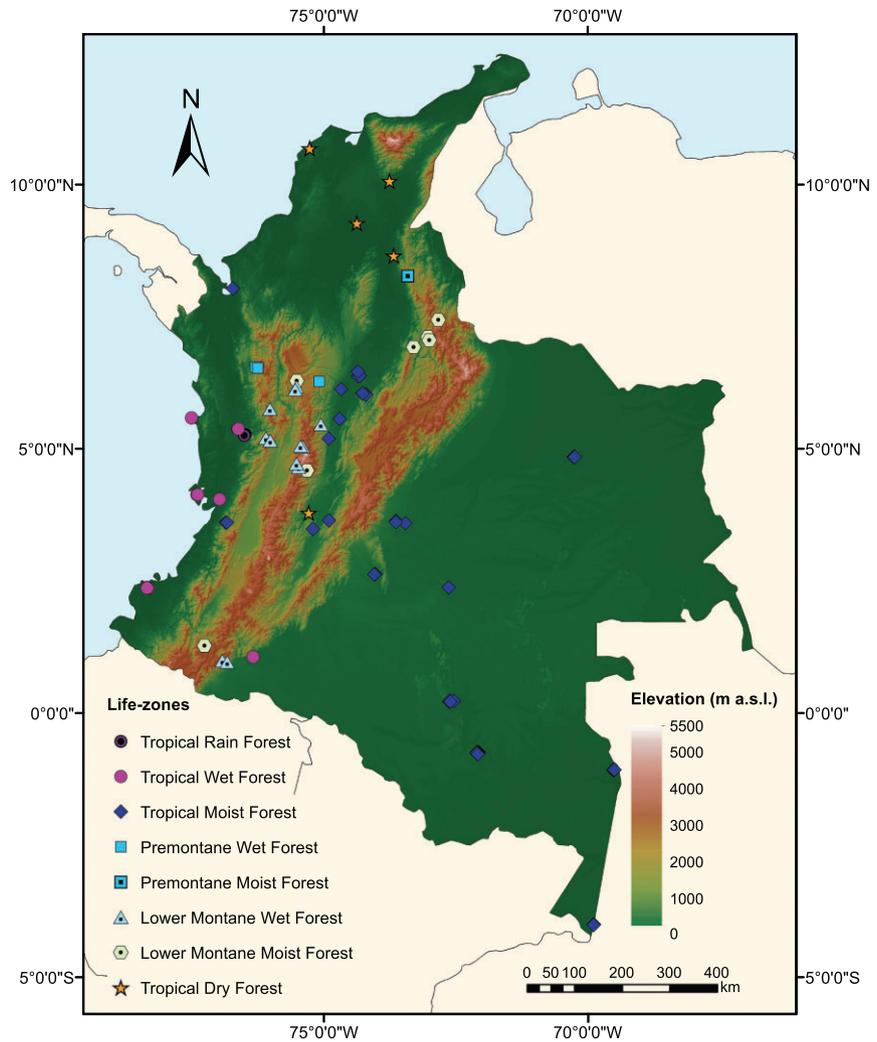


Figure 1 Distribution of the 101 one-hectare vegetation plots in Colombian Neotropical forests that were used to calculate the relative frequency and relative abundance of seed dispersal systems.

allow wind-dispersal (e.g. expanded wings, presence of kapok or tufts of hair), or without these structures but with diaspores narrower than 3 mm. Thus, anemochory included both heavy samaras (e.g. *Platypodium*; Augspurger, 1983) and dust seeds (Eriksson & Kainulainen, 2011). Hydrochory included diaspores without fleshy structures and without any characteristics that allow wind-dispersal but with the ability to float. Explosive dehiscence included those non-fleshy fruits that release seeds explosively. Myrmecochory included diaspores with seeds narrower than 3 mm and with associated fleshy structures (elaiosomes). Finally, the unassisted category was assigned to diaspores that did not show any of the previous combinations of characters or any reported dispersal mode (0.26% and 0.04% of all species and individuals, respectively). Further research may shed light on the overall dispersal vectors for tropical species, as it has been shown that, although dispersal vectors can be predicted well by morphology (Howe, 1986; Tackenberg *et al.*, 2003), they may not be mutually exclusive (Fleming *et al.*, 1993; Nathan *et al.*, 2008).

In order to show that zoochorous fruits are more costly than those dispersed abiotically, the dry weight of available fruits was measured and compared among dispersal systems for a subset of

seven plots (Fig. S1). Using SPSS 20.0 (IBM, Armonk, NY, USA), a Kruskal–Wallis test was performed to detect significant differences in fruit weight between dispersal systems, and homogeneous subsets were determined through the stepwise step-down multiple comparisons method (Campbell & Skillings, 1985).

For each plot, we obtained 19 bioclimatic variables, the SRTM 90-m elevation values (Hijmans *et al.*, 2005), and seven soil variables: bulk density, field capacity, profile available water capacity, carbon density, thermal capacity, total nitrogen density and wilting point (Global Soil Data Task Group, 2000). These variables reflect the availability of resources that could be involved in the construction of zoochorous fruits (i.e. temperature, amount of rainfall, rainfall seasonality, soil fertility and soil water availability). We assigned a Holdridge life-zone (Holdridge, 1967) to each plot using temperature and precipitation values.

In order to test the disperser-availability hypothesis, the richness of potential frugivores was obtained based on distribution maps of birds (Hilty & Brown, 2001), mammals (Emmons & Feer, 1997; Defler, 2004; Mantilla-Meluk *et al.*, 2009; IUCN, 2010) and *Chelonoidis* turtles (IUCN, 2010). We additionally

calculated a weighted richness of potential frugivores, using the volume of the frugivores as a surrogate of body size and the proportion of fruit in their diet, based on the literature (Emmons & Feer, 1997; Hilty & Brown, 2001; Defler, 2004; Mantilla-Meluk *et al.*, 2009). The volume of frugivores was calculated from their body length excluding the tail (6–197 cm in our study), and two categories of the proportion of fruit in their diet were determined (1 for primary frugivores which have diets consisting of more than 50% fruits; 0.5 for partial frugivores which have diets consisting of 25–50% fruits). In order to take into account the abundance of frugivores, we obtained the biomass of primates for a subset of 20 plots where information was available (Stevenson, 2001, 2010), most of which were located in isolated places with low historical and current hunting pressure (Amazonian region, Pacific region and some sites in the Andean region). Categories of wind speed were assigned to each plot using available maps (Ruíz & Zea, 2005), which represent the average wind speed ('1', < 1 m s⁻¹; '2', 1–2 m s⁻¹; '3', > 2 m s⁻¹) calculated from meteorological stations. The flooding regime was determined from field observations to be non-flooded, periodically flooded or permanently flooded for each plot.

Finally, based on GOOGLE EARTH satellite images, we determined three categories of fragmentation based on the percentage of remnant forest in a 5000-ha circle centred on each plot (high, < 33%; mid, 33%–66%; low, > 66%).

Data analyses

We based most analyses on endozoochory, anemochory and synzoochory, which represented 90.9% of species and morphospecies and 92.5% of all individuals. Hydrochory was used for the analysis related to the flooding regime (1.3% of the species and morphospecies, and 1.2% of the total number of individuals). The relative frequencies of dispersal systems (number of species and morphospecies per dispersal system divided by the total number of species and morphospecies per plot) and the relative abundances of dispersal systems (number of individuals per dispersal system divided by the total number of individuals per plot) were calculated as response variables (Correa-Gómez *et al.*, 2013).

In order to detect significant differences in the response variables between Holdridge life-zones, we performed Kruskal–Wallis tests, detecting homogeneous subsets through the stepwise step-down multiple comparisons method (Campbell & Skillings, 1985), using *SPSS* 20.0.

The relationships between the response variables and continuous variables available for all the plots (climatic variables, elevation, edaphic variables and raw and weighted richness of frugivores) were assessed through the elaboration of multiple regression models, using *SAM* 4.0 (Rangel *et al.*, 2010). In order to select the variables for the elaboration of these regression models, we performed multiple pairwise Spearman rank correlation tests, assessing the relationships between dispersal systems and the variables (Table S1). Spatial dependence was controlled

through the calculation of the Dutilleul's estimator (Dutilleul, 1993), reducing the degrees of freedom when spatial autocorrelation was detected.

In our models, we only included variables that had shown statistically significant correlations in previous Spearman rank correlation tests, avoiding the presence of redundant variables in the same model (i.e. $r_s \geq 0.5$) based on a Spearman rank correlation matrix constructed between all variables. In order to improve the normality and homoscedasticity in the residuals of the models, we used logarithmic and square-root transformations on response variables, and the best model for each response variable was selected based on the lowest value of the Akaike information criterion (AIC).

Moran's index (Moran's *I*) was calculated on the residuals of each selected regression model and the significance of the spatial dependence was determined by constructing spatial correlograms with 10,000 permutations. Where significant short-distance spatial autocorrelation was detected, it was corrected through spatial eigenvector mapping (SEVM), which produces spatial filters that are used as additional explanatory variables in the regression models while reducing the spatial dependence on response variables (Rangel *et al.*, 2011). An additional spatial correlogram was constructed on the residuals of the models that included spatial filters, using 10,000 permutations, to reveal whether the short-distance spatial autocorrelation had been eliminated.

We assessed whether the relationships in the previously selected multiple regression models remained after taking phylogeny into account through phylogenetically independent contrasts (Felsenstein, 1985). This method uses branch lengths and taxon relationships to calculate contrasts that can be used as statistical independent values in correlation analyses (Garland *et al.*, 1992). We constructed phylogenetic trees for each dispersal system in the software *PHYLOCOM* 4.1 (Webb *et al.*, 2008), using the master tree R20080417.new, and adjusting the branch lengths through the *BLADJ* algorithm according to reported age estimates for angiosperms (Wikström *et al.*, 2001). We adapted the script developed by Matzke & Hallinan (2011), using the R packages *APE* (Paradis *et al.*, 2004) and *PICANTE* (Kembel *et al.*, 2010), resolving polytomies in random order, and assessing the Pearson correlations between the independent contrasts derived from the mean values of explanatory variables per genus and the mean values of the relative frequency and relative abundance of dispersal systems per genus. Although these variables are not strictly heritable in a genetic sense, following Garland *et al.* (1992) plants found in the plots 'are born into environmental conditions and locations experienced by their parents at the time of birth', allowing us to use phylogenetically independent contrasts. Statistically significant results show that, throughout the plants' evolution, divergences in the relative frequency and relative abundance of dispersal systems consistently associate with divergences in the ecological variables. We forced correlations to pass through the origin and, where necessary, branch lengths were log-transformed to better fit the statistical assumptions of the test (which include normality of contrasts and absence of significant negative relationships between

standardized contrasts and branch lengths). Using EXCEL 2007, standardized contrasts of explanatory variables were plotted against standardized contrasts of dispersal systems.

In order to explore the relationships between the biomass of primates and endozoochory, we performed an additional multiple regression analysis using SAM 4.0. From the initial subset of 20 plots with available information on the biomass of primates, we obtained a total of nine sites, after averaging the response and explanatory variables in nearby plots that had equal values of primate biomass. Spearman rank correlation tests were performed between endozoochory and the continuous variables (biomass of primates, climatic variables, edaphic variables, elevation, raw and weighted richness of frugivores; Table S2). Multiple linear regression models were performed for variables that showed statistically significant relationships in these correlation tests, including only non-redundant variables in the model (i.e. $r_s \geq 0.5$) and selecting the best model based on the lowest AIC value. Short-distance spatial autocorrelation was assessed through the construction of spatial correlograms with 10,000 permutations based on the Moran's I .

Finally, we performed Kruskal–Wallis tests in order to detect significant differences between categories of flooding regime, wind speed and fragmentation, and stepwise step-down multiple comparisons were used to construct homogeneous subsets using SPSS 20.0.

RESULTS

Endozoochory was the highly represented mode of dispersal both in terms of species and of individuals, followed by anemochory and synzoochory (Table 1), showing the importance of animal-mediated seed dispersal in the tropics (Howe & Smallwood, 1982; Gentry, 1983; Jordano, 2000; Moles *et al.*, 2007). The relative frequencies of endozoochory and anemochory differed significantly among Holdridge life-zones (endozoochory, $H = 27.4$, d.f. = 6, $P < 0.001$; anemochory, $H = 42.7$, d.f. = 6, $P < 0.001$), as did the relative abundances of endozoochory and anemochory (endozoochory, $H = 19.5$, d.f. = 6, $P = 0.003$; anemochory, $H = 23.2$, d.f. = 6, $P = 0.001$). Endozoochory decreased and anemochory increased from rainy life-zones to the tropical dry forest. No statistically significant differences were found between life-zones for synzoochory (Fig. 2).

Table 1 Relative frequency (RF) and relative abundance (RA) of different seed dispersal systems in 101 one-hectare vegetation plots established in Colombian Neotropical forests. Ranges of values between the vegetation plots are shown.

Dispersal system	RF (%)	Range (%)	RA (%)	Range (%)
Endozoochory	71.2	(47.3–100)	70.2	(32.9–100)
Anemochory	14.4	(0–37.8)	13.5	(0–47.3)
Synzoochory	5.3	(0–16.8)	8.7	(0–35.4)
Hydrochory	1.3	(0–11.8)	1.2	(0–11.7)

Endozoochory (positively) and anemochory (negatively) were associated with precipitation (i.e. precipitation of the wettest month, Table 2). Additionally, field capacity, which is related to the ability of soils to retain moisture, was positively associated with the relative frequency of endozoochory, and precipitation seasonality was positively associated with the relative frequency of anemochory. Synzoochory was negatively associated with both soil carbon density and precipitation seasonality.

Short-distance spatial autocorrelation was corrected after the inclusion of spatial filters in the selected regression models (Fig. S2). When taking the phylogeny into account, standardized contrasts of response variables and explanatory variables showed significant Pearson correlations, except for the relationship between the relative abundance of synzoochory and soil carbon density (Fig. S3). This result supports the association between ecological factors and the relative frequencies and relative abundances of different dispersal systems over the course of evolution, and accounts for the consistency of our results despite a strong degree of phylogenetic inertia in fruit traits (Jordano, 1995).

No relationship was found between dispersal systems and the raw or weighted richness of frugivores, when all plots were included ($n = 101$). Using the nine sites derived from the 20 plots with available information on biomass of primates, however, the statistically significant best model for the relative abundance of endozoochory ($R^2_{\text{adj.}} = 0.62$, $\text{AIC} = -5.8$, $n = 9$, $F = 11.7$, $P = 0.011$) included the biomass of primates as the unique explanatory variable (std. coeff. = 0.79, std. error < 0.001, $t = 3.4$, $P = 0.014$), and for the relative frequency of endozoochory, the statistically significant best model ($R^2_{\text{adj.}} = 0.65$, $\text{AIC} = -22.5$, $n = 9$, $F = 13.1$, $P = 0.008$) included the weighted richness of frugivores as the unique explanatory variable (std. coeff. = 0.81, std. error < 0.001, $t = 3.6$, $P = 0.011$). No significant short-distance spatial autocorrelation was found in the residuals of these models (Fig. S4).

Hydrochory differed significantly between flooding-regime categories (relative frequency, $H = 7.34$, d.f. = 2, $P = 0.025$; relative abundance, $H = 7.33$, d.f. = 2, $P = 0.026$), reaching its highest proportion in permanently flooded plots (Fig. 3). The relative frequency of anemochory differed significantly between wind-speed categories, being higher in windy places ($H = 8$, d.f. = 2, $P = 0.019$) (Fig. 4).

Finally, the relative frequency of anemochory increased in fragmented areas ($H = 7.4$, d.f. = 2, $P = 0.024$), whereas synzoochory decreased with fragmentation (relative frequency, $H = 22.4$, d.f. = 2, $P < 0.001$; relative abundance, $H = 7.8$, d.f. = 2, $P = 0.021$) (Fig. 4).

DISCUSSION

Higher proportions of endozoochory have been found in humid areas (Howe & Smallwood, 1982; Gentry, 1983; Willson *et al.*, 1989; Jordano, 2000; Tabarelli *et al.*, 2003; Butler *et al.*, 2007; Moles *et al.*, 2007; Almeida-Neto *et al.*, 2008) and in soils with a greater ability to retain moisture (Arbeláez & Parrado-Rosselli, 2005). This could support the resource-availability hypothesis,

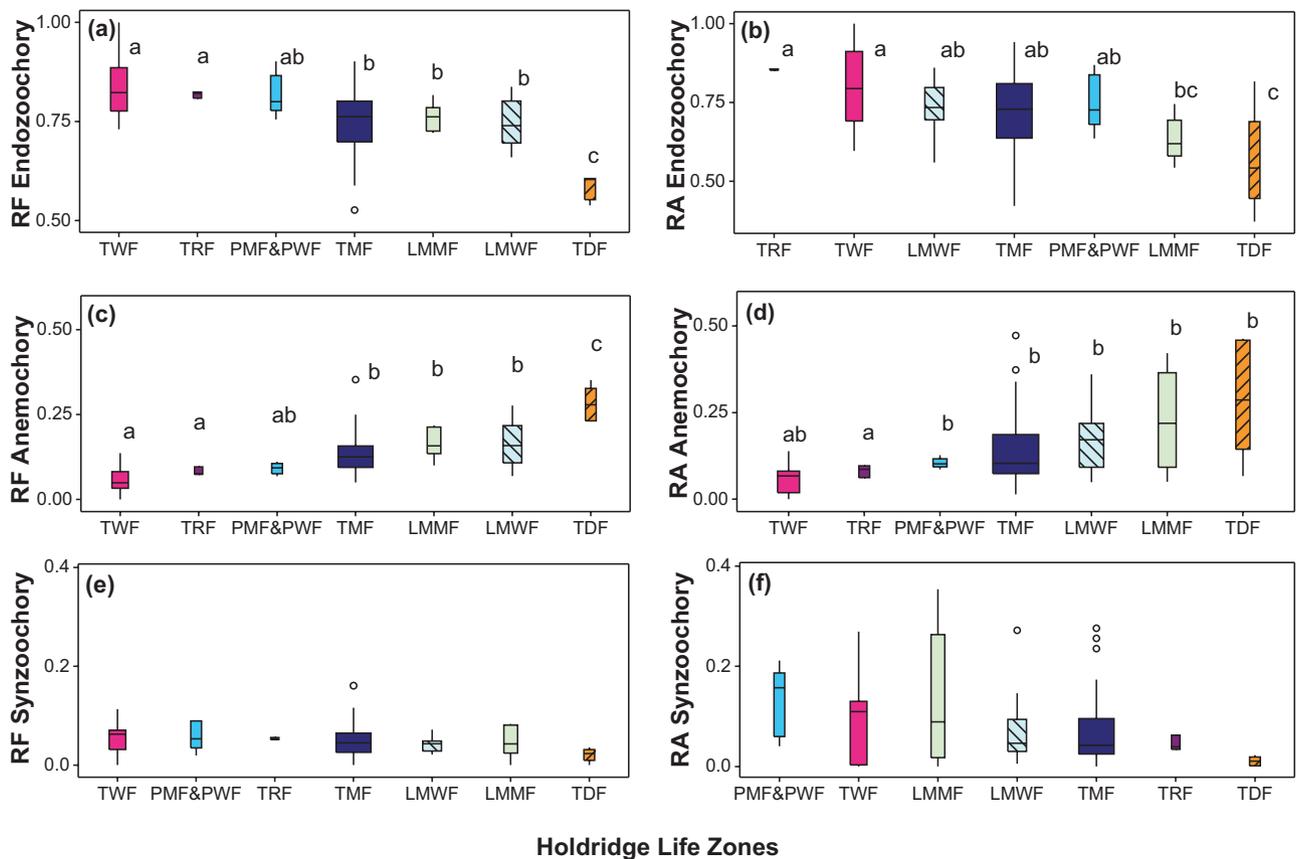


Figure 2 Box-plots of (a,c,e) the relative frequency and (b,d,f) the relative abundance of (a,b) endozoochory, (c,d) anemochory and (e,f) synzoochory in relation to Holdridge life-zones, using 101 vegetation plots in the Colombian Neotropics. Outliers are shown as circles; box width is a function of the number of plots. The letters above boxes show homogeneous subgroups based on *post hoc* tests. The *y*-axis is the relative frequency (RF) or relative abundance (RA) of each dispersal system. TDF, tropical dry forest; TMF, tropical moist forest; TWF, tropical wet forest; TRF, tropical rain forest; PMF, premontane moist forest; PWF, premontane wet forest; LMMF, lower montane moist forest; LMWF, lower montane wet forest. The single PMF plot was included in the PWF category (as ‘PMF&PWF’).

as the construction of fleshy structures may involve higher metabolic costs in terms of water consumption (Willson *et al.*, 1989), allowing fleshy-fruited species to be more frequent in areas with more water. According to this hypothesis, however, zoochorous fruits should also be more common on rich lowland soils. Our results showed no consistent patterns in relation to soil variables, elevation or temperature, suggesting that the availability of resources does not explain the proportion of endozoochorous species. The positive relationship found between the biomass of primates and the relative abundance of endozoochory, as well as that found between the weighted richness of frugivores and the relative frequency of endozoochory, shows that the proportion of endozoochory is mostly related to the availability of frugivores. This result could give support to the role of frugivore abundance in plant recruitment via dispersed seeds (García *et al.*, 2010), as well as the influence of disperser assemblages in the occurrence of animal-dispersed species with particular seed traits (e.g. seed shape) (Forget *et al.*, 2007). Although frugivores depend on fruit availability (Stevenson, 2001; Hanya *et al.*, 2011), it is probable that over evolutionary and ecological time-frames, frugivores could also

influence the demographic structure of the plants they disperse, as has been suggested by ecological studies (Wright, 1989; Godínez-Alvarez & Jordano, 2007; García *et al.*, 2010; Beck *et al.*, 2013; Galetti & Dirzo, 2013); thus, both forces probably act.

Similarly, the high proportion of anemochory in dry forests, as found in several studies (Howe & Smallwood, 1982; Tabarelli *et al.*, 2003), could be seen as the result of lower water requirements for the construction of non-fleshy structures. The lack of any relationships with elevation, temperature or soil variables, however, suggests that the availability of resources may not explain the proportion of anemochory. In fact, the occurrence of strong winds (wind speed in our study) seems to favour the frequency of anemochorous species, as suggested by other authors (Howe & Smallwood, 1982; Griffiths & Lawes, 2006). The interaction between the occurrence of strong winds, the release time of seeds and foliage shedding would also help to explain the higher proportion of anemochory in dry deciduous forests (Nathan & Katul, 2005; Wright *et al.*, 2008).

The higher proportion of synzoochory (which includes the largest seed sizes, and thus represents the most expensive type of

Table 2 Final regression models of seed dispersal systems in Colombian Neotropical forests as a function of climatic variables, elevation, edaphic variables, raw and weighted richness of frugivores, including all 101 vegetation plots. Response variables: relative frequencies of endozoochory (RFE), anemochory (RFA) and synzoochory (RFS), relative abundances of endozoochory (RAE), anemochory (RAA) and synzoochory (RAS). The explanatory variables included non-redundant factors selected from previous statistically significant Spearman rank correlation tests: precipitation of the wettest month (precipitation WM), precipitation seasonality (seasonality), soil field capacity (FC), soil carbon density (carbon) and soil bulk density (B). Where necessary, spatial filters (SF) were included in the selected models in order to control the short distance spatial autocorrelation in the residuals. Square-root ($^{1/2}$) and logarithmic (ln) transformations were used. AIC, Akaike information criterion; std., standard; coeff., coefficient.

Dispersal system	Adjusted R^2	AIC	F	Variable	Std. coeff.	Std. error	t
Endozoochory (RFE)	0.32	-240.4	15.8***	Precipitation WM	0.498	< 0.001	5.6***
				FC	0.219	< 0.001	2.6*
				SF	0.338	0.263	3.8***
Endozoochory (RAE)	0.37	-172.7	29.8***	Precipitation WM	0.483	< 0.001	5.9***
				SF	0.493	0.165	6.0***
Anemochory (RFA) ^{1/2}	0.46	-232.7	28.4***	Precipitation WM	-0.581	< 0.001	-7.0***
				Seasonality	0.292	< 0.001	3.4***
				SF	0.407	0.204	4.9***
Anemochory (RAA) ^{1/2}	0.23	-137.2	15.5***	Precipitation WM	-0.43	< 0.001	-4.8***
				B	-0.161	0.09	-1.8
Synzoochory ln (RFS + 1)	0.39	-484.6	20.6***	Seasonality	-0.532	< 0.001	-6.5***
				Carbon	-0.17	< 0.001	-2.1*
				SF	0.382	0.215	4.7***
Synzoochory (RAS) ^{1/2}	0.38	-153.4	21.1***	Seasonality	-0.321	< 0.001	-4.1***
				Carbon	-0.237	0.002	-3.0**
				SF	0.533	0.15	6.7***

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

dispersal unit) in areas with low precipitation seasonality (negatively correlated with total annual rainfall: $r_s = -0.69$, d.f. = 99, $P < 0.001$), might also suggest support for the resource-availability hypothesis. The lack of any relationships between synzoochory, elevation and temperature, in addition to the negative relationship found between synzoochory and soil carbon density (positively correlated with the soil's total nitrogen density: $r_s = 0.93$, d.f. = 99, $P < 0.001$), however, suggests that other factors are responsible for the occurrence of large-seeded species. Indeed, it has been shown that scatter-hoarding rodents (e.g. agoutis) are effective dispersers of large seeds (Jansen *et al.*, 2012) and, because they are widely distributed in Neotropical forests (Emmons & Feer, 1997), it is probable that they play a key role in the occurrence of synzoochory both in lowlands and in the mountains, within the elevation range of the vegetation plots used in our study (2–2867 m a.s.l.). It has also been found that large seeds are more frequent in infertile than in fertile soils (Parolin, 2000; ter Steege *et al.*, 2006), contrary to the expected high proportion of species and individuals with costly seeds in areas with high nutrient contents. This could be related to the high tolerance of large seedlings (which emerge from large seeds) to continuous shade (Westoby *et al.*, 2002; Baraloto & Forget, 2007), a condition that is expected to occur in forests with low disturbance rates (i.e. in forests with lower soil fertility, which are expected to be less productive) (ter Steege *et al.*, 2006).

As expected by the disperser-availability hypothesis, hydrochory was related to changes in flooding regime, showing

a higher proportion in permanently flooded plots. This expectation had been suggested by Gentry (1983), and could explain the higher proportion of hydrochorous species in Neotropical flood plains (Kubitzki & Ziburski, 1994; Umaña *et al.*, 2011).

Finally, synzoochory decreased in fragmented plots and the relative frequency of anemochory increased with fragmentation, as a probable result of the increase in pioneer species (Laurance *et al.*, 2002) with small seeds, or perhaps greater hunting pressures on mammal populations, including scatter-hoarding rodents. This local extinction of the dispersers of large seeds would cause a decrease in the populations of large-seeded species (Terborgh *et al.*, 2008; Jansen *et al.*, 2012).

CONCLUSIONS

The resource-availability hypothesis is not well supported in our study, as zoochory showed no positive relationship with lower elevation, higher temperature or higher densities of nitrogen and carbon in soils. Instead, synzoochory increased in soils with lower carbon density, in contrast to the expected high proportion of species and individuals with costly seeds in fertile soils. We hypothesize that previous findings that supported this hypothesis, based on the association between rainfall and endozoochory, might have overlooked the fact that frugivores are more abundant in productive areas

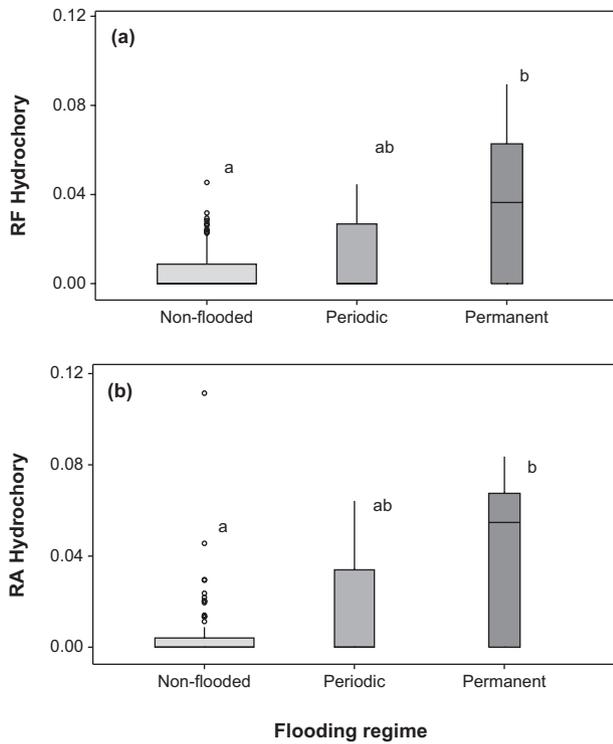


Figure 3 Box-plots of hydrochory in relation to flooding regime in the Colombian Neotropics: (a) relative frequency; (b) relative abundance. Outliers are shown as circles; box width is a function of the number of plots ($n = 101$). The letters above boxes show homogeneous subsets based on *post hoc* tests. The *y*-axis shows the relative frequency (RF) or relative abundance (RA) of hydrochory.

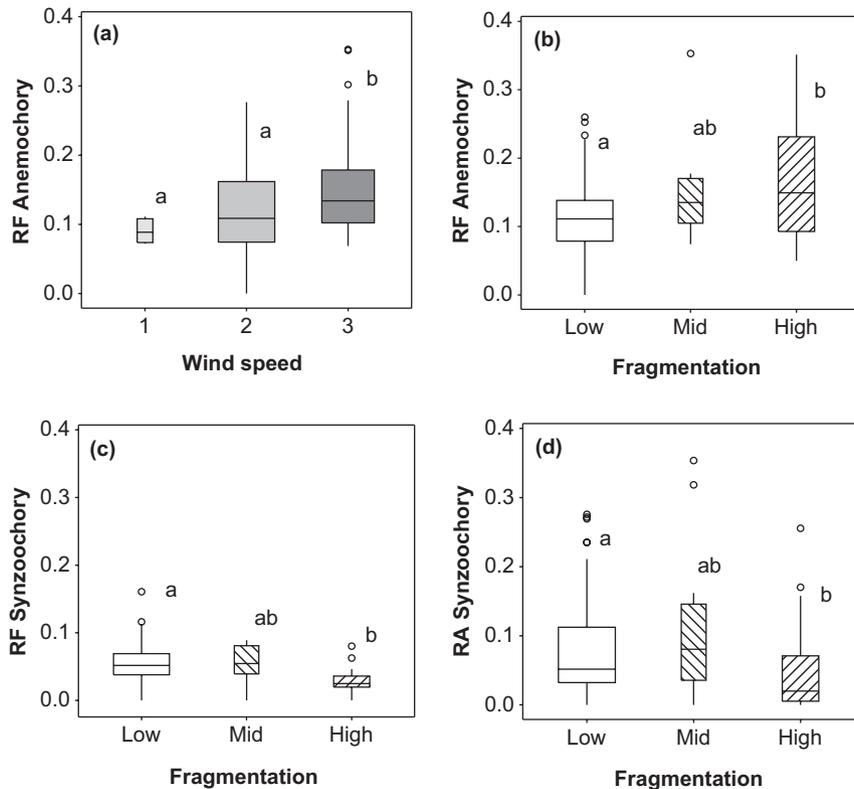


Figure 4 Box-plots of the relative frequency of anemochory in relation to wind speed and fragmentation, and for synzoochory in relation to fragmentation, in the Colombian Neotropics: (a,b) relative frequency of anemochory; (c) relative frequency of synzoochory; (d) relative abundance of synzoochory. Outliers are shown as circles; the widths of boxes is a function of the number of plots ($n = 101$); letters above boxes show homogeneous subsets based on *post hoc* tests. The *y*-axis shows the relative frequency (RF) and relative abundance (RA) of each dispersal system. The *x*-axis shows wind speed (1, $< 1 \text{ m s}^{-1}$; 2, $1\text{--}2 \text{ m s}^{-1}$; 3, $> 2 \text{ m s}^{-1}$) and fragmentation categories (defined as the proportion of remnant forest within a 5000-ha circle: high, $< 33\%$; mid, $33\text{--}66\%$; low, $> 66\%$).

(Stevenson, 2001; Hanya *et al.*, 2011) with high precipitation levels.

We conclude that the positive relationship between the biomass of key seed-dispersers (i.e. primates) and the relative abundance of endozoochory, as well as that between the weighted richness of frugivores and the relative frequency of endozoochory, along with the higher proportion of anemochory in areas with stronger winds and the higher proportion of hydrochory in permanently flooded forests, show strong support for the disperser-availability hypothesis. We hypothesize that frugivores can, over time, shape the demographic structure of the plants that they disperse. Although the availability of fruits can also influence the demographic structure of frugivores, is probable that both forces act. Further studies developed over larger spatial and temporal scales may shed light on their relative importance and/or true causality.

The high proportion of synzoochory in soils with low carbon density might be explained by the high tolerance of large seeds to continuous shade in areas with low rates of disturbance (i.e. in less productive forests with lower soil fertility) (ter Steege *et al.*, 2006). Finally, fragmentation affected large-seeded species more dramatically. This may be related to the increment in pioneer species (Laurance *et al.*, 2002) with small seeds, or to the decrease in the population density of large frugivores, including scatter-hoarding rodents, affecting the demographic structure of large-seeded plant species (Nuñez-Iturri *et al.*, 2008; Terborgh *et al.*, 2008; Stevenson, 2011).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Figure S1 Box-plots for fruit weight in relation to dispersal systems.

Figure S2 Moran's *I* spatial correlograms of the residuals in the selected models that included all the vegetation plots.

Figure S3 Relationships between standardized contrasts of dispersal systems and explanatory variables.

Figure S4 Moran's *I* results for the 20 plots with available information on primate biomass.

Table S1 Spearman rank correlation tests between response and continuous variables including all plots.

Table S2 Spearman rank correlation tests for the plots with available information on primate biomass.

BIOSKETCHES

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