RESEARCH PAPER

Vertebrate dispersal syndromes along the Atlantic forest: broad-scale patterns and macroecological correlates

Mário Almeida-Neto[1]*, Flávia Campassi[2], Mauro Galetti[2], Pedro Jordano[3] and Ary Oliveira-Filho[4]

[1]*Laboratório de Interações Insetos-Plantas, Depto. Zoologia, Instituto de Biologia, Universidade Estadual de Campinas, 13083-970, Campinas SP, Brazil*

[2]*Laboratório de Biologia da Conservação, Universidade Estadual Paulista, CP 199, 13506-900 Rio Claro, SP, Brazil*

[3]*Integrative Ecology Group, Estación Biológica de Doñana, CSIC, Apdo. 1056, E-41080 Sevilla, Spain*

[4]*Departamento de Ciências Florestais, Universidade Federal de Lavras, 37200-000 Lavras, MG, Brazil*

ABSTRACT

Aim To assess the geographical variation in the relative importance of vertebrates, and more specifically of birds and mammals, as seed dispersal agents in forest communities, and to evaluate the influence of geographical and climatic factors on the observed trends.

Location One hundred and thirty-five forest communities in the Brazilian Atlantic forest.

Methods We collected data on dispersal modes for 2292 woody species. By combining species × site with species × trait matrices, we obtained the percentages of endozoochory, ornithochory, mastozoochory and the mean fruit diameter for the local forest communities. We used Spearman's correlation to assess bivariate relationships between variables. Subsequently, we performed paired *t*-tests to verify if variations in frequency of dispersal modes and mean fruit diameter were influenced by altitude or temperature. Then, we applied multiple linear regressions to evaluate the effect of geographical and climatic variables on variation in the relative frequency of dispersal modes and mean fruit diameter across communities.

Results We found no consistent latitudinal or longitudinal trend in the percentage of vertebrate-dispersed species, neither bird- nor mammal-dispersed species along the Atlantic forest. Endozoochory was affected chiefly by annual mean rainfall, increasing towards moister sites. Forest communities located at higher altitudes had a higher percentage of bird-dispersed species. Even when sites with identical values of annual mean temperature were compared, altitude had a positive effect on ornithochory. Conversely, we found a higher percentage of mammal-dispersed species in warmer forests, even when locations at the same altitudinal belts were contrasted. Fruit diameter was clearly related to altitude, decreasing towards higher elevations.

Main conclusions This is the first analysis of a large data set on dispersal syndromes in tropical forest communities. Our findings support the hypotheses that: (1) geographical variation in the relative number of fleshy fruit species is mainly driven by moisture conditions and is relatively independent of geographical location, and (2) broad-scale trends in fruit size correspond to geographical variation in the relative importance of mammals and birds as seed dispersal agents at the community level.

*Correspondence: Mário Almeida-Neto, Depto. Zoologia, CP 6109, IB, UNICAMP, 13083-970, Campinas SP, Brazil. E-mail: marioeco@gmail.com

INTRODUCTION

Despite large variation in seed dispersal systems within and among communities, some studies have shown broad-scale, community-level trends along geographical, climatic and disturbance gradients (Howe & Smallwood, 1982; Gentry, 1995; Tabarelli & Peres, 2002; Tabarelli *et al.*, 2003; Griffiths & Lawes, 2006). The proportion of plant species dispersed by vertebrates,

for instance, has been reported to increase from dry to wet forests, from temperate to tropical regions and from higher to lower elevations (Howe & Smallwood, 1982; Willson *et al.*, 1989; Bullock, 1995; Gentry, 1995). Among the vertebrate-dispersed species, ornithochory is generally more common than mastozoochory (Gentry, 1982; Willson *et al.*, 1989). However, to our knowledge, no study has reported broad-scale trends in the relative frequency of bird- and mammal-dispersed plants along geographical or climatic gradients. Hypotheses concerning variations in dispersal spectra (i.e. the proportions of seed dispersal modes in a community) frequently invoke constraints or selective pressures related to other plant traits such as seed mass, plant size and growth form (Westoby *et al.*, 1990; Willson *et al.*, 1990; Hughes *et al.*, 1994). Some authors have suggested that the availability of dispersal vectors could be more a consequence of than a cause of the variations in dispersal spectra among communities (Hughes *et al.*, 1994; Eriksson *et al.*, 2000). Nonetheless, experimental tests for the hypotheses on broad-scale trends in dispersal modes are difficult. Because of this, most progress in this field has been made through correlative studies.

Another interesting question related to seed dispersal is whether variation in certain fruit traits also shows climatic and geographical trends, and whether these trends are consistent with those found for dispersal modes. Fruit size, for instance, is an important trait because it constrains the number of potential animal dispersers through the limitation of fruit consumption by certain frugivorous species (Wheelwright, 1985; Levey, 1987; Jordano, 1995; Githiru *et al.*, 2002). It is well documented that large-seeded species produce larger fruits (Herrera, 1987; Primack, 1987; Gill *et al.*, 1992; Jordano, 1995; Wright *et al.*, 2007). Obviously, the simplest explanation for this correlation is the physical constraint of a given fruit size over the maximum possible size of seeds it can package (Primack, 1987; Wright *et al.*, 2007). However also selective pressures acting at the seed or seedling stages can also be important elements in the elaboration of hypotheses regarding the geographical distribution of dispersal modes and associated trends in fruit size (Moles *et al.*, 2007). Some authors have postulated that seed mass is higher in shaded habitats because larger-seeded species should produce larger leaf surface area, becoming self-sufficient at lower light intensities (Salisbury, 1942; Harper *et al.*, 1970; Hammond & Brown, 1995) or, additionally, adapted for germination in dense leaf litter (Grubb & Metcalfe, 1996). Thus, if seed mass is related to the availability of light for plant germination, we should expect to find larger fruits in plant species of shaded forests compared with the fruits of species from more open forests (Lord *et al.*, 1997).

Studies performed at the local scale have found that most woody plant species in tropical rain forests have fleshy fruits whose seeds are gut-dispersed by vertebrates, whereas in tropical dry forests, a larger fraction of woody species are anemochorous (wind-dispersed) or autochorous (e.g. ballistic) (see Howe & Smallwood, 1982; Jordano, 2000 and references therein). In this study, we focus on the Brazilian Atlantic forest, the tropical forest biome with the largest latitudinal range, extending from 3° S to 33° S, and comprising several distinct forest physiognomies (Oliveira-Filho & Fontes, 2000). This particular biome is considered a global biodiversity hotspot (Mittermeier *et al.*, 2004), but currently about 92% of its original 10^6 km^2 cover has been cleared for human use (Fundação SOS Mata Atlântica *et al.*, 1998; Ministério do Meio Ambiente, 1999).

The aims of this study were to: (1) examine the broad-scale geographical variation in the relative importance of vertebrates (endozoochory), and more specifically of birds (ornithochory) and mammals (mastozoochory), as vectors of seed dispersal of woody plants in woody communities in the Atlantic forest, and (2) assess the influence of purely geographical and climatic factors on the observed trends. Furthermore, we evaluated the generality of some hypothesized trends, namely: (1) the proportion of vertebrate-dispersed plant species increases towards wetter forests, (2) bird-dispersed species are more frequent at higher altitudes, and (3) fruit size decreases with altitude. Other factors that might be postulated as potential causes of the climatic and geographical trends in seed dispersal modes include composition of the frugivore community, soil fertility, disturbance regimes and hydrological features. However, our analysis focused on hypotheses derived from the mutualistic interaction between plants and frugivores.

MATERIALS AND METHODS

Floristic and climatic data

Our data set is based on Oliveira-Filho & Fontes (2000) compilation of forest communities, with a few additions. The sources of the 135 forest community checklists used in this study are given in Appendix S1 in Supplementary Material. Only five of the 135 forest communities are not located within the official Brazilian Atlantic forest domain (CONAMA, 1992), but they are also typical Atlantic forest communities. All sites are located between 12.5° S and 25.5° S and 38.9° W and 56.5° W, and they comprise an altitudinal range from 0 to 1900 m a.s.l. (Fig. 1). Vegetation physiognomies included rain and seasonal semi-deciduous forests with annual mean rainfall varying from 771 to 3591 mm and annual mean temperature ranging from 12.9° C to 24.9° C. We obtained the following geographical variables for each forest community: latitude and longitude at the centre of the site, median altitude and shortest distance to the coast. We also compiled climatic variables from original checklist publications or from DNMet (1992) (see Table 1). Additional information on sources and methods for climatic and geographical variables were described by Oliveira-Filho & Fontes (2000). We compiled information for a total of 2292 species, with a mean richness of 153 woody species per site.

Seed dispersal syndromes

Seed dispersal syndromes were determined through direct inspection and measurements of seed and fruit traits deposited in six herbaria (Herbarium Rioclarense, HRCB; Instituto de Botânica, SP; Jardim Botânico do Rio de Janeiro, RB; New York Botanical Garden, NY; Instituto Nacional de Pesquisa da Amazônia, INPA; Royal Botanic Gardens, K) and according to
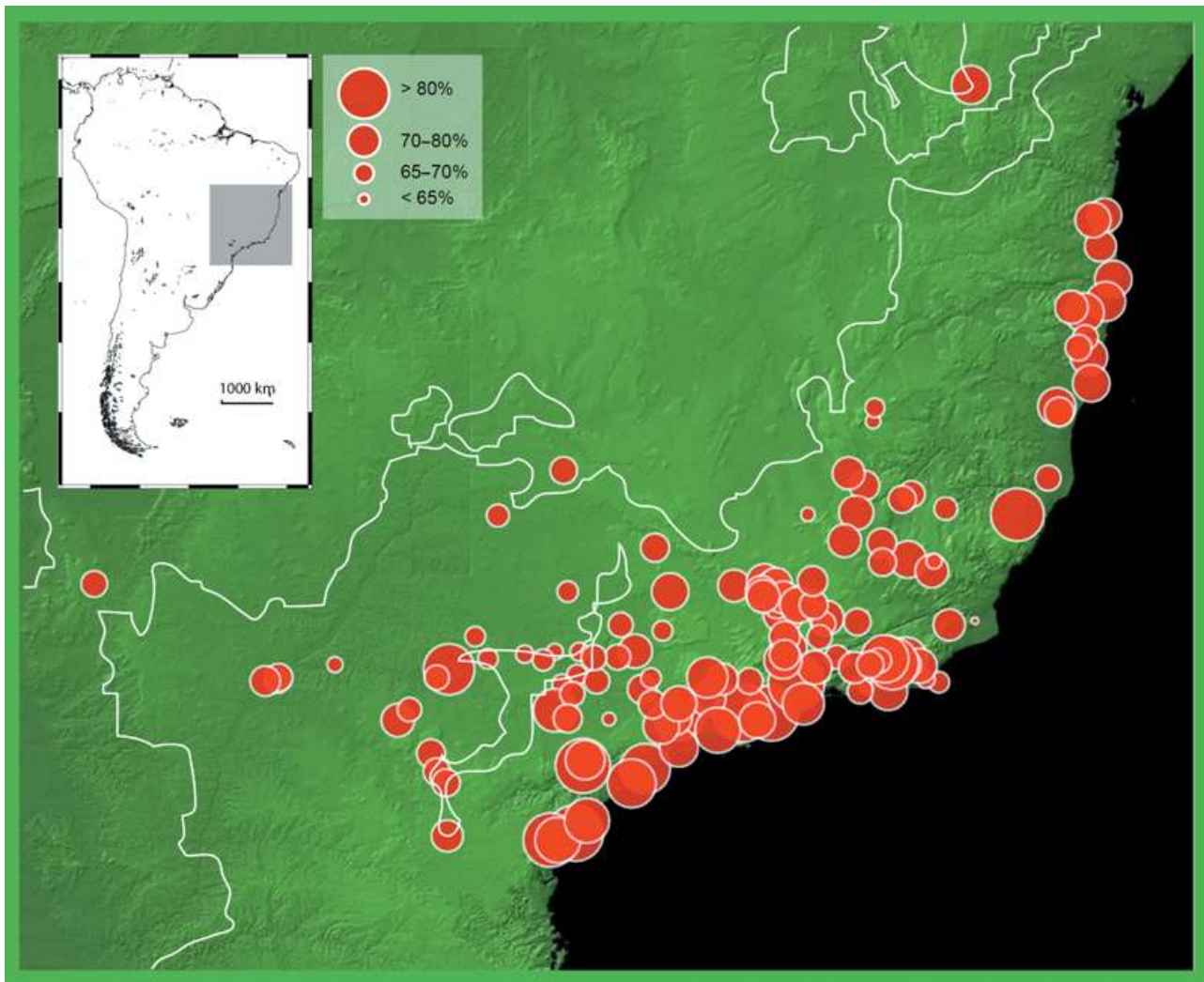
Figure 1 Distribution of the 135 forest communities along the Atlantic forest, Brazil. Circle size represents the percentage (square-root transformed) of endozoochorous woody species in each locality. The white line indicates the official limits of the Atlantic forest biome; the actual limits have been omitted for clarity but are much more reduced due to deforestation.

Table 1 Characterization of the climatic and geographical variables used in this study.

Name	Description	Mean (range)
ANNT	Annual mean temperature (°C)	20.6 (12.9–24.9)
MINT	Mean temperature of coldest month (°C)	17.0 (7.7–22.1)
RT	Mean temperature of the hottest month minus mean temperature of the coldest month (°C)	6.6 (2.4–13.3)
PPT	Annual mean precipitation (mm year^{-1})	1606 (771–3591)
PPTDM	Mean precipitation of the driest month (mm)	50.7 (6–168)
RPPT	Mean precipitation of the wettest month minus mean precipitation of the driest month (mm)	180.7 (0–489)
ALT	Approximate altitude (m)	616 (0–1900)
DFC	Distance from coast (km)	160 (1–1050)

descriptions, photos and illustrations found in the literature (e.g. Martius *et al.*, 1906; Lorenzi, 2002) as well as other data sets and field observations (van der Pijl, 1982; Jordano, 2000; M. Galetti and E. Cazetta, unpublished data). Fleshy fruits deposited in herbaria and from the literature were measured with callipers and were used as an indicator trait for endozoochory (internal animal dispersal). To distinguish between bird- and mammal-dispersed fruits, we used colour and size as indicator traits, as well as information available in the literature or personal observations. Plant species dispersed by both birds and mammals were not included in this subsequent analysis because we were not confident enough to evaluate the relative importance of these two vertebrate groups as dispersal agents. Given that our focus here was to explore the relative importance of endozoochory, distinctions of other animal dispersal modes (e.g. epizoochory and diszoochory) and types of abiotic dispersal (wind-, water- and auto-dispersed seeds) were not examined. Endozoochory by lizards and fishes was not analysed here because they do not

characterize distinct dispersal modes (Correa *et al.*, 2007; Valido & Olesen, 2007) and are not common in the Brazilian Atlantic forest (Da Silva *et al.*, 1989; Figueira *et al.*, 1994).

Statistical analyses

The percentages of vertebrate-dispersed (i.e. endozoochorous), bird-dispersed (ornithochorous) and mammal-dispersed (mastozoochorous) woody species in Atlantic forest localities were gathered from the combination of the species × site data matrix with the species × trait data matrix. We used the largest fruit diameter as a surrogate measure for fruit size for each species, which is the fruit trait that determines their main seed disperser group (Wheelwright, 1985; Jordano, 1995). Our general approach for evaluating the relative importance of geographical location and climate variables as causal explanations for the observed trends in dispersal modes was to perform multiple linear regressions with a set of non-redundant explanatory variables. We were primarily interested in developing a general model to understand the effects of each particular explanatory variable, rather than maximizing the coefficient of determination for pure prediction. However, two common problems that arise when climatic variables are used to estimate the values of a response variable over a large geographical range are collinearity and spatial autocorrelation (Legendre & Legendre, 1998; Diniz-Filho *et al.*, 2003; Graham, 2003). Collinearity biases the estimation of partial regression coefficients due to the inclusion of highly correlated independent variables in the models (Graham, 2003), whereas spatial autocorrelation biases the significance of the statistical tests by changing the number of degrees of freedom (Dutilleul, 1993). Thus, both collinearity and spatial autocorrelation can affect the selection of an adequate subset of explanatory variables when the aims of regression are description and estimation.

In order to avoid collinearity, we initially tested the correlation between all pairs of climatic and positional variables used in this study (Table 2). We used the Spearman rank coefficient to facilitate comparisons among correlations because some explanatory variables did not achieve normality even after transformations. This approach is useful for detecting redundant variables, which affect the selection of explanatory variables in multiple regressions. We also examined the bivariate correlations between the dispersal-related variables and between the explanatory and the dependent variables. We tested spatial autocorrelation for all variables, and applied Dutilleul's (1993) correction for the correlations when both variables showed significant spatial autocorrelation.

Bivariate correlations are an important step in the search for general trends, but they cannot elucidate how important each particular variable is in relation to the effects of the other variables. Thus, we evaluated the relative importance of the explanatory variables by fitting multiple linear regressions. We used the following steps to select an adequate subset of explanatory variables: (1) we included in the same model only variables whose correlation coefficient is lower than 0.6, (2) we included only variables with significant partial regression coefficients, and (3) we used the Akaike information criterion (AIC) as an objective final rule to select among the remaining models after applying criteria 1 and 2. The AIC is calculated for each model from its log-likelihood and number of parameters, and the model with the lowest AIC is the best one among the candidates (see Burnham & Anderson, 2002).

It is well known that temperature decreases at higher altitudes. However, besides its potential effects via temperature, altitude can affect dispersal-related variables through a number of other factors, such as air humidity, topography, soil depth, wind speed and availability of light at the ground layer. For this reason, we first tested whether temperature has a significant effect on the dependent variables when altitude is controlled for and, conversely, if altitude has a significant effect when temperature is controlled. We applied paired *t*-tests by contrasting the sites with the highest and lowest temperature values within altitudinal belts of 100 m, and by contrasting the sites with the highest and lowest elevations but with the same annual mean temperatures. When

Table 2 Spearman rank correlations between geographical and climatic variables. The *P*-value for each correlation was calculated taking spatial autocorrelation into account through Dutilleul's (1993) correction. All correlations were performed with 135 sites.

	ANNT	MINT	RT	PPT	PPTDM	RPPT	ALT
MINT	0.963***						
RT	−0.359***	−0.496***					
PPT	−0.295NS	−0.301NS	0.294**				
PPTDM	−0.164NS	0.144NS	0.154NS	0.517***			
RPPT	−0.457*	−0.437**	0.207*	0.369**	−0.400*		
ALT	−0.833***	−0.794***	0.111***	0.123NS	−0.453*	0.586*	
DFC	0.130NS	−0.179NS	0.082NS	−0.331**	−0.648***	0.214NS	0.379NS
LAT(S)	−0.317**	−0.383**	0.628**	0.256NS	0.456NS	0.016NS	0.015NS
LONG(W)	−0.261NS	−0.368NS	0.515NS	0.099NS	0.003NS	0.090NS	0.019NS

ANNT, annual mean temperature; MINT, temperature of coldest month; RT, temperature range; PPT, annual mean precipitation; PPTDM, precipitation of the driest month; RPPT, precipitation range; ALT, altitude; DFC, distance from coast. See Table 1 for a full description of the variables.
NS, not significant; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Table 3 Spearman rank correlations of four dispersal-related variables of woody plant communities and the respective climatic and geographical variables for 135 sites in the Brazilian Atlantic forest. The *P*-value for each correlation was calculated taking spatial autocorrelation into account through Dutilleul's (1993) correction. The percentages of ornithochorous and mastozoochorous woody species were calculated in relation to the number of endozoochorous species.

Variables	Endozoochory (%)	Ornithochory (%)	Mastozoochory (%)	Mean fruit diameter
Climatic				
ANNT	−0.195NS	−0.590***	0.625***	0.650***
MINT	−0.176NS	−0.533***	0.634***	0.652***
RT	0.196NS	0.119*	−0.327**	−0.183NS
PPT	0.505***	0.181NS	−0.097NS	−0.024NS
PPTDM	0.376***	−0.116NS	0.164NS	0.366*
RPPT	0.128NS	0.318NS	−0.271*	−0.386*
Geographical				
ALT	0.012NS	0.553**	−0.566***	−0.702***
LAT(S)	0.153NS	0.101NS	−0.292***	−0.157*
LONG(W)	−0.150NS	−0.171**	−0.303***	−0.290***
DFC	−0.478***	−0.170**	−0.188NS	−0.312NS

Abbreviations as Table 2.
NS, non-significant; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

we were able to distinguish between the effect of temperature or altitude based on the above-cited tests, we used only the variable with a significant effect in the subsequent multiple regression models.

Ecological variables measured at large geographical distances do not constitute independent observations due to spatially structured effects of extrinsic (e.g. climate, soil, topography) and intrinsic factors (e.g. metapopulation dynamics, overlap of species ranges) operating at different scales (Legendre, 1993; Koenig & Knops, 1998; Diniz-Filho *et al.*, 2003). Thus, we evaluated whether spatial autocorrelation of the dispersal-related variables was solely a consequence of their spatial dependence in relation to autocorrelated climatic and geographical variables (Legendre & Legendre, 1998). We depicted the Moran's *I* correlograms of the residuals of the multiple regression models without spatial variables, and verified whether significant spatial autocorrelation persisted at some distance interval. If not, this means that pure spatial (i.e. latitudinal and/or longitudinal) effects could be ignored. On the other hand, if spatial autocorrelation remained, we accounted for it by incorporating eigenvector-based spatial filters as explanatory variables into multiple regressions (see Borcard & Legendre, 2002; Griffith, 2003; Diniz-Filho & Bini, 2005). Diniz-Filho & Bini (2005) pointed out that this approach is better than the more conventional one based on geographical coordinates and their polynomial expansions because it captures spatial structures at different spatial scales, while the conventional method takes into account only broad-scale spatial structures. To define which eigenvectors should be used as filters, we used the criteria suggested by Griffith (2003) and Diniz-Filho & Bini (2005).

We applied an arc-sin transformation on the percentage variables to improve normality and homoscedasticity in regression residuals. The values of mean fruit diameter for each community are the mean of the logarithms of the original values for each woody species. When necessary, we used log- or square-root transformations in the explanatory variables of the multiple regression models. We performed all spatial analyses by using the software SAM 2.0 (Rangel *et al.*, 2007).

RESULTS AND DISCUSSION

Trends in endozoochory

Seventy-five per cent (1725 species) of the woody species whose dispersal syndrome could be confidently determined were classified as endozoochorous, i.e. species with seeds either regurgitated or defaecated after ingestion of the fruit by vertebrates. The percentage of endozoochorous species at the local scale ranged from 45.5% to 90.7%. We detected significant correlations between percentage of endozoochory and annual mean precipitation, whereas correlations between temperature-related variables and frequency of endozoochory along the Atlantic forest were generally non-significant (Table 3). We did not find any significant latitudinal, longitudinal or altitudinal broad-scale geographical trends in the percentage of endozoochorous species in the forest communities. However, forest communities closer to the coast showed a higher percentage of endozoochorous woody species (Fig. 1, Table 3).

Sites with the lowest annual mean temperatures had higher percentages of endozoochory than sites with the highest annual mean temperatures in 10 of the 14 altitudinal belts (Table 4). On the other hand, paired contrasts between localities at the highest and lowest altitudes with the same annual mean temperatures showed no significant difference in the percentage of endozoochory (Table 5). Based on these results, we did not include altitude as an explanatory variable in the multiple regression models of endozoochory.

Table 4 Contrast of geographical and dispersal-related variables between pairs of forest communities with the same values of annual mean temperature but located the extremes altitudes for each value of mean annual temperature. We applied the paired *t*-test to compare the mean values of each variable. We used 31 values of annual mean temperature ranging from 16.1 °C to 24.5 °C.

| | Mean values at | | | |
| | Minimum ALT | Maximum ALT | | |
Variable			*t*-value	*P*
Latitude (S)	22.3	21.2	0.32	0.0980
Longitude (W)	45.4	45.3	1.24	0.1132
Endozoochory (%)	77.5	73.5	0.78	0.2207
Ornithochory (%)	52.1	56.3	−1.76	0.0446
Mastozoochory (%)	29.1	24.6	0.74	0.2323
Mean fruit diameter	1.00	0.93	2.16	0.0194

ALT, altitude.

Table 5 Contrast of geographical and dispersal-related variables between pairs of forest communities located at the same 100-m altitudinal bands but with the maximum and minimum values of mean annual temperature in each altitudinal band. We applied the paired *t*-test to compare the mean values of each variable. We used 14 altitudinal bands ranging from 0–100 m to 1300–1400 m.

| | Mean values at | | | |
| | Minimum ANNT | Maximum ANNT | | |
Variable			*t*-value	*P*
ANNT	18.24	21.78	8.44	< 0.0001
Latitude (S)	23.36	20.17	−3.51	0.0019
Longitude (W)	46.63	44.01	−2.10	0.0279
Endozoochory (%)	80.6	72.3	3.44	0.0022
Ornithochory (%)	56.2	54.5	0.47	0.3240
Mastozoochory (%)	23.8	27.4	−1.83	0.0452
Mean fruit diameter	0.958	0.952	0.34	0.3704

ANNT, annual mean temperature.

The percentage of endozoochorous species showed positive spatial autocorrelation at closer distance intervals, with a decrease in the Moran's *I* values at 400-km intervals (Fig. 2a). The non-spatial regression model for endozoochory included only annual mean precipitation and distance from the coast, but the residuals of this model still retained both positive and negative spatial autocorrelation (Fig. 2a). Therefore, we included the eigenvector-based spatial filters to account for spatial auto-correlation in the regression models. The new regression models, including the spatial filters as explanatory variables, explained 45% of the variation in the percentage of endozoochorous woody species across sites and did not show any significant spatial autocorrelation (Fig. 2a, Table 6). Annual mean precipitation

Table 6 Multiple regression models of four dispersal-related variables associated with 135 forest communities in the Atlantic forest. The selection of the variables was done for description and estimation instead of forecasting. Spatial filters were incorporated as explanatory variables in the regression models of endozoochory and ornithochory.

Dependent variable Explanatory variable	Standard coefficient	*P*	*r*²	Adjusted *r*²
Endozoochory (%)	Overall *F* = 27.0, *P* < 0.0001, *R*² = 45.4%			
PPT	0.445	< 0.0001	0.158	0.286
DFC	−0.181	0.001	0.017	0.033
Ornithochory (%)	Overall *F* = 41.5, *P* < 0.0001, *R*² = 51.6%			
ALT	0.727	< 0.0001	0.312	0.421
DFC	−0.450	< 0.0001	0.205	0.324
Mastozoochory (%)	Overall *F* = 51.5, *P* < 0.0001, *R*² = 43.8%			
ANNT	0.647	< 0.0001	0.403	0.410
DFC	−0.162	0.014	0.035	0.057
Mean fruit diameter	Overall *F* = 149.8, *P* < 0.0001, *R*² = 52.1%			
ALT(sqrt)	−0.728	< 0.0001	0.521	0.521

Sqrt, square-root transformed.
ANNT, annual mean temperature; PPT, annual mean precipitation;
ALT, altitude; DFC, distance from coast.
See Table 1 for full descriptions of the variables.

had a positive effect on the percentage of endozoochorous species and explained most of its variation along the Atlantic forest (Table 6).

Our findings show that the relative importance of vertebrates as seed dispersers increases in forest communities located at sites with higher rainfall. We also found an additional negative effect of distance from the coast on the relative frequency of endozoo-chorous woody species. Since continentality is inversely related to air humidity, we hypothesized that humidity is the key factor affecting the percentage of endozoochory. Similar results have been previously reported in the literature (e.g. Gentry, 1982; Howe & Smallwood, 1982; Willson *et al.*, 1989; Tabarelli *et al.*, 2003), but as far as we know this is the first large-scale study relating seed dispersal modes in a continuous biogeographical range of relatively homogeneous tropical forest (i.e. not including hetero-geneity due to the inclusion of various forest biomes). Therefore, our analysis supports a prominent effect of rainfall on the frequency of endozoochory in the woody flora, after controlling for purely geographical trends and discontinuities due to biogeo-graphical differences in forest biomes. Bullock (1995) also suggested that the percentage of endozoochorous species is related to rainfall via moisture because sites with similar rainfall regimes but with lower soil drainage resulting from topography have reduced endozoochory. Although the majority of studies on seed dispersal modes, including this one, did not elucidate the particular mechanisms favouring or constraining endozoochory, they reported consistent patterns providing positive and negative support for specific hypotheses. For instance, studies reporting strong associations between moisture and endozoochory have
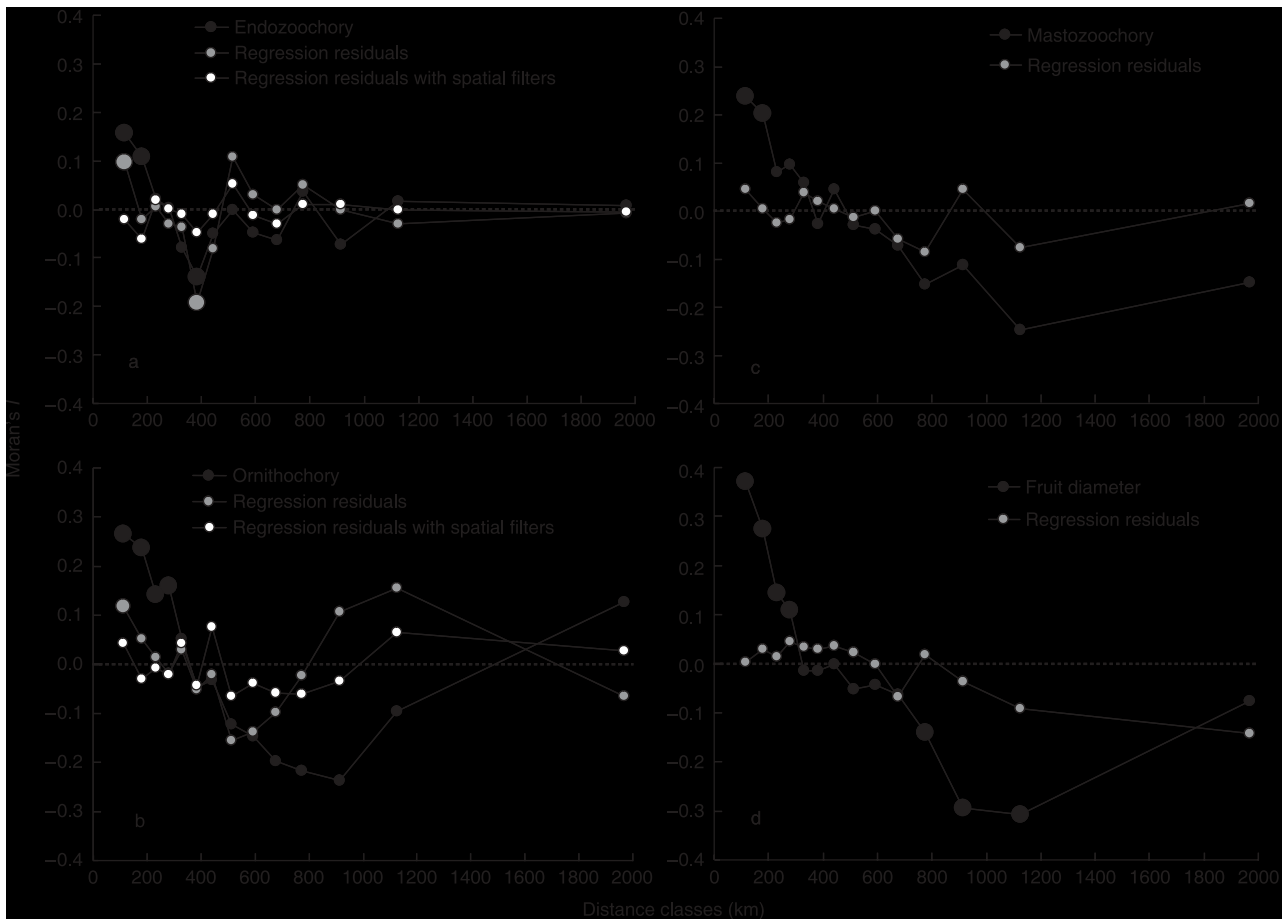
Figure 2 Spatial correlograms for the four seed dispersal-related variables for 135 sites of the Brazilian Atlantic forest: (a) endozoochorous woody species (%), (b) ornithochorous woody species (%), (c) mastozoochorous woody species (%), and (d) mean fruit diameter. Larger circles represent significant values after Bonferroni sequential correction ($\alpha_{initial}$ = 5%). Positive and negative Moran's *I* indicate whether the values of a variable are more or less similar, respectively, for pairs of sites at each distance interval.

been cited as support for the metabolic costs hypothesis (Willson *et al.*, 1989). According to this hypothesis, fleshy fruit production is not positively selected at sites with low soil moisture and fertility because of the high metabolic costs of the biochemical constituents of edible pulps.

Although some studies have shown a latitudinal trend in the relative frequency of endozoochorous plant species (Willson *et al.*, 1989; Lord *et al.*, 1997; Moles *et al.*, 2007), we did not detect any clear latitudinal gradient in the importance of vertebrates as dispersal agents in a latitudinal range spanning 12.5°. If latitudinal gradients in seed dispersal modes emerge as a consequence of remarkable contrasts between climatic variables, then its absence in our data can be explained by the fact that the forest areas included in this study make up a relatively homogeneous biogeographical and floristic assemblage. Although the Atlantic forest biome shows a pronounced variation in vegetation physiognomies and floristic composition across its north–south distribution (Oliveira-Filho *et al.*, 2006), this study included only two main forest physiognomies (rain and semi-deciduous forests) that constitute a more homogeneous subset compared with broader latitudinal gradients that show a much more marked turnover of

vegetation types (Moles *et al.*, 2007). Another relevant effect, which is still poorly understood, is how the historic process moulded each community (especially during the Late Pleistocene) along this ample biogeographical gradient. Some of the communities sampled are probably located within documented Pleistocene refuge areas which now correspond to areas with a high frequency of endozoochorous species (e.g. the Serra do Mar refuge and the Southern Bahia refuge). Moreover, it is probable that the previously documented latitudinal gradients in the percentage of endozoochory in fact represent a contrast between tropical and temperate regions instead of an actual gradual decrease in the frequency of this syndrome from equatorial to polar regions (but see Moles *et al.*, 2007, for such a trend in seed mass).

The relative importance of birds vs. mammals

The majority of the vertebrate-dispersed woody species in the Atlantic forest have their seeds preferentially dispersed by birds. Among all recorded endozoochorous woody species, 51% (879) are ornithochorous, 20% (338) are mastozoochorous, 7% (126) are dispersed by both birds and mammals and 22% (382) could

not be confidently classified in a subsyndrome due to lack of information on fruit morphology or interaction records with frugivores. The relative importance of birds and mammals as seed dispersal agents in local communities ranged from 26.9% to 75.2% and from 12.4% to 46% of the endozoochorous woody species, respectively. The mean percentage of bird-dispersed species (53.9%) was two times higher than that of mammal-dispersed species (26.1%) in the forest communities. Gentry (1982) also reported a 2-to-1 ratio of bird- to mammal-dispersed species in the Neotropics. Only four out of the 135 forest communities had more mammal- than bird-dispersed woody species (see Appendix S1).

Obviously, it was expected that ornithochory and mastozoochory had almost opposite patterns, because they represent two components of a composite variable of three components (mixed-dispersed species is the third one). The percentages of ornithochory and mastozoochory were, respectively, negatively and positively related to mean annual temperature and mean temperature of the coldest month (Table 3), but only the mastozoochory value showed a significant trend with latitude (Table 3). The relative frequency of ornithochory increased with altitude, whereas the frequency of mastozoochory was higher at lower elevations (Table 3).

If only the bivariate correlations were inspected, we should conclude that both ornithochory and mastozoochory are actually influenced by the same geographical and climatic factors. However, our subsequent analyses to distinguish whether temperature or altitude influences the percentage of bird- and mammal-dispersed woody species revealed interesting differences. The forest communities at Atlantic forest sites with the lowest annual mean temperatures within the 100-m altitudinal bands had a relatively lower frequency of mastozoochory than sites with highest annual mean temperatures within the same altitudinal bands, but we did not find any significant difference in the percentage of ornithochorous species (Table 4). In fact, the opposite results were found when the effect of altitude is tested by contrasting pairs of forest communities at the lowest and at the highest elevations with the same values of annual mean temperature. In this case, only the percentage of bird-dispersed species was significantly affected by altitude (Table 5). These results are reinforced by the significant negative correlation between percentage of mammal-dispersed species and latitude, while percentage of ornithochory showed no consistent trend with latitude. If temperature also had a strong influence on ornithochory, then we should expect a significant correlation with latitude.

Both the frequency of ornithochorous and the frequency of mastozoochorous species showed positive spatial autocorrelation at closer distance intervals with a decrease in the Moran's *I* values at 900-km intervals (Fig. 2b,c). Significant spatial autocorrelation also remained in the non-spatial regression model for ornithochory that included altitude and distance from the coast (Fig. 2b). After accounting for spatial autocorrelation through the inclusion of two spatial filters, the regression model explained 51.6% of the variation in the percentage of bird-dispersed species in the forest communities (Table 6). Altitude had a clear positive effect on the relative importance of birds as seed dispersers, whereas

distance from coast was negatively related to proportion of ornithochorous species (Table 6). The non-spatial regression model for mastozoochory included mean annual temperature and distance from the coast, and no significant spatial autocorrelation persisted in its residuals (Fig. 2c). This model explained 43.8% of the variation in the percentage of mammal-dispersed species, with annual mean temperature explaining 41% of this variation.

Why does the relative importance of birds as seed dispersers increase at higher elevations? A proper answer to this question depends on the evaluation of the altitudinal ranges of the vertebrate-dispersed plants and their mammal and bird dispersers. However, the strong relationship between altitude and fruit diameter (see below) can be an important clue to understand why birds had a greater relative importance as seed dispersers at higher elevations. Large fruits tend to be swallowed by large frugivores and fruits dispersed by mammals are typically larger than bird-dispersed fruits (Willson *et al.*, 1989; Jordano, 1995, 2000; Donatti *et al.*, 2007). High-altitude regions may lack large mammalian frugivores (especially primates) and vertebrate-dispersed fruits in these areas may be under strong selection deriving from a frugivore community dominated by frugivores with a small gape size, such as birds.

Patterns in fruit size

Mean fruit diameter showed a marked negative correlation with altitude, but was weakly related to latitude and longitude (Table 3). The woody species from forest communities at warmer sites had larger fruits than species from colder sites (Table 3). However, this correlation seems to be more related to altitude than temperature, because the forest communities located at lower altitudes had greater mean fruit diameter than those with identical values of annual mean temperature, but located at higher altitudes (Table 4). This result is supported by the absence of any significant difference in fruit diameter between pairs of communities with the lowest and highest annual mean temperatures in the same altitudinal belts. Nonetheless, we do not discard the hypothesis that altitude affects fruit diameter through effects mediated by other temperature variables besides annual mean temperature, such as daily and annual variations in temperature or other adverse climatic conditions that could influence seed size and, consequently, fruit diameter.

Mean fruit diameter showed positive spatial autocorrelation at closer distance intervals, with a marked decrease in the Moran's *I* values at 1200-km intervals (Fig. 2d). Altitude (square-root transformed) was the unique explanatory variable included in the regression model for mean fruit diameter and it explained 52.1% of the variation in this fruit trait across the forest communities in the Brazilian Atlantic forest (Table 6). When using only altitude as an independent variable, we removed all significant spatial autocorrelation in mean fruit diameter (Fig. 2d). As shown in the bivariate correlations, mean fruit diameter of the woody species decreases at higher elevations.

Apparently contrary to a recent study on latitudinal trends in seed mass (Moles *et al.*, 2007), we found no consistent variation

in mean fruit diameter from lower to higher latitudes. However, Moles *et al.* (2007) showed that latitude explains only 0.2% of the variation in seed mass if the effects of growth form, vegetation type, dispersal syndrome and net primary productivity were accounted for. Since we evaluated only vertebrate-dispersed woody species from tropical forests (trees and shrubs), major factors associated with latitudinal gradients in seed mass were probably previously incorporated in our data. In addition, we analysed a single mean value of fruit diameter per site, whereas Moles *et al.* (2007) used the values of seed mass for each species × site combination to perform their regression model. This distinct approach and our relatively small latitudinal range (12.5° S to 25.5° S) compared to that of Moles *et al.* (0° S to 60° S) could explain why we did not detect a significant effect of latitude on mean fruit size.

Why do Atlantic forest communities at higher altitudes have smaller fruits than lowland forests? There is no simple answer to this question because fruit size is strongly related to other plant traits, such as seed and plant size (Herrera, 1987; Primack, 1987; Gill *et al.*, 1992; Jordano, 1995; Wright *et al.*, 2007). Thus, any trend in fruit size can be explained by hypotheses related to seed and/or plant size. Leishman *et al.* (2000) found that the relationship between large seeds and shaded habitats is the strongest pattern of seed mass variation in relation to environmental factors (but see Metcalfe & Grubb, 1997). Baker (1972) found consistent decrease in seed weight at higher elevations in Californian mountains and argued that the length of the growing season decreases with elevation, reducing the availability of photosynthate and selecting for smaller seeds as an alternative strategy to reducing output. This hypothesis, however, cannot apply to our results, because both the maximum altitude and the altitudinal range of this study are considerably smaller than those described by Baker (1972).

Concluding remarks

The Brazilian Atlantic forest encompasses an enormous diversity of vertebrate-dispersed plant species. It spans a wide latitudinal gradient where there is no evidence for a consistent trend in the relative frequency of endozoochory, except in relation to rainfall. On the other hand, variations in the relative frequency of mammal- and bird-dispersed woody species were significantly related to annual mean temperature and altitude, respectively. The relative importance of vertebrates and, more specifically, of birds and mammals as seed dispersal agents in Atlantic forest communities appears to be mostly related to local variations in rainfall, elevation and temperature, which also account for the tremendous diversity of vertebrate-dispersal adaptations in these forests.

ACKNOWLEDGEMENTS

REFERENCES

Baker, H.G. (1972) Seed weight in relation to environmental conditions in California. *Ecology*, **53**, 997–1010.

Borcard, D. & Legendre, P. (2002) All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling*, **153**, 51–68.

Bullock, S.H. (1995) Plant reproduction in neotropical dry forests. *Seasonally dry tropical forests* (ed. by S. Bullock, H. Mooney and E. Medina), pp. 277–297. Cambridge University Press, Cambridge, UK.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical-theoretic approach*, 2nd edn. Springer-Verlag, New York.

CONAMA-Conselho Nacional do Meio Ambiente – Brasil (1992) *Resoluções CONAMA. 1984–1991: Resolução número 20 de 18 de junho de 1986.*

Correa, S.B., Winemiller, K.O., López-Fernández, H. & Galetti, M. (2007) Evolutionary perspectives on seed consumption and dispersal by fishes. *Bioscience*, **57**, 748–756.

Da Silva, H.R., Britto-Pereira, M.C. & Caramaschi, U. (1989) Frugivory and seed dispersal by *Hyla truncata*, a neotropical treefrog. *Copeia*, **3**, 781–783.

Diniz-Filho, J.A.F., Bini, L.M. & Hawkins, B.A. (2003) Spatial autocorrelation and red herrings in geographical ecology. *Global Ecology and Biogeography*, **12**, 53–64.

Diniz-Filho, J.A.F. & Bini, L.M. (2005) Modelling geographical patterns in species richness using eigenvector-based spatial filters. *Global Ecology and Biogeography*, **14**, 177–185.

DNMet (1992) *Normais climatológicas (1961–1990)*. Departamento Nacional de Meteorologia, Ministério da Agricultura, Brasília, Brazil.

Donatti, C.I., Galetti, M., Pizo, M.A., Guimarães, P.R. & Jordano, P. (2007) Living in the land of ghosts: fruit traits and the importance of large mammals as seed dispersers in the Pantanal, Brazil. *Seed dispersal: theory and its application in a changing world* (ed. by A.J. Dennis, E.W. Schupp, R.J. Green and D.W. Westcott), pp. 104–123. CAB International, Wallingford, UK.

Dutilleul, P. (1993) Modifying the *t*-test for assessing the correlation between two spatial processes. *Biometrics*, **49**, 305–314.

Eriksson, O., Friis, E.M. & Löfgren, 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.

Figueira, J.E.C., Vasconcellos-Neto, J., Garcia, M.A. & de Souza, A.L.T. (1994) Saurocory in *Melocactus violaceus* (Cactaceae). *Biotropica* **26**, 295–301.

Fundação SOS Mata Atlântica/INPE/Instituto Socio-ambiental (1998) *Atlas da evolução dos remanescentes florestais da Mata Atlântica e ecossistemas associados no período de 1990–1995*. Fundação SOS Mata Atlântica/INPE/Instituto Socio-ambiental (ISA), São Paulo.

Gentry, A.H. (1982) Patterns of neotropical plant species diversity. *Evolutionary Biology*, **15**, 1–84.

Gentry, A.H. (1995) Diversity and floristic composition of neotropical dry forests. *Seasonally dry tropical forests* (ed. by H. Bullock, H.A. Mooney and E. Medina), pp. 146–194. Cambridge University Press, Cambridge, UK.

Gill, A.M., Brooker, M.I.H. & Moore, P.H.R. (1992) Seed weights and numbers as a function of fruit size and subgenus in some *Eucalyptus* species from south-western Australia. *Australian Journal of Botany*, **40**, 103–111.

Githiru, M., Lens, L., Bennur, L.A. & Ogol, C. (2002) Effects of site and fruit size on the composition of avian frugivore assemblages in a fragmented afrotropical forest. *Oikos*, **96**, 320–330.

Graham, M.H. (2003) Confronting multicollinearity in ecological multiple regression. *Ecology*, **84**, 2809–2815.

Griffith, D.A. (2003) *Spatial autocorrelation and spatial filtering. Gaining understanding through theory and visualization.* Springer-Verlag, Berlin.

Griffiths, M.E. & Lawes, J.L. (2006) Biogeographic, environmental, and phylogenetic influences on reproductive traits in subtropical forest trees, South Africa. *Ecography*, **29**, 614–622.

Grubb, P.J. & Metcalfe, D.J. (1996) Adaptation and inertia in the Australian tropical lowland rain forest flora; contradictory trends in intergeneric and intrageneric comparisons of seed size in relation to light demand. *Functional Ecology*, **10**, 512–520.

Hammond, D. & Brown, V. (1995) Seed size of woody plants in relation to disturbance, dispersal, soil type in wet neotropical forests. *Ecology*, **76**, 2544–2561.

Harper, J.L., Lovell, P.H. & Moore, K.G. (1970) The shapes and sizes of seeds. *Annual Review of Ecology and Systematics*, **1**, 327–356.

Herrera, C.M. (1987) Vertebrate-dispersed plants of the Iberian Peninsula: a study of fruit characteristics. *Ecological Monographs*, **57**, 305–331.

Howe, H.F. & Smallwood, J. (1982) Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, **13**, 201–228.

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.

Jordano, P. (1995) Angiosperm fleshy fruits and seed dispersers: a comparative analysis of adaptation and constraints in plant–animal interactions. *The American Naturalist*, **145**, 163–191.

Jordano, P. (2000) Fruits and frugivory. *Seeds: the ecology of regeneration in plant communities* (ed. by M. Fenner), pp. 125–166. CAB International, Wallingford, UK.

Koenig, W.D. & Knops, J.M.H. (1998) Testing for spatial autocorrelation in ecological studies. *Ecography*, **21**, 423–429.

Legendre, P. (1993) Spatial autocorrelation: trouble or a new paradigm? *Ecology*, **74**, 1659–1673.

Legendre, P. & Legendre, L. (1998) *Numerical ecology*, 2nd edn. Elsevier, Amsterdam.

Leishman M.R., Wright, I.J., Moles, A.T. & Westoby, M. (2000) The evolutionary ecology of seed size. *The ecology of regeneration in plant communities* (ed. by M. Fenner), pp. 31–58. CAB International, Wallingford, UK.

Levey, D. (1987) Seed size and fruit-handling techniques of avian frugivores. *The American Naturalist*, **129**, 471–485.

Lord, J., Egan, J., Clifford, T., Jurado, E., Leishman, M., Williams, D. & Westoby, M. (1997) Larger seeds in tropical floras: consistent patterns independent of growth form and dispersal mode. *Journal of Biogeography*, **24**, 205–211.

Lorenzi, H. (2002) *Árvores brasileiras: Manual de identificação e cultivo de plantas arbóreas do Brasil*, vols 1 & 2, 4th edn. Instituto Plantarum, Nova Odessa, Brazil.

Martius, C.F.P. von, Endlicher, S., Eichler, A.G. & Urban, J. (eds) (1906) *Flora Brasiliensis*. München, Wien, Leipzig, Germany. 15 volumes.

Metcalfe, D.J. & Grubb, P.J. (1997) The ecology of very small-seeded shade-tolerant trees and shrubs in lowland rain forest in Singapore. *Functional Ecology*, **11**, 215–221.

Ministério do Meio Ambiente (1999) *Diretrizes para a política de conservação e desenvolvimento sustentável da Mata Atlântica*. Caderno número 13. Brasília, DF, Brazil.

Mittermeier, R.A., Robles-Gil, P., Hoffman, M., Pilgrim, J.D., Brooks, T.M., Mittermeier, C. G., Lamoreux, J.L. & da Fonseca, G.A.B. (2004) *Hotspots revisited: earth's biologically richest and most endangered terrestrial ecoregions*. CEMEX, Mexico City.

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.

Oliveira-Filho, A.T. & Fontes, M.A. (2000) Patterns of floristic differentiation among Atlantic Forest in southeastern Brazil and the influence of climate. *Biotropica*, **32**, 793–810.

Oliveira-Filho, A.T., Jarenkow, J.A. & Rodal, M.J.N. (2006) Floristic relationships of seasonally dry forests of eastern South America based on tree species distribution patterns. *Neotropical savannas and dry forests: plant diversity, biogeography and conservation*, (ed. by R.T. Pennington, J.A. Ratter and G.P. Lewis), pp. 159–192. CRC Press, Boca Raton, FL, USA.

van der Pijl, L. (1982) *Principles of dispersal in higher plants*, 3rd edn. Springer-Verlag, Berlin.

Primack, R.B. (1987) Relationships among flowers, fruits, and seeds. *Annual Review of Ecology and Systematics*, **18**, 409–430.

Rangel, T.F.L.V.B., Diniz-Filho, J.A.F. & Bini, L.M. (2007) Towards an integrated computational tool for spatial analysis in macroecology and biogeography. *Global Ecology and Biogeography*, **15**, 321–327.

Salisbury, E.J. (1942) *The reproductive capacity of plants*. Bell and Sons, London.

Tabarelli, M. & Peres, C.A. (2002) Abiotic and vertebrate seed dispersal in the Brazilian Atlantic forest: implications for forest regeneration. *Biological Conservation*, **106**, 165–176.

Tabarelli, M., Vicente, A. & Barbosa, D.C.A. (2003) Variation of seed dispersal spectrum of woody plants across a rainfall gradient in north-eastern Brazil. *Journal of Arid Environments*, **53**, 197–210.

Valido, A. & Olesen, J.M. (2007) The importance of lizards as seed dispersers. *Seed dispersal: theory and its application in a changing world* (ed. by A.J. Dennis, E.W. Schupp, R.J. Green and D.W. Westcott), pp. 124–147. CAB International, Wallingford, UK.

Westoby, M., Rice, B. & Howell, J. (1990) Seed size and plant growth form as factors in dispersal spectra. *Ecology*, **71**, 1307–1315.

Wheelwright, N.T. (1985) Fruit size, gape width, and the diets of fruit-eating birds. *Ecology*, **6**, 808–818.

Willson, M.F., Irvine, A.K. & Walsh, N.G. (1989) Vertebrate dispersal syndromes in some Australian and New Zealand plant communities, with geographic comparisons. *Biotropica*, **21**, 133–147.

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.

Wright, I.J., Ackerly, D.D., Bongers, F., Harms, K.E., Ibarra-Manriquez, G., Martinez-Ramos, M., Mazer, S.J., Muller-Landau, H.C., Paz, H., Pitman, N.C.A., Poorter, L., Silman, M.R., Vriesendorp, C.F., Webb, C.O., Westoby, M. & Wright S.J. (2007) Relationships among ecologically important dimensions of plant trait variation in seven neotropical forests. *Annals of Botany*, **99**, 1003–1015.

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Details of the 135 sites used in the study.

This material is available as part of the online article from:
http://www.blackwell-synergy.com/doi/abs/10.1111/j.1466-8238.2008.00386.x
(This link will take you to the article abstract).

Please note: Blackwell Publishing is not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

BIOSKETCHES

Mário Almeida-Neto is a post-doctoral researcher at Universidade Estadual de Campinas, Brazil. He is especially interested in plant–animal interactions and spatial patterns.

Flávia Campassi is a former masters student with M. Galetti and her main interest is in geographical patterns of seed dispersal modes.

Mauro Galetti is the research leader of the Laboratório de Biologia da Conservação and founder of the Phenology and Seed Dispersal Group at Universidade Estadual Paulista at Rio Claro, Brazil.

Pedro Jordano is research professor at the Integrative Ecology Group, Estación Biologica de Doñana, CSIC, Seville, Spain. His main interest is in the evolutionary ecology of plant–animal mutualistic interactions of seed dispersal and pollination.

Ary T. Oliveira-Filho is research professor at the Federal University of Lavras, Brazil. His main interest is phytogeography and plant community ecology.

Editor: Thomas Gillespie