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Variation of seed dispersal spectrum of woody plants across a rainfall gradient in north-eastern Brazil

M. Tabarelli*, A. Vicente & D. C. A. Barbosa

Departamento de Botânica, Universidade Federal de Pernambuco, Recife, Pernambuco 50670-091, Brazil

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This study tests the hypothesis that the percentage of tree and shrub species within categories of seed dispersal, fruit size and type is directly related to rainfall in the caatinga vegetation, a tropical dry forest of the north-eastern Brazil. The percentage of vertebrate-dispersed species ranged from 11% in a 246-mm year\(^{-1}\) plot to 53.6% in a 663-mm year\(^{-1}\) plot. In addition, the percentage of berry species was positively correlated with annual rainfall, whereas the percentage of drupe species was negatively correlated. Among the group of vertebrate-dispersed species, a significant increase was found in the percentage of Myrtaceae species (0–16.7%) from dry to moist plots. Our results support trends described in the literature reporting gradual and predictable changes in seed dispersal mode in neotropical forests located across rainfall gradients.

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Introduction

Several studies have identified remarkable differences between dry and moist neotropical forests in terms of vegetation structure, woody plant species composition, plant species richness, reproductive biology and diversity of plant life forms (Frankie et al., 1974; Gentry, 1982a, 1983, 1988; Gentry & Dodson, 1987; Bullock, 1995; Medina, 1995; Pennington et al., 2000). For example, lowland dry forests have about 50–70 plant species <2.5 cm diameter in 0.1-ha plots, semievergreen forests have 100–150 species, whereas moist forests have 200–250 species (Gentry, 1988). Neotropical dry forests usually also have lower percentages of woody plant species dispersed by vertebrates, of species pollinated by generalist pollinators and of evergreen species when compared with more humid forests (Howe & Smallwood, 1982; Bullock, 1995).

More than remarkable differences between dry and moist forests, the studies by Murphy & Lugo (1986), Gentry (1995) and Medina (1995) support the idea of predictable and gradual changes in the structure of woody plant communities (i.e. species richness and composition, frequency of species within categories of life form and life-history strategies) along rainfall gradients in neotropical forests. According to Medina (1995), along a dry–moist forest gradient, we should expect a reduction in the
number (and percentage) of woody deciduous species and an increase in the number of evergreen woody plant species and C\textsubscript{3} epiphytes. The review by Bullock (1995) showed some evidence that strategies of pollination and seed dispersal change gradually from dry to moist forests.

The caatinga vegetation is a kind of dry forest (sensu Mooney et al., 1995; Pennington et al., 2000) and scrub vegetation that occurs in north-eastern Brazil (IBGE, 1985; Sampaio, 1995). The caatinga vegetation ranges from well-developed stands of dry forest with canopy trees 17 m tall and 2220–28,020 plants ha\textsuperscript{-1} (stem diameter at soil level \(\geq 3\) cm) to 5 m-tall scrub types with 619 plants ha\textsuperscript{-1} (Sampaio, 1996). Such variation in vegetation structure is conditioned by soil type and topography, human disturbance and, most important, by the amount of annual rainfall (Sampaio & Salcedo, 1993; Sampaio, 1995) that ranges from 240 to 900 mm throughout the caatinga vegetation (IBGE, 1985; Lins, 1989). In certain regions of caatinga vegetation, average annual rainfall explained 86\% of the variation in the height of woody plants (Sampaio et al., 1981). Several studies (e.g. Andrade-Lima, 1981; Santos et al., 1992; Sampaio, 1995) have also documented changes in woody plant species composition associated with variation in the vegetation structure and physical environment. However, we should also expect predictable and gradual changes in the percentage of trees and shrubs within different categories of growth form, seed dispersal, pollination mode and phenology in plots of caatinga vegetation situated across rainfall gradients.

This study tests the hypotheses that in the caatinga vegetation the percentage of vertebrate-dispersed tree and shrub species gradually increases along a rainfall gradient (i.e. from dry to moist plots). In addition, among the vertebrate-dispersed species, the percentage of large- and fleshy-fruited species gradually increases, whereas the percentage of species with small fruits and with partially sclerocarpic fruits decrease along the rainfall gradient. We quantified the percentage of species within categories of seed dispersal, fruit size and fruit type sampled in 20 plots of the caatinga vegetation located across a rainfall gradient of 246–694 mm year\textsuperscript{-1}. Differences on seed dispersal, fruit size and type are analysed at two spatial scales: between-plots and between-precipitation categories. The relationships between seed dispersal mode, fruit morphology, taxonomic composition and annual rainfall are discussed. Finally, we discuss the way that geographically proximal ecosystems, like the Atlantic rain forest, may affect the frequency of vertebrate-dispersed tree and shrub species with particular fruit types in the caatinga vegetation.

**Methods**

*Caatinga and the study sites*

The caatinga vegetation of Brazil (hereafter caatinga) includes several woodland vegetation types from seasonally tropical dry forest (sensu Mooney et al., 1995; Pennington et al., 2000) to scrub vegetation (Sampaio, 1995). Caatinga covers 730,000 km\textsuperscript{2} of north-eastern Brazil and represents a distinctive feature of the Brazilian semi-arid or caatinga region (IBGE, 1985, Fig. 1). Vegetation types are spread over sedimentary basins, mountains and plateau (IBGE, 1985). Diversified geology and relief support a large number of soil types including lithosols, regosols, latosols and sand soils (Sampaio, 1995). Throughout the caatinga region, vegetation is constrained by annual rainfall which ranges from 240 to 900 mm (Fig. 1), and which falls within 3–7 months (IBGE, 1985; Lins, 1989). Bordering or completely surrounded by caatinga, there are some high plateau, where annual rainfall exceeds 1200 mm. Tracts of the Atlantic rain forest cover these high plateau, and they are locally named *brejo* forests (sensu Andrade-Lima, 1982; Lins, 1989). Thus, caatinga and Atlantic forest border each other for hundreds of kilometres.
In the caatinga, richest woody plant families are Leguminosae, Euphorbiaceae, Compositae, Solanaceae, Boraginaceae and Cactaceae (Rodal & Melo, 1999; Pennington et al., 2000). At present, 322 woody plant species have been recorded for the caatinga vegetation (Rodal & Melo, 1999). Among them, at least 57 species are widely distributed among the neotropical dry forests (Pennington et al., 2000). Sampaio (1995) provided an overview about caatinga.

In order to test the hypotheses, we used published plant surveys conducted in 20 different plots of caatinga rather than surveys carried out by ourselves. Plots were located inside a 160,000-km$^2$ polygon including the States of Piauí, Pernambuco, Paraíba, Alagoas and Sergipe, at distances from 100 to 800 km from the Atlantic Ocean. Plant surveys were conducted at sites with average annual rainfall ranging from 246 to 694 mm, and with different soil types (Table 1). These plant surveys represented the best-published information available on woody plant species composition at the local level and they covered a large part of the rainfall gradient observed in the caatinga (246–900 mm year$^{-1}$ for caatinga vegetation). Plant surveys were conducted based on different methods, but they used plant sample criteria (from 5 cm DBH to all woody plant species, Table 2) that permitted them to record a representative portion if not all tree and shrub species found at each plot.

Seed dispersal, fruit size and type vs. annual rainfall

All tree and shrub species reported from the 20 plots were classified into classes of seed dispersal, fruit size and fruit type on the basis of: (1) a reasonably good knowledge of their fruit morphology; (2) detailed accounts of species life-history traits provided in the literature (van Roosmalen, 1985; Barroso et al., 1999); and (3) checking herbarium specimens.
Table 1. Main characteristics of the 20 plots of caatinga vegetation analysed in this study

<table>
<thead>
<tr>
<th>Plot</th>
<th>Location (Lat. S, Long. W)</th>
<th>Elevation (m)</th>
<th>Rainfall* (mm year⁻¹)</th>
<th>Soil type†</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cabaceiras</td>
<td>7°29′–36°17′</td>
<td>500</td>
<td>246</td>
<td>Non-calcic brown, litholic</td>
</tr>
<tr>
<td>Barra de São Miguel</td>
<td>7°45′–36°19′</td>
<td>500</td>
<td>363</td>
<td>Non-calcic brown, litholic</td>
</tr>
<tr>
<td>Serra Branca</td>
<td>7°29′–36°39′</td>
<td>500</td>
<td>386</td>
<td>Non-calcic brown, litholic</td>
</tr>
<tr>
<td>São João do Cariri</td>
<td>7°23′–36°51′</td>
<td>500</td>
<td>386</td>
<td>Non-calcic brown, litholic</td>
</tr>
<tr>
<td>Vale do Moxotó</td>
<td>8°30′–37°38′</td>
<td>400</td>
<td>400</td>
<td>Quartz sand, litholic,</td>
</tr>
<tr>
<td>Santa Maria da Boa Vista</td>
<td>8°45′–39°50′</td>
<td>453</td>
<td>454</td>
<td>Latosol</td>
</tr>
<tr>
<td>Canindé</td>
<td>9°37′–37°51′</td>
<td>280</td>
<td>529</td>
<td>Cambisol, non-calcic brown</td>
</tr>
<tr>
<td>Poço Redondo</td>
<td>9°48′–37°41′</td>
<td>230</td>
<td>542</td>
<td>Regosol, solonetz</td>
</tr>
<tr>
<td>Brejo da Madre de Deus</td>
<td>8°09′–36°19′</td>
<td>627</td>
<td>553</td>
<td>Regosol</td>
</tr>
<tr>
<td>Petrolina</td>
<td>9°02′–40°14′</td>
<td>337</td>
<td>570</td>
<td>Cambisol</td>
</tr>
<tr>
<td>Custódia</td>
<td>8°06′–37°40′</td>
<td>500</td>
<td>574</td>
<td>Regosol, non-calcic brown</td>
</tr>
<tr>
<td>Parnamirim</td>
<td>8°04′–39°30′</td>
<td>400</td>
<td>580</td>
<td>Podzol, non-calcic brown</td>
</tr>
<tr>
<td>Alagoinha</td>
<td>8°27′–36°44′</td>
<td>762</td>
<td>584</td>
<td>Lithic, podzolic</td>
</tr>
<tr>
<td>Sertânea</td>
<td>8°04′–37°16′</td>
<td>450</td>
<td>600</td>
<td>Regosol, non-calcic brown</td>
</tr>
<tr>
<td>Buíque†</td>
<td>8°35′–37°15′</td>
<td>835</td>
<td>600</td>
<td>Quartz sand</td>
</tr>
<tr>
<td>Ibimirim</td>
<td>8°39′–37°35′</td>
<td>600</td>
<td>631</td>
<td>Quartz sand</td>
</tr>
<tr>
<td>Serra Talhada</td>
<td>7°57′–38°17′</td>
<td>500–700</td>
<td>650</td>
<td>Cambisol, litholic</td>
</tr>
<tr>
<td>Nossa Senhora da Glória</td>
<td>10°13′–37°25′</td>
<td>291</td>
<td>663</td>
<td>Podzolic</td>
</tr>
<tr>
<td>São Raimundo Nonato</td>
<td>8°44′–42°29′</td>
<td>600</td>
<td>688</td>
<td>Latosol</td>
</tr>
<tr>
<td>Caruaru</td>
<td>8°14′–35°55′</td>
<td>537</td>
<td>694</td>
<td>Regosol, litholic</td>
</tr>
</tbody>
</table>

*Data provided by the authors of each plant survey.
†Refers to predominant soil types.
‡Refers to a particular type of caatinga.
Table 2. *Sampling effort and criteria used in the plant surveys carried out at the 20 plots of caatinga vegetation considered in this study*

<table>
<thead>
<tr>
<th>Plot</th>
<th>Sample size (no. of individuals)</th>
<th>Sampling criteria*</th>
<th>No. of woody plant species</th>
<th>Vegetation height (m)†</th>
<th>Source of floristic data</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cabaceiras</td>
<td>0·1 ha (297)</td>
<td>All woody species</td>
<td>9</td>
<td>6</td>
<td>Lira (1979)</td>
</tr>
<tr>
<td>Barra de São Miguel</td>
<td>0·1 ha (74)</td>
<td>All woody species</td>
<td>7</td>
<td>3</td>
<td>Lira (1979)</td>
</tr>
<tr>
<td>Serra Branca</td>
<td>0·2 ha (335)</td>
<td>All woody species</td>
<td>9</td>
<td>7</td>
<td>Lira (1979)</td>
</tr>
<tr>
<td>São João do Cariri</td>
<td>0·2 ha (315)</td>
<td>All woody species</td>
<td>10</td>
<td>7·5</td>
<td>Lira (1979)</td>
</tr>
<tr>
<td>Vale do Moxotó</td>
<td>0·42 ha (257)</td>
<td>5 BSD</td>
<td>16</td>
<td>—</td>
<td>Rodal (1984)</td>
</tr>
<tr>
<td>Santa Maria da Boa Vista</td>
<td>?</td>
<td>All woody species</td>
<td>65</td>
<td>—</td>
<td>Drumond <em>et al.</em> (1982)</td>
</tr>
<tr>
<td>Canindé</td>
<td>0·45 ha (1664)</td>
<td>3 BSD</td>
<td>29</td>
<td>16</td>
<td>Fonseca (1991)</td>
</tr>
<tr>
<td>Poço Redondo</td>
<td>0·3 ha (1029)</td>
<td>3 BSD</td>
<td>31</td>
<td>15</td>
<td>Fonseca (1991)</td>
</tr>
<tr>
<td>Brejo da Madre de Deus</td>
<td>1 ha (2828)</td>
<td>3 BSD</td>
<td>26</td>
<td>—</td>
<td>Andrade (2000)</td>
</tr>
<tr>
<td>Petrolina</td>
<td>1·4 ha (2234)</td>
<td>3 BSD</td>
<td>38</td>
<td>14</td>
<td>Nascimento (1998)</td>
</tr>
<tr>
<td>Custódia</td>
<td>1 ha (2180)</td>
<td>5 BSD</td>
<td>35</td>
<td>15</td>
<td>Aráujo <em>et al.</em> (1995)</td>
</tr>
<tr>
<td>Parnamirim</td>
<td>0·2 ha (640)</td>
<td>All woody species</td>
<td>22</td>
<td>12</td>
<td>Santos (1987)</td>
</tr>
<tr>
<td>Alagoinha</td>
<td>1 ha (flora)</td>
<td>All woody species</td>
<td>26</td>
<td>—</td>
<td>Griz &amp; Machado (2001)</td>
</tr>
<tr>
<td>Sertânea</td>
<td>1 ha (4977)</td>
<td>3 BSD</td>
<td>28</td>
<td>9</td>
<td>Figueirêdo (2000)</td>
</tr>
<tr>
<td>Buque</td>
<td>(400)</td>
<td>3 BSD</td>
<td>79</td>
<td>9</td>
<td>Gomes (1999)</td>
</tr>
<tr>
<td>Ibimirim</td>
<td>?</td>
<td>All woody species</td>
<td>60</td>
<td>—</td>
<td>Rodal <em>et al.</em> (1999)</td>
</tr>
<tr>
<td>Serra Talhada</td>
<td>0·3 ha (flora)</td>
<td>All woody species</td>
<td>40</td>
<td>—</td>
<td>Ferraz <em>et al.</em> (1998)</td>
</tr>
<tr>
<td>Nossa Senhora da Glória</td>
<td>0·4 ha (1086)</td>
<td>5 DBH</td>
<td>29</td>
<td>15</td>
<td>Souza (1983)</td>
</tr>
<tr>
<td>São Raimundo Nonato</td>
<td>1 ha (5827)</td>
<td>3 BSD</td>
<td>40</td>
<td>9·5</td>
<td>Lemos (1999)</td>
</tr>
<tr>
<td>Caruaru</td>
<td>0·6 ha (2286)</td>
<td>3 BSD</td>
<td>42</td>
<td>19</td>
<td>Alcoforado-Filho (1993)</td>
</tr>
</tbody>
</table>

*Refers to the minimum size in cm of diameter at breast height (DBH) or basal stem diameter (BSD) of plants sampled.
†Refers to maximum plant height.
Seed-dispersal modes were defined according to mutually exclusive categories describing the following life-history traits: (1) vertebrate-dispersed species: those producing diaspores attached to a fleshy pulp, aril, or other features typically associated with vertebrate dispersal agents (endozoochorous species sensu van Roosmalen, 1985); and (2) abiotically dispersed species: those presenting winged seeds, plumes, or other wind-dispersal devices that slow the rate of seed fall; or those dispersed entirely by free fall or propelled explosively by a fruit that opens suddenly or by a trip lever. This last category includes the secondarily ant-dispersed species of Euphorbiaceae (elaiosome-bearing seeds, e.g. Manihot and Jatropha), as they are primarily autochoric species (Webster, 1994; Machado et al., 1997).

Vertebrate-dispersed species were further classified in relation to fruit size according to the following size classes: (1) fruits smaller than 0·6 cm in length; (2) fruits sizing of 0·6–1·5 cm; (3) fruits sizing of 1·6–3·0 cm; and (4) fruits larger than 3·0 cm in length. We use these categories because there is a great deal of intra-specific variation in fruit size within these size classes for a large proportion of the woody plant species in the Atlantic forest and caatinga (Barroso et al., 1999; Silva & Tabarelli, 2000; M. Tabarelli, unpublished data). For convenience, we simply refer to fruits within these increasingly larger size classes as small, medium-sized, large and very large. Fruits of vertebrate-dispersed species were also classified as: (1) berry, monocarp or pseudo-fruit (fleshy fruits); and (2) drupe, pod or capsule (partially sclerocarpic fruits) according to van Roosmalen (1985).

We also grouped the species from the 20 plots within the following categories of annual rainfall: (1) 400 mm (2 plots, 70 spp., 400–454 mm), (2) 500 mm (7 plots, 108 spp., 529–584 mm); and (3) 600 mm (7 plots, 192 spp., 600–694 mm). Species in 300 and 200 mm categories were not included because several taxa had classification limited to generic level. For each plot and precipitation category — the two spatial levels of analysis — we thus obtained the percentage of trees and shrubs within each category of dispersal mode, fruit size and type. Distribution of abiotically and vertebrate-dispersed species in terms of rainfall gradient and in space (i.e. number of plots) was analysed. For each species, we calculated the difference between maximum and minimum rainfall at which each species was recorded, and the number of plots each species was recorded.

In order to examine the relationships between seed dispersal mode, taxonomic composition and annual rainfall, we quantified the number (and proportion) of species within the Myrtaceae in each plot, and in the three categories of rainfall described above (400, 500 and 600 mm categories). Analysis was restricted to Myrtaceae because other families and genera had a small number of vertebrate-dispersed species recorded, which was incompatible to statistical analysis. We also excluded Cactaceae species from all the analyses because our hypotheses are valid for forest tree and shrubs of tropical dry forests.

Statistical analysis

We examined the relationship between the percentage of species within modes of seed dispersal, fruit size and fruit type and average annual rainfall (between-plot differences) using Spearman rank correlation coefficients (Sokal & Rohlf, 1995). Differences in the percentage of species among categories of average annual rainfall (between-precipitation category differences) were examined by G-test (Sokal & Rohlf, 1995). Differences between abiotically and vertebrate-dispersed species in terms of distribution across the rainfall gradient and space were analysed by Mann–Whitney tests (Sokal & Rohlf, 1995). We also used a Spearman rank correlation coefficient to examine the relationship between the percentage of Myrtaceae among the vertebrate-dispersed species and average annual rainfall (between-plot differences). A G-test was used to analyse the distribution of Myrtaceae species within the categories of annual rainfall.
rainfall (between-precipitation category differences). All analyses were carried out using the SYSTAT 6.0 software package (Wilkinson, 1996).

In all the analyses, we compared plots from different sites and we were unable to control for some differences in the surrounding vegetation matrix, plot size, sample size and sampling criteria, which could introduce some bias in our results. However, such differences are expected to explain any trend detected only if differences in the surrounding matrix, plot size, sample size and sampling criteria varied linearly across the rainfall gradient, which was decidedly not the case. We, therefore, assume that between-plots and -precipitation categories differences regarding dispersal mode and fruit morphology (i.e. size and type) are primarily associated with rainfall rather than particular differences between sites, plot size or methods. If this is true, then the trends uncovered should share similar causal relationships at both spatial scales.

Results

Seed dispersal, fruit size and type vs. annual rainfall

In the 20 plots, 107 vertebrate-dispersed species and 162 abiotically dispersed species were recorded (39.7% and 60.3%, respectively). The percentage of vertebrate-dispersed species ranged from 11% in a 246-mm year\(^{-1}\) plot to 53.6% in a 663-mm year\(^{-1}\) plot and a positive correlation was found between average annual rainfall and the percentage of vertebrate-dispersed species (Fig. 2; \(r_s = 0.66, p < 0.01, N = 20\)). In addition, the percentage of vertebrate-dispersed species ranged from 21.4% in the 400 mm category to 40.7% in the 600 mm category (Fig. 3), which represented a significant increase of ca. 90% along the gradient of annual rainfall (\(G = 8.2, \text{df} = 3, p = 0.01\)).

Among the vertebrate-dispersed species middle-sized and very large fruits prevailed (46.7% and 25.2%, respectively). Significant correlation between fruit size and rainfall was not found at any spatial level (i.e. between-plots and -precipitation categories), although the percentage of small fruit species decreased from 20% in 400 mm to 13.2% in 600 mm category, and large fruit species increased from 6.6% to 14.5%, respectively (Fig. 4). Berry and drupe were the most common fruit types among vertebrate-dispersed species (32.7% and 28.9%, respectively), followed by capsule (21.5%), pod (8.4%), and others (i.e. monocarp plus pseudo-fruit, 8.4%).

![Figure 2](image_url)

**Figure 2.** Relationship between percentage of vertebrate-dispersed species and average annual rainfall in the caatinga vegetation of Brazil (\(N = 269\)).
the plot level, the percentage of berry-fruited species was positively correlated with annual rainfall, whereas the percentage of drupe-fruited species was negatively correlated (Fig. 5, $r_s = 0.73$, $p < 0.001$, $N = 20$; $r_s = -0.55$, $p = 0.01$, $N = 20$). Berry- and drupe-fruited species prevailed among precipitation categories, but in contrast to
what we found at the plot level no significant trends were observed from 400 to
600 mm category (Fig. 6).

Abiotically dispersed species had wider distribution across the rainfall gradient and
in space compared to vertebrate-dispersed species ($U = 6946.5, p = 0.01; U = 7222.1,
$ = 0.02$). Among abiotically dispersed species, 27.4% occurred along portions of the
rainfall gradient with more than 100 mm of variation and 44% were recorded in at
least two plots. In contrast, 85% of vertebrate-dispersed species were distributed along

**Figure 5.** Relationships between percentage of berry- and drupe-fruited species, and average
annual rainfall in the caatinga vegetation of Brazil.

**Figure 6.** Percentage of species with different fruit type within categories of average annual
rainfall in the caatinga vegetation of Brazil. Numbers above each vertical bar represent the
number of species examined in each category of annual rainfall.
portions of the rainfall gradient with less than 100 mm of variation and 73.8% were restricted to a single plot.

**Taxonomic composition**

Among the 107 vertebrate-dispersed species recorded, Myrtaceae was the richest family (14 spp., 13.1% of all sampled species within this dispersal mode) followed by Boraginaceae (8 spp.), Erythroxylaceae (7), Euphorbiaceae (6), Solanaceae (5), and Leguminosae (5). The most speciose genera within the vertebrate-dispersed flora were Cordia (7 spp.), Erythroxylum (7), Eugenia (6), Sapium (6) and Solanum (5). The percentage of vertebrate-dispersed species belonging to Myrtaceae was not correlated with annual rainfall at plot level. However, Myrtaceae had no species at plots receiving <500 mm of annual rainfall, and only one species (2.5%) in 500 mm category, whereas it represented 16.7% (13 spp.) of all vertebrate-dispersed species in the 600 mm category (the highest category of annual rainfall). These numbers represented a significant increase of Myrtaceae species along the rainfall gradient ($G = 28.8; \text{df} = 2; p < 0.0001$). Despite the relative importance of Myrtaceae species, the positive correlation between the percentage of vertebrate-dispersed species and annual rainfall remained significant at any spatial level after they were excluded from the analyses ($r_s = 0.58; p < 0.006, N = 20$).

**Discussion**

**Seed dispersal, fruit size and type vs. annual rainfall**

The data analysed here were gathered from the literature and collected by different methods. These differences may have introduced some bias in our results, mainly in between-plot differences, which should be analysed with caution. However, uncontrolled variables would not explain the major trends found in this study. Our study showed a high percentage of abiotic dispersal among tree and shrub species throughout the caatinga. This finding is similar to those of more local studies by Machado et al. (1997), Barbosa et al. (2001) and Grize et al. (2001), which reported a predominance of abiotically dispersed species (anemochoric plus autochoric species) in the caatinga vegetation. Compared to the surrounding Atlantic forest, where vertebrate-dispersed species can reach over 90% of all tree and shrub species (Tabarelli & Peres, 2002), seed dispersal mediated by vertebrates was much less common in the caatinga vegetation.

More notably, we found a gradual increase in the percentage of vertebrate-dispersed species and of berry species associated with an increase in average annual rainfall. Comparing the driest vs. the moistest plot, the percentage of vertebrate-dispersed species was increased by six-fold. Among woody floras from rainfall categories, the relative importance of vertebrate-dispersed species was increased by a half over a range of 300 mm. Similarly, Barbosa et al. (2001) analysed plant collections from regional herbarium and reported that the caatinga vegetation in the Agreste region ($>600$ mm year$^{-1}$, Lins, 1989) had a higher richness of vertebrate-dispersed trees and shrubs than in the Sertao region ($<600$ mm year$^{-1}$), respectively, 33% and 15%.

In the caatinga region, reduction in annual rainfall is positively associated with both the duration and year-to-year variation of the rainy season (Sampaio, 1995). In addition, it is also associated with higher local place-to-place variation in rainfall and with higher frequencies of drought periods (IBGE, 1985). Droughts are usually defined as those years in which the annual rainfall is less than 30% of the long-term average (Sampaio, 1995). Low-rainfall areas within the caatinga region, or those areas where rainfall is erratic, would not be the best habitats for those trees and shrubs species that produce and have to maintain small or large fleshy fruits.
(i.e. moist-but-soft-skinned fruit) due to the long dry season and high evaporation/insolation during the moist season.

In fact, water appears to be important for producing fleshy fruits, since several studies in tropical forests (dry and moist) and savannas showed a positive relationship between fleshy fruits produced by trees and shrubs and fruiting in the rainy season (Janzen, 1967; Lieberman, 1982; Gottsberger & Silberbauer-Gottsberger, 1983; Rathcke & Lacey, 1985; Mantovani & Martens, 1988; Morellato et al., 1989; Bullock, 1995; Medina, 1995; Machado et al., 1997; Oliveira, 1998; Ribeiro & Tabarelli, 2002). This is also true for caatinga vegetation, in which Machado et al. (1997) and Griz & Machado (2001) registered a concentration of fleshy-fruit trees and shrubs fruiting during the rainy season. According to Bullock (1995), not only is rainfall correlated with the frequency of zoochory in trees, but also sites that are drier and moister because of local topography, support lower and higher frequencies of zoohchorous tree species, respectively.

We should also mention that local and regional frequency of vertebrate-dispersed species may be influenced by both the behaviour and abundance of vertebrate seed dispersers (see Machado et al., 1997, Griz & Machado, 2001). Whatever the cause or causes (still quite uncertain), our results provide strong support for the trends emerging from literature, of a gradual and predictable change in seed dispersal modes and fruit morphology in neotropical forests across rainfall gradients within regions of strong seasonality.

Annual rainfall, taxonomic composition, and vertebrate-dispersed species

Myrtaceae species accounted for 12.6% of all vertebrate-dispersed species sampled in the 20 caatinga plots analysed in this study and we found a strong increase in the occurrence of Myrtaceae species along the annual rainfall gradient. Our results also suggested a similar pattern for vertebrate-dispersed species within Annonaceae, Rutaceae and Leguminosae (sensu lato) families, but we did not have enough data to properly test it. Myrtaceae species are usually shrub to small evergreen trees (<10 cm DBH) that grow up in lower strata (shade-tolerant species), and more rarely reach the vegetation upper strata (Tabarelli et al., 1999). Species of this family usually produce berries >1.5 cm length, and the pulp contains over 80% of water (Moermond & Denslow, 1985). Thus, Myrtaceae species appear to explain part of the trends we found regarding the frequency of both seed dispersal mode and fruit type across rainfall gradients in the caatinga vegetation.

Myrtaceae is the most speciose woody plant family in the Brazilian Atlantic forest (Mori et al., 1983, Lima & Guedes-Bruni, 1997), which is a species diversity centre for this family in South America (Landrum, 1981, 1986; Gentry, 1982b). For brejos — the Atlantic forest ‘islands’ within the arid caatinga region (Andrade-Lima, 1982) — incomplete information reveals at least 35 Myrtaceae species (Sales et al., 1998). In contrast to what is observed in the Atlantic forest, Myrtaceae is poorly represented in caatinga vegetation (Rodal & Melo, 1999). Thirteen (92.9%), from the 14 Myrtaceae species that we analysed in this study, were restricted to 1–2 plots of caatinga in the moistest portion of the rainfall gradient (i.e. <600 mm year\(^{-1}\)), whereas they are frequent in the Atlantic forest plots. Similarly, vertebrate-dispersed tree species of Leguminosae analysed in this study (species of Hymenaea and Swartzia) were only recorded in the caatinga sites, which received more than 500 mm year\(^{-1}\) of rainfall and have also been widely recorded in the Atlantic forest (Siqueira, 1994; Lorenzi, 1998; Sales et al., 1998).

These considerations lead us to hypothesize that the frequency of vertebrate-dispersed species along rainfall gradients in the caatinga vegetation depends partially of the species from surrounding Atlantic forest, such as Myrtaceae and Leguminosae species. More specifically, several vertebrate-dispersed species may have suitable
habitats in *brejos* and in the continuous Atlantic forest, from which they colonize the surrounding or the moistest sites covered by caatinga vegetation. This hypothesis is also supported by the fact that vertebrate-dispersed species had narrower distribution on both the rainfall gradient and in space when compared to abiotically dispersed species. Further studies should investigate species distribution within families or genus, which are notable for having several fruit types and dispersal modes, in order to improve the understanding about the contribution of the Atlantic forest for vertebrate seed dispersal in caatinga. Our results not only confirm the relationships between seed dispersal, fruit morphology and rainfall in very seasonal forests, but they show the utility of studying plant community organization in relation to environmental gradients.

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References


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