Abiotic and vertebrate seed dispersal in the Brazilian Atlantic forest: implications for forest regeneration

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Abstract

This study documents the proportion of woody plant species having different modes of seed dispersal, and classes of seed and fruit size at 16 Atlantic montane forest plots of southeastern Brazil (23–24°S). These plots represent six chronosequences (from 5-year-old to old-growth forest) of forest regeneration following small-scale shifting agriculture. Our results indicate that there is a gradual but predictable increase in the number of woody plant species relying on vertebrate-mediated seed dispersal in increasingly older plots. Moreover, the percentage of plant species bearing small seeds and fruits (<0.6 cm in length) was more than halved from earlier to older forest plots, while the percentage of plant species producing middle-sized seeds and fruits at least doubled. Plant species belonging to the Melastomataceae, Myrsinaceae, Rubiaceae and Flacourtiaceae comprised a large proportion of the small-seeded and fruit species (33–53%), and largely occurred in early successional forest plots (5–30 years old). In contrast, species belonging to the Myrtaceae and Lauraceae represented most of the species (51–72%) bearing medium-sized seeds and fruits (0.6–1.5 cm in length), and occurred primarily in the old-growth forests. Shifts in the relative importance of dispersal strategies during the regeneration process of Atlantic montane forest, as well as in diaspore size appear to be related to the balance between early successional and shade-tolerant species associated with particular life forms and plant families. Finally, we discuss the relationships between the species richness of Myrtaceae and Lauraceae trees, seed dispersal by medium to large vertebrates, and possible regeneration scenarios for the Atlantic forest. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Brazilian Atlantic forest; Forest regeneration; Frugivorous vertebrates; Seed dispersal; Species richness

1. Introduction

Animal-mediated seed dispersal is usually the most important mechanism of propagule dissemination in tropical forests where a vast proportion of the woody plant species are dispersed by vertebrates rather than wind, water, or other abiotic processes (e.g. van Roosmalen, 1985; Charles-Dominique, 1993). Although seeds of most tropical forest plants are dispersed by vertebrates, the relative importance of different dispersal mechanisms is considerably different between neotropical and paleotropical forests (Howe and Smallwood, 1982; Richards, 1996), evergreen and deciduous forests (Gentry, 1995), and early successional and mature forests (Brown and Lugo, 1990). In general, the proportion of vertebrate-dispersed species is greater in wet, late-successional or mature forests (Howe and Smallwood, 1982). This is particularly the case of species-rich neotropical forests, where as many as 87–90% of the woody plant species in a local flora produces diaspores that are gut-dispersed by vertebrates (Peres and van Roosmalen, 2002). Previous studies in Amazonian forests (Uhl, 1987; Nepstad et al., 1996; Vieira et al., 1996) and the Brazilian Atlantic forest (Tabarelli and Mantovani, 1999a) suggest that tree and shrubs species dispersed by abiotic means are gradually replaced by those dispersed by vertebrates throughout the forest regeneration process. Among the vertebrate-dispersed species, those in early secondary forests producing small fruits and seeds appear to be gradually replaced by those producing medium to large fruits and seeds in increasingly older forests (Howe and Smallwood, 1982; Richards, 1996; Vieira et al., 1996).

This gradual increase in the species richness and abundance of vertebrate-dispersed woody plant species

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from early to late-successional forests reinforces the pantropical notion that forest regeneration processes that are able to preserve most, if not all, plant species in the source flora rely heavily on effective seed dispersal by frugivorous vertebrates (cf. Nepstad et al., 1996; Vieira et al., 1996; Corlett, 1998; Guaricata and Pinard, 1998; Duncan and Chapman, 1999). For example, natural succession in small, degraded forest fragments in Singapore is unlikely to restore the original plant species composition (Corlett and Turner, 1997). Large-seeded forest trees are simply unable to colonise new patches of secondary forests because their large-bodied vertebrate dispersers are now locally extinct. Birds in Indomalayan fragmented forest landscapes typically have gaping widths of 10–15 mm, and are thus too small to ingest whole seeds of most forest fruits. Bird species with larger gaping widths and large mammals capable of dispersing large-seeded fruits are highly vulnerable to selective hunting, fragmentation and habitat loss (Corlett, 1998). Likewise, in northern Thailand, seedling recruitment rates of two vertebrate-dispersed plant species in abandoned agricultural clearings are severely limited by low rates of seed dispersal (Hardwick et al., 1997). In the island of La Réunion, large-seeded (>20 mm) fleshy-fruit species show very low colonisation rates and are missing from young lava flows (Thébaud and Strasberg, 1997), perhaps because of the extremely impoverished frugivore fauna following an alarming number of large-vertebrate extinctions in the last three centuries (Cox et al., 1991). It remains to be seen, however, whether or not large-seeded plants can adjust to the loss of key seed-dispersal services.

The Brazilian Atlantic forest is one of the highest global priorities for conservation (Myers et al., 2000), with only 7% of the original pre-Columbian forest cover of over 1.2x10^6 km^2 still standing (Brown and Brown, 1992; Myers et al., 2000). Most of the remaining forest was retained within private properties (Viana et al., 1997), and continues to be disturbed by a combination of shifting agriculture, logging and wildfires (Oliveira et al., 1994) as well as degradation of small forest fragments (Gascon et al., 2000). Human disturbance typically creates a vegetation mosaic where early and late-successional forests are converted to subsistence and cash crops and later abandoned to natural forest succession (Tabarelli and Mantovani, 1999a). Over large tracts of the remaining Atlantic forest, large-bodied frugivorous vertebrates, such as primates, toucans, cracids, and large cotingas, have been extirpated or significantly reduced in numbers (Almeida et al., 1995; Galetti et al., 1997; Silva and Tabarelli, 2000). It is therefore possible that background rates of vertebrate-mediated seed delivery have been significantly reduced thus delaying, curbing, or precluding forest regeneration so that late-successional forests will never be able to attain the full complement of plant species typical of original old growth forests.

Here we examine the proportion of woody plant species occurring within different modes of seed dispersal, and classes of fruit and seed size within 16 Atlantic montane forest plots (comprising six sites) of southeastern Brazil at different stages of regeneration. These 16 plots represent six chronosequences (ranging from 5-year-old to old-growth forest) of forest regeneration following clear-cuts in shifting agriculture plots. We examine three questions on the relationship between seed dispersal and forest regeneration: (1) are wind and water-dispersed species replaced by those dispersed by vertebrates in the course of the forest regeneration process? (2) are small-seeded species gradually replaced by large-seeded counterparts? and (3) are small-fruit species gradually replaced by those producing large fruits? The relationships between seed dispersal mode, regeneration strategy, plant life form, and taxonomic groupings are also discussed. Finally, we discuss the relationships between the species richness of Myrtaceae and Lauraceae trees, seed dispersal by medium to large vertebrates, and possible regeneration scenarios for old secondary stands of the Brazilian Atlantic forest regarding woody plant species richness and composition.

2. Methods

2.1. Forest chronosequences

We selected a set of published plant inventories conducted in 16 Atlantic forest plots of varying regeneration stages or ages, located at six different sites (Fig. 1). All sites are located between 1 and 100 km inland from the coastline and along the slopes of the Serra do Mar knifefridge within three neighbouring states of southeastern Brazil: Rio de Janeiro, São Paulo, and Paraná (23–24° S; Table 1). According to the Köppen’s classification system, the regional climate is humid-temperate, lacking a demarcated dry season. Mean rainfall at all study sites ranged from 1400 to 2767 mm year^-1, with the wettest and the driest periods of the year in December–March, and July–August, respectively. The predominant soil types at all sites are lithosols and podzols (Radambrasil, 1983). The vegetation is best described as tropical montane rain forest at elevations of 100–1100 m a.s.l., which comprise one of the major Atlantic forest types (submontane and montane categories of Veloso et al., 1991). Detailed descriptions of the plant species composition in these forests can be found elsewhere (Melo and Mantovani, 1994; Guedes-Bruni et al., 1997).

The 16 forest plots considered here were located either within (13 plots in five sites: Cubatão, Intervales, Iporanga, Macaé de Cima, Santa Virgínia) or along the boundaries of protected areas (three plots in one site: Morretes; Table 1), which still harbour large patches of
continuous forest with their typical plant and vertebrate species composition. The smallest of these protected areas—Macaé de Cima Biological Reserve—encompasses 7200 ha of Atlantic montane forest surrounded by 35,000 ha of continuous forest (Lima and Guedes-Bruni, 1997). The largest one—Serra do Mar State Park—protects 360,000 ha of continuous forest, including the Santa Virgínia Reserve (Lima and Capobianco, 1997). These 16 plots represent six chronosequences of forest plots left to regenerate (ranging from 5-year-old to old-growth forest) following slash-and-burn agriculture. These were selected for this analysis based on the best available floristic data and information on past history of land use (Table 2). Prior to floristic surveys, the primary forest at all regenerating forest plots had been clear-felled, burned and used for subsistence crops for 2–10 years, and subsequently abandoned to revert to secondary forest. The plots ranged from 1 to 5 ha in size, according to detailed site descriptions provided by the authors of the different studies which were conducted on the basis of different methods. However, plant sampling criteria used in these studies [from 6 cm
diameter at breast height (DBH) to all woody plants taller than 1 m] were considered to be appropriate to record a representative set of tree and shrub species occurring at each plot.

2.2. Seed dispersal mode

All woody plant species sampled within each plot were classified according to two mutually exclusive modes: (1) vertebrate-dispersed species, or those producing diaspores adhered to a fleshy pulp, aril, or other features typically associated with vertebrate dispersal agents; and (2) species dispersed by abiotic means, or 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 bursts suddenly open (van der Pijl, 1982).

Vertebrate-dispersed species were further classified in relation to seed size according to the following size-classes: (1) seeds smaller than 0.6 cm in length; (2) seeds sizing 0.6–1.5 cm; (3) seeds sizing 1.6–3.0 cm; and (4) seeds larger than 3.0 cm in length. Vertebrate-dispersed species were also classified in relation to fruit size according to the same categories described above. “We use these categories because there is a great deal of intraspecific variation in fruit and seed size within these size classes for a large proportion of the woody plant species in the Atlantic forest (Reitz, 1965; Barroso et al., 1999; Silva and Tabarelli, 2000; M. Tabarelli, unpublished data). Given the nature of the flora in the Atlantic forest, these size-classes are assumed to represent natural categories, although this has never been adequately tested. For convenience, we simply refer to seeds and fruits within these increasingly larger size-classes as small, medium-sized, large and very large.

Classification of plant species according to seed-dispersal mode and seed and fruit size classes was based on (1) our own knowledge of the flora sampled in relation to fruit and seed morphology; (2) detailed accounts of species life history traits available in the literature (e.g., Flora Neotropica, Reitz, 1965; van Roosmalen, 1985; Lorenzi, 1998; Barroso et al., 1999); and (3) inspection of herbarium specimens at the herbaria of Instituto de Botânica de São Paulo, Brazil.

2.3. Plant species composition

In order to examine the relationships between seed dispersal mode (vertebrate vs. abiotic dispersal), seed and fruit size, plant species composition and stage of forest succession, we quantified the number (and proportion) of species within the Melastomataceae, Rubiaceae, Flacourtiaceae, Myrsinaceae, Lauraceae and Myrtaceae in early secondary (5–30 years old) and old-growth forests. These six families were selected because (1) they are widely distributed in the Atlantic montane forest, (2) they often account for over half of the woody plant species richness in plots of this forest, and (3) there are vast records on literature about the natural history of their species (Klein, 1980; Silva and Leitão Filho, 1982; Mori et al., 1983; Lima and Guedes-Bruni, 1997; Tabarelli, 1997; Tabarelli and Mantovani, 1999b).

2.4. Data analysis

We examined the relationship between age of forest plots and the proportion of species with different dispersal modes using Spearman rank correlations (Siegel, 1979). For each site, between-plot differences in the proportion of species in different dispersal modes were examined using log-likelihood ratio ($G$) tests (Sokal and Rohlf, 1995). We used the same procedures to examine the relationship between age of forest plots and the relative species richness of different size classes of fruits and seeds.

In the absence of precise historical records on the old-growth forest plots sampled, these were assumed to be approximately 120 yrs old, given the history of deforestation and forest fragmentation in the region and the minimum amount of time required for complete regeneration of Atlantic montane forests following shifting agriculture (Klein, 1980). $G$-tests were also used to examine differences in the frequency of species occurrence of Melastomataceae, Rubiaceae, Flacourtiaceae,
Myrsinaceae, Lauraceae and Myrtaceae between the early secondary (5–30 years old) and old-growth forests. All analyses were performed using SYSTAT 6.0 (Wilkinson, 1996).

We also applied the percentage of species within these six families in the 16 plots to a detrended correspondence analysis (DCA; sensu Hill and Gauch, 1980), using CANOCO version 3.11.5 (ter Braak, 1987–1992). If the percentage of plant species within these families varied linearly from younger to older forests, plots would be expected to cluster in the DCA primarily according to their age, rather than geographic region, physical proximity, or elevation.

In most of the analyses we compare plots both within and among different sites. At the first spatial scale, between-plot differences are expected to be correlated only with the age of forest plots since sampling method, sampling effort and overall plot size were identical. At the second level of comparisons, 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 age of forest plots which was decidedly not the case. We therefore assume that between-plot differences regarding dispersal mode and percentage of species within categories of seed and fruit size are primarily associated with forest age rather than particular differences between sites, plot size or methods. If this is true than the trends uncovered should share similar causal relationships at both spatial scales.

3. Results

3.1. Abiotic vs. vertebrate seed dispersal

Vertebrate seed dispersal mode prevailed in all 16 forest plots. However, this was highly variable across sites ranging from 52.9% of the species in a 5-year-old plot at Intervales to 98.7% in an old growth plot at Santa Virgínia. There was a strong positive correlation between the age of forest plots and the percentage of vertebrate-dispersed plant species within them ($r_s=0.84$, $n=16$, $P<0.001$; Fig. 2). This correlation remained significant after the four old-growth plots were discarded from the analysis ($r_s=0.78$, $n=12$, $P<0.001$), suggesting that there was a trend throughout different stages of forest succession. At three different sites (Iporanga, Macaé and Santa Virginia) the proportion of vertebrate-dispersed species significantly increased from the youngest to the oldest forest plots ($G$ tests; $P<0.05$ in all possible pairwise comparisons).

3.2. Small vs. medium-sized seeds and fruits

Small ($<0.6$ cm) and medium-seeded (0.6–1.5 cm) plant species prevailed in all forest plots, ranging from 24.6% to 72.2% (small-seeded) and from 14.3 to 59.2% (medium-seeded) of the species sampled (Fig. 3). Large
and very large-seeded species thus represented a relatively small percentage of all the species sampled in the floras of the 16 plots (<25%). We also found a strong negative correlation between the age of forest plots and the percentage of small-seeded plants as it was reduced by three thirds throughout the successional process ($r_s = -0.83$, $n = 16$, $P = 0.0001$). In contrast, the percentage of medium-seeded plant species was positively correlated with the age of forest plots ($r_s = 0.85$, $n = 16$, $P = 0.0001$). Mirroring the pattern shown for seed dispersal mode, these correlations remained highly significant even after old-growth plots were removed from the analyses ($r_s = -0.73$, $n = 12$, $P = 0.006$; $r_s = 0.78$, $n = 12$, $P = 0.002$).

A similar pattern was also found for fruit size, since plant species bearing small to medium-sized fruits prevailed in all forest plots (>60% of all species, Fig. 4). Furthermore, species bearing small-fruits were significantly reduced in numbers from younger to older forest plots ($r_s = -0.76$, $n = 16$, $P = 0.0005$), whereas the percentage of plant species bearing medium-sized fruits was positively correlated with the age of forest plots ($r_s = 0.67$, $n = 16$, $P < 0.004$). In four sites sampled the percentage of woody species bearing either small seeds or fruits was significantly reduced from younger to older forest plots, whereas in three sites the percentage of plant species bearing medium-sized seeds and fruits significantly increased from younger to older plots (Table 3, within-site comparisons).

### 3.3. Plant family composition of forest plots

In the early successional forest plots within the six sites sampled (Cubatão, Santa Virginia, Macaé, Morretes, Iporanga and Intervales), plant species belonging to the Melastomataceae, Rubiaceae, Flacourtiaceae and Myrsinaceae comprised between 25 and 42% of all species dispersed by any vertebrate. Species belonging to these families were far more common in these early successional plots than in old-growth plots ($G = 8.92$; d.f. = 1; $P = 0.003$). On the other hand, species belonging to medium-seeded families such as the Lauraceae and Myrtaceae comprised between 33 and 41% of all vertebrate-dispersed species in the old-growth forests occurring in four sites sampled (Cubatão, Santa Virginia, Macaé de Cima and Morretes). The species richness of these families was therefore significantly higher in old-growth than in early successional forests ($G = 22.9$; d.f. = 1; $P < 0.001$).

### 3.4. Ordination of forest plots

The first two axes of the DCA explained 67.6% of the variance within the species data at the level of families (sum of all eigenvalues = 0.142, $\lambda_1 = 0.075$, $\lambda_2 = 0.017$). The figure of 67.6% of the total variance explained by the first two DCA axes of an unconstrained ordination compares favourably with that of most other neotropical forest plant communities examined to date. The next two axes of the DCA explained only a further 2.9% of the variance in the species data ($\lambda_3 = 0.004$, $\lambda_4 = 0.000$), and were thus discarded.

Most late-successional and old-growth plots clustered together on the second DCA axis irrespective of the location at which they were sampled (Fig. 5). This convergence according to forest age thus provides marked evidence that the frequency of occurrence of Melastomataceae, Rubiaceae, Flacourtiaceae, Myrsinaceae,
Lauraceae and Myrtaceae species varied according to the age of forest plots, rather than their geographic region, proximity or elevation. In particular, this convergence primarily reflects the greater density of Lauraceae and Myrtaceae tree species in late-successional and old-growth plots as opposed to young second-growth which tended to be largely dominated by understory shrub and small trees belonging to the Melastomataceae, Rubiaceae, Myrsinaceae and Flacourtiaceae. One late-successional plot (Iporanga), however, was identified as an outlier somewhat resembling the floristic composition of a younger forest plot sampled in the same region.

4. Discussion

4.1. Shifts in species composition, seed dispersal mode and diaspore size

The data analysed here were gathered from several studies conducted on the basis of different methods and sampling effort, and within plots of different size. It is possible that these differences may have introduced some bias in our results, mainly in the between-site comparisons which should be interpreted with caution. However, it is unlikely that differences in sampling methods and plot size would significantly influence the patterns uncovered as these were the same regardless of whether we compare plots within or between sites. Our results therefore support the notion that there are predictable shifts in species composition and seed dispersal strategies throughout the regeneration process of Atlantic montane forest.

More specifically, increasingly older plots were associated with both a greater proportion of woody plant species relying on animal dispersal agents, and of vertebrate-dispersed species bearing medium-sized seeds and fruits. In contrast, early successional plots were associated with a greater proportion of species dispersed by abiotic means and of vertebrate-dispersed-species bearing small seeds and fruits. Small-fruit species represented between 24.4 and 58.8% of the species in early

Fig. 4. Relationship between the age of 16 montane Atlantic forest plots and the percentage of woody plant species in different classes of fruit size.

Table 3
Percentage of vertebrate-dispersed woody species in different seed and fruit size-classes in the 16 plots sampled

<table>
<thead>
<tr>
<th>Site</th>
<th>Age of forest plots (year)</th>
<th>Percentage of plant speciesa</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Seeds &lt;0.6 mm</td>
<td>Seeds 0.6–1.5 cm</td>
</tr>
<tr>
<td>Cubatão</td>
<td>15, old growth</td>
<td>44, 28.5*</td>
</tr>
<tr>
<td>Intervales</td>
<td>5, 13, 18</td>
<td>71.4, 52.6, 54.5</td>
</tr>
<tr>
<td>Iporanga</td>
<td>5, 15, 50</td>
<td>72.2, 60.6, 40.5*</td>
</tr>
<tr>
<td>Macaé de Cima</td>
<td>30, old growth</td>
<td>46.6, 44.5</td>
</tr>
<tr>
<td>Morretes</td>
<td>13, 15, old growth</td>
<td>58.8, 54.5, 35.1*</td>
</tr>
<tr>
<td>Santa Virginia</td>
<td>18, 40, old growth</td>
<td>65.1, 43.4, 24.6*</td>
</tr>
</tbody>
</table>

* G-test pairwise comparisons, P < 0.05.

a Ordered from the youngest to the oldest forest plot.
secondary forests (5–30-year-old) and between 8.7 and 23.3% of the species in the old-growth forests. In the Atlantic montane forest, the most species-rich plant families associated with small seeds and fruits are the Melastomataceae, Rubiaceae, Flacourtiaceae and Myrsinaceae (Reitz, 1965; Silva and Tabarelli, 2000). These families occurred primarily within early secondary forests. Most of these species are represented by large shrubs or small trees (DBH < 10 cm) and are usually classified as pioneer or early successional species (cf. Klein, 1980; Denslow et al., 1990; Baider et al., 2001). These families typically produce sugar-rich berries or drupes smaller than 5 mm in diameter and the seeds of which are primarily dispersed by small frugivores (Moermond and Denslow, 1985; Dalling and Wirth, 1998).

In contrast, species belonging to the Myrtaceae and Lauraceae comprised a large proportion of the flora bearing medium-sized seeds and fruits in the survey sites, including 33 and 41% of all vertebrate-dispersed species in the four old-growth plots. The most species-rich genera in the forests surveyed—Eugenia, Myrcia, Marlierea, Ocotea, Nectandra and Cryptocarya—are all shade-tolerant trees, even in early secondary forests (Vattimo, 1979; Tabarelli, 1997). However, the greatest levels of species richness for these genera are found within old-growth forests (Klein, 1980; Silva and Leitão Filho, 1982; Pessoa et al., 1997; Tabarelli and Mantovani, 1999a). For example, in the Morretes site we recorded one, three, and 16 species of Myrtaceae in increasingly older forests (13, 25-year-old and old-growth forest) accounting for 4, 7, and 21% of the species sampled, respectively. At the Santa Virginia Reserve this family represented between 8.9 and 27% of the species sampled in a 18-year-old and an old-growth forest, respectively.

We therefore hypothesise that shifts in the relative importance of dispersal strategies (vertebrate vs. abiotic) during the regeneration process of Atlantic montane forest, as well as in diaspore size (small vs. medium-sized seeds and fruits) are related to the balance between early successional and shade-tolerant species associated with specific life forms (large shrubs vs. trees) and the frequency of species within particular plant families (Melastomataceae, Rubiaceae, Flacourtiaceae and Myrsinaceae vs. Lauraceae and Myrtaceae).

In the Atlantic forest and elsewhere in the neotropics, fruits of Melastomataceae, Rubiaceae, Flacourtiaceae and Myrsinaceae are usually consumed by small passerines such as manakins and tangaras (Pipra, Tachyphonus, Thraupis; Moermond and Denslow, 1985; Stiles and Rosselli, 1993; Sick, 1997, Loiselle and Blake, 1999; Develey and Peres, 2000). For example, at least seven tanager species are known to eat fruits of 

\[
\text{Leandra barbinervis}, \text{Leandra levigata} \text{ and } \text{Miconia rigidiacaulis} \text{ (Melastomataceae species) in southern Atlantic montane forest (Rodrigues, 1995).} 
\]

In contrast, fleshy fruits of Myrtaceae and Lauraceae trees in the montane Atlantic forest are usually consumed by howler monkeys (Alouatta fusca) and woolly spider monkeys (Brachyteles arachnoides), cootingas (Procnias, Tijuca), toucans (Ramphastos), aracaris (Pteroglossus, Baillonius) and cracids (Penelope, Pipile; Petroni, 1993; Galetti, 1995; Galetti and Pizo, 1996; Höfling and Camargo, 1996; Sick, 1997). For example, woolly spider monkeys, the largest neotropical primates, have been recorded feeding on fruits of at least 14 species of Myrtaceae in a montane forest reserve of southeast Brazil, and seed passage over long retention times through their digestive tract effectively increased germination rates of at least four Myrtaceae species (Moraes, 1992).

Studies in other neotropical forests also suggest that seeds of Myrtaceae and Lauraceae trees are primarily dispersed by medium to large-bodied arboreal frugivores (i.e. primates and large-gaped birds). In French Guiana and Surinam, seeds of Eugenia and Campnosia trees, two species-rich Myrtaceae genera, are primarily dispersed by tamarins, capuchins, howlers and spider monkeys (van Roosmalen, 1985). Likewise, Myrtaceae seeds are frequently ingested by primates ranging in size from tamarins to woolly monkeys throughout lowland Amazonia (Terborgh, 1983; Peres, 1993, 1994). In Mesoamerican forests, quetzals, toucans and bellbirds are the main dispersers of some 40 tree species of Lauraceae (Moermond and Denslow, 1985;
In this study we did not quantify rates of seed removal for the Myrtaceae and Lauraceae by different animal species, or determine how seed dispersal might affect plant recruitment at both local and regional scale. However, if we accept that (1) seeds of Myrtaceae and Lauraceae trees are primarily dispersed by mid-sized to large frugivores and (2) some of these species could face severe recruitment bottlenecks in the absence of seed dispersal services (Wenny and Levey, 1998; Silva and Tabarelli, 2000), then it becomes imperative to examine the fabric of plant–animal interactions mediating the regeneration ecology of the Brazilian Atlantic forest since these two families contribute with a large proportion of the tree species richness throughout this region (Klein, 1980; Gentry, 1982; Mori et al., 1983; Leitão Filho, 1992; Tabarelli, 1997).

The remaining Brazilian Atlantic forest cover is largely represented by small forest fragments surrounded by a hostile matrix of crops and pastures (Brown and Brown, 1992; Coimbra-Filho and Câmara, 1996; Ranta et al., 1998; Tabarelli et al., 1999). For example, the remaining forest cover in the state of Pernambuco consists of over 20,000 fragments, 48% of which are smaller than 10 ha and 85% are smaller than 50 ha (Ranta et al., 1998). Likewise, over 99% of the 100,000 forest fragments in the State of Rio de Janeiro are smaller than 500 ha (Gascon et al., 2000). Indeed several regions of the Atlantic forest are best described as huge archipelagos of small forest remnants in contrast to the sites of continuous tracts of montane Atlantic forest. In these archipelagos, regenerating and mature forest remnants are vulnerable to continuing disturbance since most of them occur within private properties (Viana et al., 1997) and are subjected to shifting agriculture, selective logging and wildfires that have maintained a successional mosaic, particularly in the last 300 years (Andrade-Lima, 1970; Brown and Brown, 1992; Coimbra-Filho and Câmara, 1996; Tabarelli and Mantovani, 1999a). This means that much of the Atlantic forest regeneration is expected to occur after remnants are partially or totally converted into agricultural land and subsequently abandoned to revert to secondary forest.

Unfortunately, local extinction of large vertebrates by habitat fragmentation, habitat loss and overhunting is an ongoing process over much of the remaining Atlantic forest (Almeida et al., 1995; Galetti et al., 1997; Cianciello, 1999; Cullen et al., 2000). In many cases, local extinction of large-bodied vertebrates are a result of both habitat fragmentation and subsistence hunting because small fragments accommodate small populations, are more accessible to hunters, and cannot be easily recolonised from surrounding source populations exposed to low levels of hunting pressure (Robinson, 1996; Silva and Tabarelli, 2000; Peres, 2001). Most of the Atlantic forest vertebrate species that are vulnerable to local extinction within fragments are large-bodied or relatively specialised frugivores (e.g. primates, cracids, cotingas, and toucans), whose seed dispersal services are often associated with a large proportion of medium to large-seeded plant species (e.g. Myrtaceae, Lauraceae).

The composition of the seed disperser fauna appear to be one of the major filters for the seedling recruitment in successional forest landscapes since effective dispersal agents can greatly enhance successful colonisation of new secondary forest patches (Corlett and Turner, 1997; Duncan and Chapman, 1999). Previous studies in the old colonisation frontier of eastern Brazilian Amazonia have demonstrated that forest regeneration following cattle ranching and shifting agriculture can be restricted by the low availability of forest tree seeds (Uhl, 1987; Vieira et al., 1996). In the Paragominas region, trees with the highest establishment probability in abandoned pastures are those bearing seeds smaller than 0.18 g which are carried by small birds and bats (Nepstad et al., 1996). In a comparison between rare and abundant tree species recorded in a successional Amazonian forest mosaic, Vieira et al. (1996) found that trees classified as rare usually had seeds larger than 10 g. Similar dispersal-limitation scenarios have been proposed for other fragmented tropical forest regions where assemblages of large frugivorous vertebrates in small fragments appear to represent nested subsets of the regional species pool still retained by large fragments or remaining expanses of continuous forest (e.g. Kattan and Alvarez-López, 1996; Restrepo et al., 1997; Warbuton, 1997; Chapman and Oderdonk, 1998).

In light of the present state of most the Atlantic forest, our results should prompt additional studies on the extent to which: (1) seedling recruitment in the Myrtaceae and Lauraceae species is limited by a lack of effective seed dispersal services at both local and regional scales; (2) forest regeneration relies on seed delivery from adjacent forest patches and mediated by medium to large vertebrates; and (3) the increasingly fragmented Brazilian Atlantic forest faces widespread dispersal-limitation scenarios. As a working hypothesis to be tested in further studies we conjecture that the species richness of woody plants in old secondary forests could eventually be reduced by as much as one half because of seed delivery and plant recruitment failures in Myrtaceae and Lauraceae species resulting from the local extirpation of medium to large vertebrates in highly fragmented portions of the Brazilian Atlantic forest.

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