

Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeastern Brazil

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Abstract

Habitat fragmentation is a major cause of biodiversity erosion in tropical forests. The Brazilian Atlantic forest has both high species richness and a long history of anthropogenic disturbance, beginning with colonial agriculture in the sixteenth century. Here we examine the species composition and guild structure of woody plants within five montane Atlantic forest fragments of the Tiet River basin, State of São Paulo, southeastern Brazil, ranging from 5 to 7900 ha in area. We found a negative relationship between fragment size and the relative importance of tree and shrub species that (1) depend on abiotic modes of seed dispersal, (2) are shade-intolerant, and (3) occupy the forest canopy. As fragment size decreased, there was a marked rise in the relative importance of ruderal species, primarily in the Compositae, Euphorbiaceae, Solanaceae, and Leguminosae. There also was a 9% average decline in smaller fragments in relative importance of Myrtaceae, Lauraceae, Sapotaceae, and Rubiaceae, which are the main sources of fleshy fruits for vertebrate frugivores in these forests. Our results suggest that predictable shifts in plant guild structure occur as tropical forest fragments are reduced in size, and that small fragments may become dominated by edges and the surrounding habitat matrix. We suggest that small forest fragments will be unlikely to preserve intact plant and animal assemblages of Brazil's Atlantic coastal forest © 1999 Elsevier Science Ltd. All rights reserved.

Keywords: Atlantic forest; Brazil; Edge effects; Habitat fragmentation; Guild composition; Ruderal species

1. Introduction

Forest fragmentation causes many physical and biological changes as a result of habitat loss and insularization (Lovejoy et al., 1986; Laurance, 1990). As forest landscapes become increasingly fragmented, populations of forest species are reduced, dispersal and migration patterns are interrupted, ecosystem inputs and outputs are altered, and previously isolated core habitats become exposed to external conditions, all of which result in a progressive erosion of biological diversity (Terborgh and Winter, 1980; Tilman et al., 1994). The creation of abrupt forest edges exposed to open habitats can severely modify local microclimatic conditions, increase tree mortality, and promote the establishment of non-forest species (Lovejoy et al., 1986; Kapos, 1989; Laurance et al., 1998a). Predictable shifts in the abundance and composition of plant species should also occur, in large part because of greater recruitment or

lower mortality of light-dependent gap specialists along forest edges (Murcia, 1995; Laurance et al., 1998b).

Many consequences of forest fragmentation may have prolonged lag effects and require a sufficient “relaxation” period, with communities passing through a series of transitional states before final equilibrium conditions are reached (Simberloff, 1976; Tilman et al., 1994; Terborgh et al., 1997). Responses to insularization and habitat loss are thus best assessed in older fragments that have had adequate time to equilibrate (cf. Turner et al., 1996; Kellman et al., 1997). The Brazilian Atlantic forest contains mainly older fragments (> 50 years) and has one of the highest levels of plant and animal endemism of any continental tropical forest (Klein, 1980; Prance, 1982a,b; Brown, 1987; Leitão Filho, 1994; Thomas et al., 1998). Of 127 woody species described for this region in the *Flora Neotropica* monographs, 68 (56%) are endemic (Mori et al., 1981), including 39 species in the Chrysobalanaceae alone (Prance, 1987). In addition to a large number of endemic plants, the Atlantic forest exhibits remarkably high plant diversity which may rival or exceed that of Amazonian forests

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(Silva and Leitão Filho, 1982; Mori et al., 1983; Martins, 1989; Peixoto and Gentry, 1990; Joly et al., 1991; Brown and Brown, 1992; Leitão Filho, 1994).

Following a history of severe and repeated anthropogenic disturbance since the sixteenth century, the Atlantic forest has been reduced to several thousand fragments accounting for only 8% of its pre-Columbian extent, which once encompassed some 12% of the Brazilian territory (SOS Mata Atlântica and INPE, 1993). Although this relentless fragmentation process has been curbed in recent decades, it has by no means been halted. For example, some 11% of the surviving Atlantic forest cover was lost between 1985 and 1990, leaving only 285,000 ha of forest remaining (SOS Mata Atlântica and INPE, 1993). While alarming from a conservation perspective, this intensely fragmented landscape with both old and new isolates provides an excellent opportunity for fragmentation studies (Brown and Brown, 1992; Viana and Tabanez, 1995; Tabarelli and Mantovani, 1997b).

This study evaluates the effects of habitat fragmentation on the structure and composition of woody plant guilds in Atlantic forest fragments that vary considerably in size (5–7900 ha). Guild structure is defined in terms of functional groups that relate to seed-dispersal mode, regeneration requirements, and height of mature individuals in the forest (*sensu* Giller, 1984). In particular, we determine whether and how the composition of different plant guilds varies with fragment size. We also consider the long-term viability of fragments remaining in the Brazilian Atlantic forest.

2. Methods

2.1. The forest fragments

This study examines the plant communities in five fairly well studied Atlantic montane forest fragments of the Atlantic Plateau within the Tietê River basin, State of São Paulo, southeastern Brazil. The fragments are located on the outskirts or just outside the urban perimeter of the city of São Paulo, ca. 100 km inland from the Atlantic coast (Fig. 1), at 700–850 m elevation (Table 1). All five fragments are relatively old (isolated for > 50 years) and range from 5 to 7900 ha. They have comparable histories and with one exception have been set aside as protected areas for periods of 50–100 years (Vuono, 1985; Gandolfi et al., 1995).

Predominant soil types in the study sites are latosols and podzols (Radambrasil, 1983), and the regional climate is humid-temperate lacking a demarcated dry season, according to Koeppen's classification (Gomes, 1992). Mean rainfall throughout this area is ca. 1400 mm year⁻¹, with the wettest and driest periods of the year between December–March and July–August,

respectively (São Paulo, 1972). The primary vegetation in this region is best classified as tropical montane rain forest (Whitmore, 1990), considered one of the major Atlantic forest formations [Veloso et al., 1991; see Baitello et al. (1992) and Rossi (1994) for descriptions of woody species].

The five fragments were selected because they had the best available floristic data for forests in the Tietê River basin (Baitello and Aguiar 1982; Vuono 1985; Baitello et al., 1992; Gomes, 1992; Aragaki and Mantovani, 1993; Knobel, 1995; Rossi, 1994; Gandolfi et al., 1995). Three fragments were small (5–14 ha), one was medium-sized (370 ha), and one was large (7900 ha). These fragments have a similar physical environment, are < 100 km apart, and once apparently contained similar plant communities characteristic of this region (Table 1). Although protected for as long as 100 years, illegal hunting of large vertebrates and selective extraction of the edible palm (*Euterpe edulis*) may have occurred occasionally in recent decades. The only exception is the smallest fragment (Cumbica Forest, Guarulhos), which was completely cleared in 1985 and no longer exists. For this site, we relied on detailed data on plant species composition collected prior to destruction (Gandolfi et al., 1995). All fragments were surrounded by urban development for > 50 years prior to their floristic inventories, and are considered spatially independent as they are located at least 5 km apart from one another.

2.2. Woody plant guilds

We compiled available data on woody plant species composition for each fragment on the basis of five comparable floristic inventories conducted by ourselves or other investigators (Vuono, 1985; Aragaki and Mantovani, 1993; Rossi, 1994; Tabarelli, 1994; Gandolfi et al., 1995; see Table 2). All inventories employed quadrats of varying sizes to sample the central portions of fragments or at least 30 m from forest edges. Although the two smallest fragments were exhaustively surveyed, most sampling focused in the central areas, with peripheral areas near edges being deliberately avoided. Woody species within each fragment were classified according to two broad classes each for (1) seed-dispersal mode, (2) typical height of adults, and (3) regeneration niche, based on our personal knowledge and detailed accounts of species life history traits provided by Reitz (1965). Between-fragment differences in the proportion of species in each guild were assessed using *G*-tests for independence, with Williams' correction for sample size (Sokal and Rohlf, 1995). The functional groups (hereafter termed guilds) were defined as follows:

Seed-dispersal: (1) zoochoric species: those producing diaspores attached to a fleshy pulp, aril, or other features typically associated with vertebrate dispersal agents; and (2) species dispersed by abiotic mechanisms,

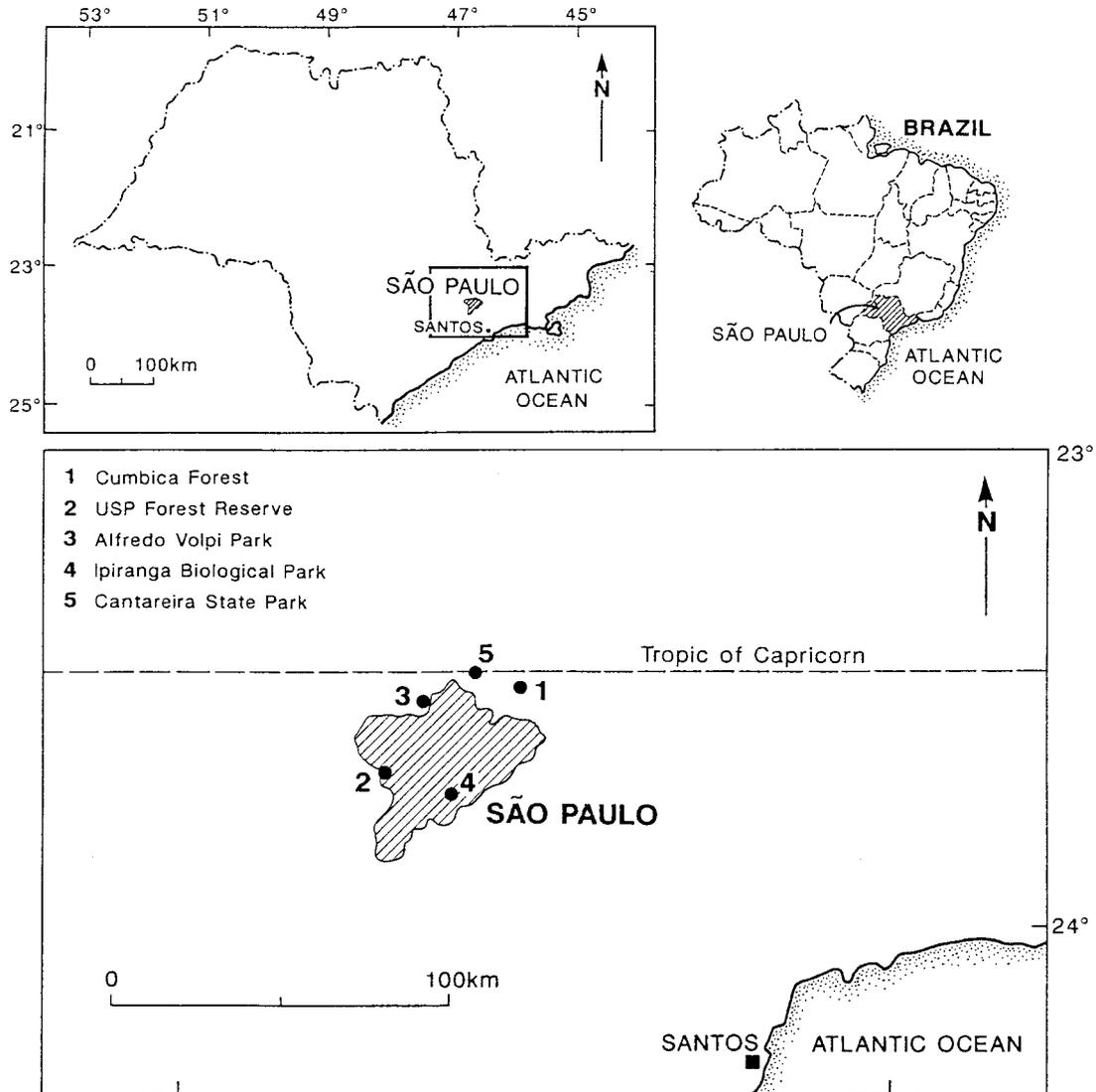


Fig. 1. Location of the five montane Atlantic forest fragments examined in this study.

Table 1
Characteristics of five montane Atlantic forest fragments surveyed in the Tietê River basin, São Paulo State, Brazil

Fragment ^a	Size (ha)	Location (latitude S, longitude W)	Elev. (m)	Rainfall ^b (mm/year)	Source of data
Cumbica Forest	5	23°25', 46°28'	740	1479	Gandolfi et al. (1995)
USP Forest Reserve	10	23°33', 46°43'	745	1428	Rossi (1994)
Alfredo Volpi Park	14	23°35', 46°42'	760	1420	Aragaki and Mantovani (1993)
Ipiranga Biological Park	370	23°39', 46°37'	800	1477	Vuono (1985)
Cantareira State Park	7900	23°22', 46°26'	850	1431	Tabarelli (1994)

^a All fragments were at least 50 years old and surrounded by an urban landscape.

^b Mean annual rainfall over at least 5 years.

which include anemochoric species (those presenting winged seeds, plumes, or other wind-dispersal devices that slow the rate of seed fall) and autochoric species (those dispersed entirely by free fall or propelled explosively by a

fruit that opens suddenly or by a trip-lever; van der Pijl, 1982).

Plant height: (1) understory species: consisting of small trees and shrubs occurring in lower forest strata

Table 2
Sampling effort and criteria used during floristic inventories in five Brazilian Atlantic forest fragments

Forest fragment	Sample size (no. of individuals)	Sampling criteria ^a	No. of woody plant species
Cumbica Forest	12,998	≥ 1.5 m height	158
USP Forest Reserve	> 1000	All woody plants	104
Alfredo Volpi Park	300	≥ 3.2 DBH	94
Ipiranga Biological Park	1008	≥ 4.8 DBH	157 ^b
Cantareira State Park	776	≥ 3.2 DBH	112

^a Refers to the minimum size (height or diameter at breast height) of plants sampled.

^b Some closely related taxa were identified only to genus level, thus underestimating the total number of species sampled.

(< 6 m); and (2) canopy species: occurring in the highest layer of the forest, including emergent trees.

Regeneration niche: (1) shade-tolerant species: those capable of regenerating in the shaded understory of mature forest; and (2) shade-intolerant species: those requiring high light environments provided by treefall gaps and forest edges as viable regeneration sites (Hartshorn, 1978). Some shade-intolerant species were also classified as ruderal species (sensu Grime, 1977) because they are particularly successful in disturbed habitats including forest edges and large canopy gaps.

3. Results

3.1. Effects of fragment size

The five fragments clearly differed in the proportions of species in guilds with varying light requirements at the seedling and sapling stage ($G_{\text{adj}}=24.4$, d.f. = 4,

$P < 0.001$), growth form ($G_{\text{adj}}=17.3$, d.f. = 4, $P=0.001$), and dispersal syndrome ($G_{\text{adj}}=21.5$, d.f. = 4, $P < 0.001$; G -tests for independence). The two smallest fragments had the highest proportions of shade-intolerant and canopy species dispersed by abiotic means (Fig. 2), and these guilds declined in importance as fragment size increased. Compared to the largest fragment, the smallest fragment had significantly more shade-intolerant ($G_{\text{adj}}=16.5$, d.f. = 1, $P < 0.001$) and canopy species ($G_{\text{adj}}=13.2$, d.f. = 1, $P=0.003$), and those relying on wind or ballistic seed dispersal ($G_{\text{adj}}=16.6$, d.f. = 1, $P < 0.001$). The largest fragment had the highest proportions of vertebrate-dispersed, understory, and shade-tolerant species. There also were negative but non-significant correlations between fragment size and the relative proportion of shade-intolerant ($r_s = -0.50$, $P=0.32$), forest canopy ($r_s = -0.70$, $P=0.16$), and abiotically dispersed species ($r_s = -0.90$, $P=0.072$).

3.2. Prevalence of ruderal species

A total of 66 ruderal species were sampled in the five fragments, with the Solanaceae, Compositae, Leguminosae, and Euphorbiaceae containing the most species (Table 3). Over half of all identified ruderal species (52%) were abiotically dispersed, a substantially higher frequency than expected based on the woody plant community in the largest fragment (8%), which presumably best approaches the conditions of continuous forest ($G_{\text{adj}}=40.3$, d.f. = 1, $P < 0.001$). All ruderal plants were forest canopy and shade-intolerant species, and generally thrived best in high-light environments provided by the forest edge and large canopy gaps.

Ruderal species were considerably more prevalent in small fragments and their species richness was negatively correlated with fragment size ($r_s = -0.93$, $P=0.037$;

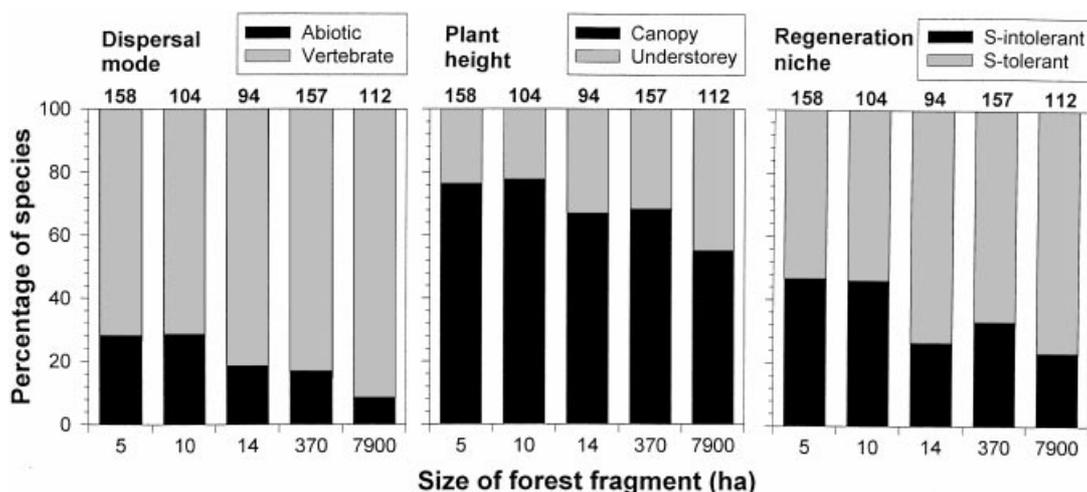


Fig. 2. Plant species richness in five montane Atlantic forest fragments of varying size in relation to their seed dispersal mode, height of mature individuals in the forest, and seedling regeneration niche. Numbers above each vertical bar represent the total number of species examined in each sample.

Table 3
Ruderal woody species occurring at five montane Atlantic forest fragments, State of São Paulo, Brazil

Family and species	Family and species
Anacardiaceae	Leguminosae
<i>Schinus terebinthifolius</i> Raddi	<i>Senna macranthera</i> (Colladon) I. and B.
Cecropiaceae	<i>Senna multijuga</i> (Rich.) I. and B.
<i>Cecropia adenopus</i> Mart.	<i>Senna speciosa</i> (Colladon) I. and B.
<i>Cecropia glazioui</i> Snethl.	Loganiaceae
<i>Cecropia hololeuca</i> Miq.	<i>Strychnos brasiliensis</i> (Spreng.) Mart.
<i>Cecropia pachystachya</i> Trécul	Melastomataceae
Clethraceae	<i>Tibouchina mutabilis</i> Cogn.
<i>Clethra scabra</i> Pers.	<i>Tibouchina pulchra</i> Cogn.
Compositae	<i>Tibouchina sellowiana</i> Cogn.
<i>Baccharis dracunculifolia</i> DC.	Myrsinaceae
<i>Baccharis schultzii</i> Baker	<i>Rapanea ferruginea</i> (Ruiz et Pav.) Mez
<i>Baccharis semiserrata</i> (Steud.) G.M. Barroso	Myrtaceae
<i>Eupatorium vauthierianum</i> A. DC.	<i>Psidium cattleianum</i> Sabine
<i>Gochmatia polymorpha</i> (Less.) Cabr.	Rutaceae
<i>Piptocarpha axillaris</i> Baker	<i>Zanthoxylum rhoifolium</i> Lam.
<i>Piptocarpha macropoda</i> Baker	Solanaceae
<i>Piptocarpha oblonga</i> (Gard.) Baker	<i>Athenaea picta</i> (Mart.) Sendtn.
<i>Piptocarpha sellowii</i> Baker	<i>Capsicum flexuosum</i> Sendtn
<i>Senecio glaziovii</i> Baker	<i>Cestrum schlechtendalii</i> D. Don.
<i>Symphopappus</i> sp.	<i>Cestrum sessiliflorum</i> Schott.
<i>Vernonia diffusa</i> Less	<i>Sessea brasiliensis</i> Tol.
<i>Vernonia discolor</i> Less	<i>Solanum argenteum</i> Dun.
<i>Vernonia polyanthes</i> Less	<i>Solanum bullatum</i> Vell.
Euphorbiaceae	<i>Solanum concinnum</i> Schott. ex Sendtn
<i>Croton celtidifolius</i> Baill.	<i>Solanum erianthum</i> D. Don.
<i>Croton floribundus</i> Spreng.	<i>Solanum granuloso-leprosum</i> Sun.
<i>Croton macrobothrys</i> Baill.	<i>Solanum inaequale</i> Vell.
<i>Sapium klotzchianum</i> (Müel. Arg.) Huber	<i>Solanum robustum</i> Wendl.
<i>Sapium glandulatum</i> (Vell.) Pax.	<i>Solanum rufescens</i> Sendtn.
Clusiaceae	<i>Solanum swartzianum</i> Roem. et Schultz
<i>Vismia brasiliensis</i> Choisy	<i>Solanum variable</i> Mart.
Leguminosae	Styracaceae
<i>Anadenanthera colubrina</i> (Vell.) Bren. (Min.)	<i>Styrax camporum</i> Pohl.
<i>Cassia ferruginea</i> (Schrad.) Schrad. ex DC.	Ulmaceae
<i>Cassia leptophylla</i> Vog.	<i>Trema micrantha</i> (L.) Blume
<i>Dalbergia brasiliensis</i> Vog.	Verbenaceae
<i>Lonchocarpus subglaucescens</i> Mart. ex Benth.	<i>Aegiphila obducta</i> Vell.
<i>Machaerium rictitans</i> (Vell.) Benth.	<i>Aegiphila sellowiana</i> Cham.
<i>Machaerium villosum</i> Vog.	<i>Lantana brasiliensis</i> Link
<i>Machaerium aculeatum</i> Raddi	<i>Lantana</i> aff. <i>fulcata</i> Lindl.
<i>Piptadenia gonoachanta</i> (Mart.) Macbride	

Fig. 3). Nevertheless, the largest of the three small fragments had a lower proportion of ruderal species than did the medium-sized fragment. This is partly due to a sampling artifact, in that several understory species in the medium-sized fragment were identified only to genus level, thereby overestimating the proportion of ruderal species.

In contrast, the species richness of plants in vertebrate-dispersed families that provide key sources of fleshy fruits for birds and mammals in the Atlantic forest — including the Myrtaceae, Lauraceae, Sapotaceae and Rubiaceae — declined from 38.9 and 35.7% of the species in the medium and large fragments, respectively, to as few as 15.4% in one of the small fragments.

4. Discussion

4.1. Floristic effects of fragment size

Our findings demonstrate that fragments of the montane Atlantic forest of southeastern Brazil differ in the guild structure of their plant assemblages, and that these changes are related to fragment size. Given the limited available data, we were unable to compare relative abundances of species in different guilds, but earlier studies (Aragaki and Mantovani, 1993; Tabarelli, 1994) suggest that our conclusions would have been strengthened had patterns of abundance been taken into account. Our analysis is also limited because it was

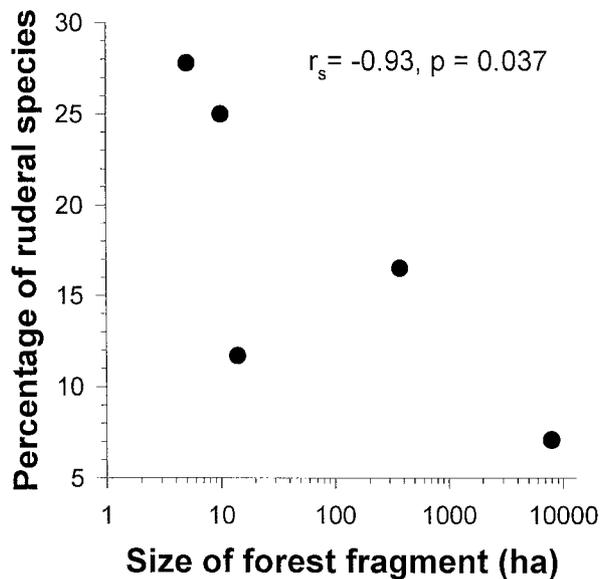


Fig. 3. Percentage of ruderal plant species in the local flora of five montane Atlantic forest fragments.

based on just five fragments, and because plant assemblages in each fragment were not sampled with identical methods. However, the observed differences among fragments are clear and generally support results from other studies of fragmented tropical forests (e.g. Lovejoy et al., 1986; Laurance et al., 1997, 1998b). Small forest fragments have a greater edge to area ratio and are intrinsically more susceptible to colonization of plants and animals from surrounding, human-dominated habitats (Janzen, 1986; Bierregaard et al., 1992; Gascon et al., 1999). Fragments can be bombarded with diaspores of exotic or weedy species that may be incorporated into the remaining plant community, sometimes eliminating species confined to the forest interior (Janzen, 1986).

The establishment and maintenance of ruderal and exotic species are clearly related to structural and microclimatic changes in fragmented forests (Janzen, 1986; Lovejoy et al., 1986; Kapos, 1989; Laurance, 1991; Malcolm, 1994). Greater levels of solar radiation in open habitats outside fragments increase air temperature, wind speed, and light availability, resulting in lower air and soil humidity near the fragment edge (Zuidema et al., 1996). Disturbance-adapted species may slowly modify the floristic and guild composition of the original forest by dispersing into natural treefall gaps near forest edges (Janzen, 1986). Rates of tree mortality and canopy-gap formation also tend to increase near edges after fragmentation (Laurance et al., 1998a). Small forest fragments, particularly those under 10 ha, can effectively consist entirely of edge habitat, and given time may not be structurally or floristically distinguishable from forest edge (Kapos, 1989; Zuidema

et al., 1996; Viana et al., 1997). The three smallest fragments in this study were characterized by an irregular canopy, a high density of treefall gaps and dead trees, and hyperabundant vines, lianas, and bamboo species (Vuono et al., 1982; Vuono, 1985; Gandolfi et al., 1995), all of which are associated with edge effects (Murcia, 1995). This indicates that fragment size is a major determinant of changes in woody plant composition and guild structure.

4.2. Intrusion of ruderal species

Ruderal species in the five fragments were mainly members of the Solanaceae, Compositae, Leguminosae and Euphorbiaceae (Table 3), with species richness of these families increasing in smaller fragments. This may result from enhanced conditions for dispersal and seedling recruitment for wind-dispersed species in small fragments, or inadequate dispersal and regeneration sites for vertebrate-dispersed species. It appears that size of relatively old montane Atlantic forest fragments is a major determinant of their woody species guilds, and that key components of the flora of small fragments (<10 ha) cannot be distinguished from that of edge habitats. Because the progressive increase in ruderals, small fragments will tend to converge in composition, preserving only a limited and highly biased subset of the original plant community (cf. Patterson, 1987).

The ruderal plant species we studied appear to be good indicators of disturbed forest, which clearly increases near forest edges (Loefgren, 1898; Burkart, 1979; Klein, 1980; Mantovani, 1993; Tabarelli et al., 1993). The occurrence of most ruderal species in the Atlantic forests is not related to natural disturbances caused by treefall gaps (Costa and Mantovani, 1992; Negrelle, 1995; Tabarelli, 1997; Tabarelli and Mantovani, 1997a). These species are usually missing from forest sites without large-scale anthropogenic disturbances and are rarely detected in detailed soil seed-bank profiles in intact forest (Baider, 1994). Rather, the successful establishment of these species appears to depend on human disturbances, including forest fragmentation, or large-scale natural disturbances such as landslides (Mendonça et al., 1992; Leitão Filho, 1993). This strengthens the suggestion that anthropogenic disturbance in tropical habitats has greatly expanded colonization opportunities for ruderal and pioneer species (Gómez-Pompa, 1971; Brown and Brown, 1992). This appears to have promoted the diversification of plants normally associated with large-scale natural disturbance, leading to the evolution of commensal species with life histories now more intimately tied to anthropogenic disturbance (Gómez-Pompa, 1971; Kellman, 1980).

Because many ruderal plants are shade-intolerant species of the canopy relying primarily on wind and

ballistic seed dispersal, between-site differences in guild composition appear to result from their greater dispersal and establishment potential in small fragments. The level of species richness within the ruderal guild has been used to reconstruct disturbance histories of a number of different sites (Klein, 1980; Whitmore, 1990; Gómez-Pompa et al., 1991). Anthropogenic disturbances such as selective logging and slash-and-burn agriculture cause structural changes in vegetation similar to those of forest edges and will also tend to favor ruderal species. The successful establishment of these species may precede declines in the population size of forest-interior species, which could eventually be driven to local extinction (cf. Zuidema et al., 1996).

4.3. Viability of small Atlantic forest fragments

Given the striking changes in plant communities observed in smaller fragments in this study and elsewhere in southeastern Brazil (e.g. Viana et al., 1997), a key concern is whether such small fragments can preserve biological communities typical of the original Atlantic forest. Changes in the composition of woody plants may affect the abundance and persistence of other plant and animal groups in fragments (Terborgh, 1992). A decline in abundance and richness of vertebrate-dispersed plants would almost certainly cause a reduction in vertebrate frugivores (Peres, 1999). Smaller fragments had lower fruit availability and lower abundance and species richness of frugivorous birds such as cracids, toucans, and bellbirds in montane forests of Costa Rica (Guidon, 1995) and the Colombian Andes (Kattan and Alvarez-López, 1995). In this study, we found a marked decline from the largest to smallest fragment in the relative number of Myrtaceae, Lauraceae, Rubiaceae, and Sapotaceae species, the families considered most important to vertebrate frugivores in the Atlantic forest (Moraes, 1992; Petroni, 1993; Galetti, 1996). Although we have no data on the frugivore communities in our five fragments, it is very plausible that a decrease in the abundance and diversity of fleshy fruits will ultimately lead to an impoverished vertebrate community. Understanding the effects of fragmentation on biodiversity is an essential ingredient for successful forest conservation programs. The remaining 8% of the original pre-Columbian Atlantic forest cover is mainly confined to small fragments (Brown and Brown, 1992), most of which are now private or governmental protected areas (DPRN, 1991). Over 40% of the 239 existing Atlantic forest reserves are less than 500 ha in area, and 32% of those are under 100 ha (Lima and Capobianco, 1997). Protected areas within the Atlantic forest plateau of São Paulo State are also mostly smaller than 500 ha (DPRN, 1991). Indeed, the bulk of remaining fragments along the entire north-south axis of the Atlantic forest are small to very

small (SOS Mata Atlântica and INPE, 1993; Jorge and Garcia, 1997). In the northern Brazilian state of Pernambuco, for example, some 48% of fragments are under 10 ha in size, while only 7% are larger than 100 ha (Ranta et al., 1998). Although no mammal or bird species has yet been declared regionally extinct in the Atlantic forest (Brown and Brown, 1992; Brooks and Balmford, 1996), our results clearly suggest that small fragments are likely to differ markedly in composition from the original forest (Viana and Tabanez, 1995; Viana et al., 1997; Tabarelli and Mantovani, 1997b). Thus, the existing network of protected areas may be unable to maintain regional species diversity and representativeness, especially if additional fragments are lost and fragmented landscapes are left unmanaged.

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