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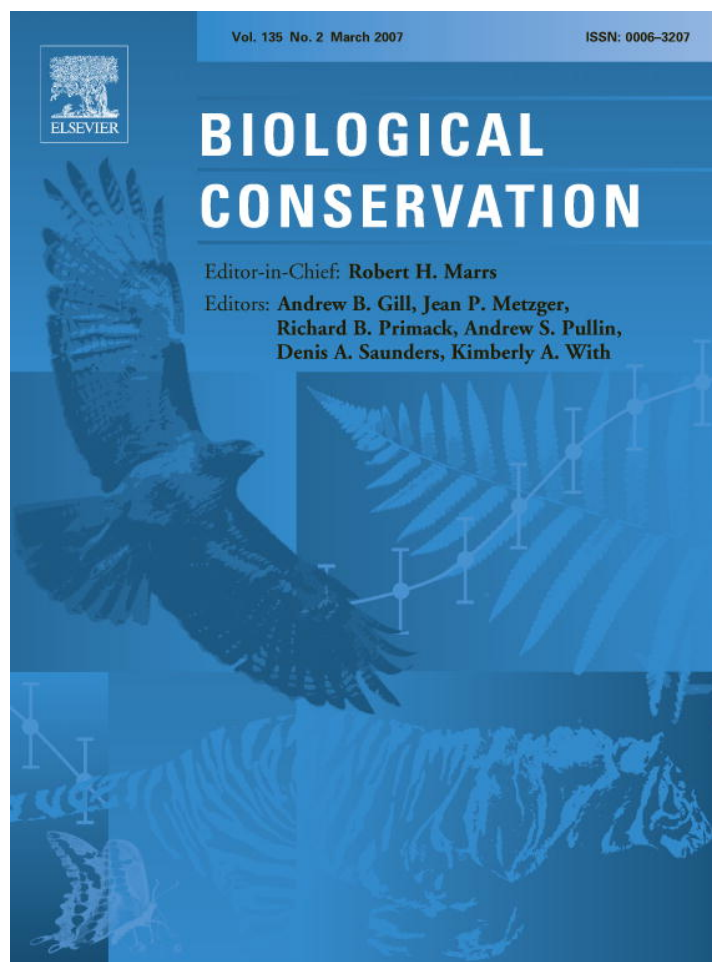
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Tree species composition and similarity in semideciduous forest fragments of southeastern Brazil

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ABSTRACT

This study investigates the influence of fragment size on tree species composition, species richness and on individual groups of species within 11 semideciduous forest fragments in southeastern Brazil. We compared same-sized samples of 500 trees from 10 fragments <100 ha, allocated to three size categories, with three 500-tree samples collected in different areas within a large forest, used as a reference forest. The variation in species richness, in the proportion of species/individuals in dispersal modes, and in the proportion of rare species was not related to fragment size. Nonetheless, comparisons between the mean values of these variables of each fragment size categories, using 95% confidence intervals, showed a wider range of variation within the category of small-sized fragments than in the other size categories. NMS ordination plot also suggested the absence of a relationship between fragment area and tree species composition. However, multiple regressions using the scores from the NMS ordination as response variables, and area and disturbance intensities as predictor variables, suggested that the interaction of area and disturbance might be a good predictor of species composition. Pre-existing environmental heterogeneity and geographical proximity also appeared to play a role in the variations of forest composition among the fragments studied. Our results demonstrated the high conservation value of small forest fragments.

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1. Introduction

Tropical forest fragmentation has been described as one of the main causes of diminishing biological diversity (Turner, 1996). An important aspect of this process is change in forest area and the impact of this change on species number and composition. However, it is still poorly understood for tropical ecosystems how the composition of tree species varies with landscape components such as forest patch size.

Fragmentation exposes previously isolated core habitats to the conditions of a different surrounding ecosystem (Kapos,

1989). The so-called 'edge effect' can modify the former microclimate conditions, eliminating more-sensitive species and promoting establishment of successional and non-forest species (Kapos et al., 1997; Laurance et al., 1998). Area reduction can influence species persistence in fragments, by promoting the collapse of small populations via demographic or genetic events (Shafer, 1981; Pimm et al., 1988). Moreover, in the fragmented landscape, pollination and dispersal mechanisms, as well as migration patterns, can be interrupted or altered, influencing plant species reproduction and opportunities for expansion (Aizen and Feinsinger, 1994; Benitez-

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Malvido, 1998). All these changes may result in shifts in plant species composition. The changes tend to be more accentuated in smaller fragments, which are proportionately more affected by the edge effect, because of their higher edge:interior ratio, and because they support smaller populations than do larger fragments (Laurance and Yensen, 1991; Goodman, 1987).

Among the few studies that have explicitly attempted to find a relationship between remnant area and tree species composition in tropical forests, some did find such a relationship (Tabarelli and Mantovani, 1999; Hill and Curran, 2001; Ross et al., 2002), and some did not (Haig et al., 2000; Balasubramaniam, 2003). Several factors may affect the influence of area. For instance, the occurrence of disturbance events and the inherent environmental heterogeneity among patches can act in conjunction with area, influencing species composition in forest fragments and blurring the detection of an area effect alone (Ross et al., 2002). Moreover, many consequences of forest fragmentation are time-related and require a “relaxation” period before final equilibrium conditions are reached (MacArthur and Wilson, 1967; Vellend et al., 2006). However, the long-term effects of fragmentation on tropical floras are barely known because of the scarcity of studies focusing on forest remnants isolated for a century or more (Turner et al., 1996).

The fragmentation process in Campinas County in southeastern Brazil, where this study was carried out, began in the 18th century. The once predominant and continuous semideciduous forests currently occupy only 2.55% of the county's total area. They are distributed in 197 fragments, most of which are smaller than 10 ha in area (Santin, 1999). The conservation value of such forest fragments in southeastern Brazil has been questioned by many authors, who consider their floras so modified by anthropogenic disturbances that they no longer represent remnants of the original ecosystem (Tabanez et al., 1997; Tabarelli and Mantovani, 1999; Durigan et al., 2000). However, considering that most of the remaining fragments are small and disturbed, it is important to evaluate the degree to which these fragments contribute to the preservation of biological communities typical of the original forests (Turner and Corlett, 1996).

The major aim of this study was to investigate whether and how tree species composition varies with forest fragment size. However, investigating fragmentation effects in regions where the fragmentation occurred long before the original forests could be studied, as in southeastern Brazil, can be challenging, because there is no longer any continuous forest at the regional scale for secure comparisons. The only option is to compare larger to smaller fragments, keeping in mind that small fragments are remnants of a formerly larger forest. Samples taken randomly in different areas within a large forest will most likely differ from each other in terms of species composition. This variation may often be related to environmental heterogeneity, such as different soil types, topography, and water availability, among others (Cooper, 1926; Oliveira-Filho et al., 1994; Vormisto et al., 2004). After fragmentation, environmental heterogeneity may be maintained, still driving species composition, but many other factors, such as described above, begin to influence the newly created forest fragments. Shifts in the original species composition

are to be expected, and smaller fragments most likely will differ from the continuous forest or from larger fragments. For example, the proportion of rare species (i.e., those with small populations) is expected to decrease with fragment size (Hill and Curran, 2001). Moreover, as the response to forest fragmentation is very species-specific (Boecklen and Gotelli, 1984; Dupré and Ehrlén, 2002), small fragments would show reduced richness of animal-dispersed species, as observed by Tabarelli and Mantovani (1999), and higher proportions of wind-dispersed species, which could benefit in fragmented landscapes (Howe and Smallwood, 1982).

However, when comparing tree species composition within small fragments and between small and large fragments, one could expect two different scenarios. In the first, species composition would vary greatly between smaller fragments, because in addition to the previous environmental heterogeneity, fragmentation effects would operate differently in each patch, depending on their particular features, such as shape, edge orientations, matrix occupations, and frequency and intensity of disturbance events, which are stochastic (Laurance and Yensen, 1991; but see Saunders et al., 1991 for a review). Nonetheless, the smaller fragments would differ from the larger ones. The second possibility is that small fragments would converge in species composition, because only a limited subset of species would be able to survive in the new habitat, as predicted by Patterson (1987). As a result, small fragments would present similar floras when compared to each other, which in turn would differ markedly from larger fragments or to randomly selected areas within a very large forest. Moreover, if an area effect does exist, i.e., the effects of forest fragmentation decrease with increasing fragment area, we would expect that same-sized fragments would be more similar among each other, in terms of species composition, than to fragments from other size classes or to areas randomly sampled within a very large forest.

More specifically, in this study we wanted to answer the following questions: Is the variation in species composition among forest fragments related to their size? Do the proportions of individuals and species in dispersal modes and rare species differ between fragments of different sizes? Is the variation among forest fragments greater than between areas randomly chosen within a large or continuous forest? Are same-sized fragments more similar to each other than to fragments from other size classes?

2. Methods

2.1. Study area

The forest fragments studied were located within or just outside the perimeter of the Environmental Protection Area (EPA) of Campinas County (Área de Proteção Ambiental – APA – do município de Campinas), state of São Paulo, southeastern Brazil (22°45'–23°00' S, 47°00'–47°12' W) (Fig. 1). The climate is classified as Köppen's Cwag'-temperate type, i.e., mild rainy with a mild, dry winter. Mean rainfall is ca. 1409 mm year⁻¹ (Mello et al., 1994), irregularly distributed throughout the year, with a dry season from June through August and a rainy season from December through February. The mean monthly temperatures range from 23.3 °C (February) to 17.3 °C (July)

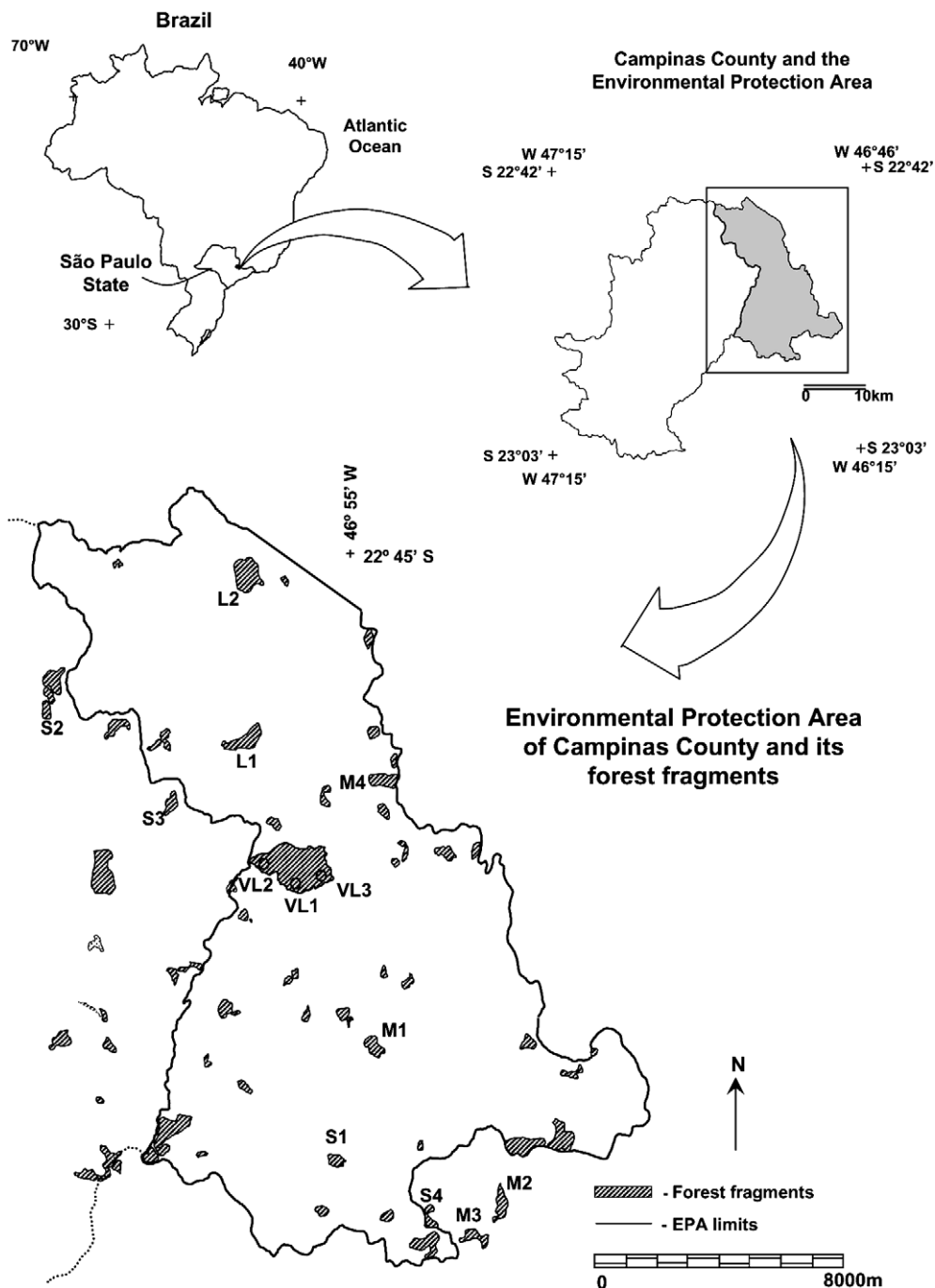


Fig. 1 – Locations of the 11 forest fragments studied in Campinas County, southeastern Brazil. S1–S4: small fragments; M1–M4: medium fragments; L1–L2: large fragments; VL1–VL3: samples taken in the very large forest.

(Mattos, 1996). According to the Brazilian soil taxonomy system, the soils are classified as Red-Yellow Podzol or Red Latosol, and the topography ranges from slightly hilly to strongly hilly and mountainous (Oliveira et al., 1999) (Table 1).

The primary vegetation in this region is semideciduous seasonal forest (Veloso et al., 1991; see Santos, 1998; for descriptions of woody species). The most dominant families at the studied fragments are Apocynaceae, Fabaceae, Meliaceae, Euphorbiaceae, Caesalpiniaceae, Mimosaceae, and Rutaceae. The most dominant species are *Esenbeckia leiocarpa*, *Piptadenia gonoacantha*, *Trichilia clauseni*, *Croton floribundus*, *Gallesia integ-*

rifolia, *Lonchocarpus muehlbergianus*, and *Aspidosperma polyneuron* (K. Santos, unpublished data). The current landscape consists of a patchwork of annual and perennial crops, pastures, reforestation projects, and small human settlements.

The process of fragmentation of the semideciduous forests in the region began in the 18th century. The major clearance and forest destruction, which occasioned the isolation of the fragments studied, occurred with the expansion of coffee cultivation during the 19th century. These fragments have been isolated for at least 100 years (Christofolletti and Federici, 1972; Mattos, 1996; Miranda, 1996).

Table 1 – Characteristics of the 11 fragments studied in Campinas County, southeastern Brazil

Fragment ^a	Area (ha)	Altitude (m)	Soil type ^b	Topography ^c	Disturbance ^d
S1	12.4	887	RYP 22	SHM	Moderate
S2	13.2	658	RL4	SH	Very strong
S3	13.4	674	RYP 20	HSH	Moderate
S4	12.5	808	RYP 22	SHM	Moderate
M1	19.9	885	RYP 22	SHM	Strong
M2	21.0	777	RYP 22	SHM	Moderate
M3	20.0	717	RYP 22	SHM	Moderate
M4	25.2	733	RYP 22	SHM	Moderate
L1	41.8	739	RYP 8	SHM	Strong
L2	63.4	650	RYP 20	HSH	Very strong
VL1	244.9	653	RYP 22	SHM	Moderate
VL2	244.9	660	RYP 22	SHM	Moderate
VL3	244.9	756	RYP 22	SHM	Strong

a Fragments are presented by increasing size (S1–S4: small fragments; M1–M4: medium fragments; L1–L2: large fragments; VL1–VL3: samples taken in the 244.9 ha fragment).

b According to the Brazilian soil taxonomy system, the soils are classified as Red-Yellow Podzol of three different types: RYP 8, RYP 20, and RYP 22, or Red Latosol: RL 4.

c The topography ranges from slightly hilly (SH) or hilly and slightly hilly (HSH), to strongly hilly and mountainous (SHM).

d Estimated by personal observations and information from local residents referring to the last 10 years. “Moderate disturbance” means fragments that were free of signs of disturbance, such as logging or fires and/or with no information about disturbances available from the local residents. “Strong disturbance” means fragments with a history of fire near the edge or in small parts of the fragment area. “Very strong disturbance” corresponds to fragments that were burned over most of their area during the last 10 years, and/or were repeatedly burned in small sections.

The forest fragments were chosen on the basis of their size, physiological similarity, ease of access, and authorization from the landowners. The history of disturbance of the fragments was investigated by reference to publications (Mattos, 1996; Miranda, 1996; Santin, 1999); aerial photographs dating from the late 1960s and from 1972, 1994, and 2000; interviews with landowners; and personal observations (Table 1). There is only one record of forest management within these fragments. It refers to fragment S1, where, according to the landowner, the forest has been protected against fire and liana infestations have been controlled for the past 30 years.

2.2. Experimental design

This study compares species composition and similarity of semideciduous forest fragments in an area with a relatively long history and high degree of fragmentation. To investigate the influence of patch area on species composition, we first tested for effects on species numbers and on individual groups of species, and secondly compared the similarity among fragments, considering the species composition as a whole.

We compared the species composition of same-sized samples of 500 trees from 10 fragments <100 ha, with three 500-tree samples collected in different areas within a very large forest (Fig. 1, Table 1). Hereafter these samples are referred to as VL1, VL2, and VL3. We used these samples as references, assuming that they were less affected by the fragmentation process, and that the variation among them cannot be related to forest size. Thus, if the variation in species composition among the samples from the very large forest is similar to that observed between the fragments <100 ha, this variation cannot be related to fragment area. Moreover, to test the hypothesis that the extent of fragmentation effects dimin-

ishes as patch sizes increase, we investigated the species composition of fragments <100 ha divided into three size-categories as follows: four small (12 and 13.5 ha), four medium-sized (19 and 25.5 ha), and two large (41.8 and 63.3 ha) (Table 1, Fig. 1).

To assess the influence of patch area on individual groups of species, we divided species into groups based on their (1) abundance; (2) frequency; and (3) seed-dispersal mode. These dispersal modes are zoochoric (animal-dispersed species), anemochoric (wind-dispersed species), and autochoric (self-dispersed species), based on fruit and/or seed morphology (Van der Pijl, 1982).

In each forest fragment, we surveyed 125 sampling points, using the point-centered quarter method (Cottan and Curtis, 1956). This procedure consists of dividing each sampling point into four quarters by a pair of perpendicular lines. In each quarter, the nearest tree of 10 cm diameter at breast height (DBH) or larger was recorded, totaling 4 individuals per sampling point and yielding a sample of 500 individuals per fragment. The sampling points were placed every 15 m along transects crossing similar areas, in terms of size, in all the forest fragments.

We attempted to sample a standardized area of each fragment, in order to isolate the effect of area from other variables, such as edge effects. We also attempted to minimize the influence of environmental heterogeneity by placing transects in areas with similar environmental features, such as slope, altitude, soil, and drainage conditions. We also avoided other types of vegetation within fragments, such as gaps and edge-affected areas (defined as a strip 20 m inward from the forest margin).

Collecting was done mainly from April through September 2000. Identification followed the usual taxonomic techniques, and the classification system proposed by Cronquist (1981).

Vouchers have been deposited in the UEC Herbarium (Departamento de Botânica, Universidade Estadual de Campinas).

2.3. Data analysis

We used two different approaches to assess the influence of patch area on species richness (expressed as number of species), and on the species groups. First, we tested for effects on the entire range of fragment sizes using least squares linear regressions in the software Systat v.11 (Systat Software, Richmond CA). Second, we compared fragment size categories using the mean values and 95% confidence intervals of these variables. In these comparisons, the samples from the very large forest were used as reference points to represent the range of the analyzed variables in a forest which presumably has been less affected by the fragmentation process. The large fragments had to be excluded from these comparisons, because of the small number of fragments in this category. In the linear regressions, only a mean value for the very large forest samples was considered, because the three samples were taken within the same forest fragment (i.e., they were not independent). All values in percentages were arcsine-square-root-transformed prior to calculations of means, standard errors, confidence intervals, and linear regression analysis.

We used non-metric multidimensional scaling (NMS) in PC-ORD version 4.0 (McCune and Mefford, 1999) with the quantitative version of Sørensen's distance measure to investigate the similarity among forest fragments. This ordination method displays the most similar fragments in the plot as the points plotted closest together, and the fragments with the least similarity are represented with the points located farthest apart. NMS is well suited for non-normal data and does not assume linear relationships among variables (McCune and Grace, 2002). The method performs an iterative search for the placement of entities on a small number of dimensions (axes), to maximize the rank correspondence between similarity in the original n -dimensional hyperspace and distances in the ordination space (McCune and Grace, 2002). Only species having more than five individuals in the total were included in the NMS analysis.

We ran separate multiple regression analyses using axis 1 and axis 2 scores from the NMS ordination as response variables, and area and disturbance intensities (Table 1) as predictor variables. The multiple regression analyses should show which environmental variables are most highly correlated with the community patterns contained in the ordination axis scores. Area values were log-transformed before all the regression analyses in order to eliminate potential nonlinearities in the relationship.

Preliminary investigations on similarity relationships among forest fragments using the Jaccard index and cluster analysis (average linkage method – UPGMA) performed on FITOPAC (Shepherd, 1988), suggested that the geographical distance among fragments could be negatively related to the similarities among forest fragments. In order to further investigate this hypothesis, a Mantel test was performed with PC-Ord version 4.0 (McCune and Mefford, 1999) to quantify the correlation between the floristic distance matrices, calculated

using Sørensen's similarity coefficient, with the geographical distance among fragments in kilometers (Supplementary Table 1).

Because our fragments do not differ only in their sizes, i.e. some variation in soil and topography types also occurs; we performed multiple regressions (just as described above), using soil and topography types as dummy variables to test for their influence on the analyzed variables. The variations in soil and topography were not correlated to the variations in the species composition (results not shown).

3. Results

3.1. Species richness and groups of species

A total of 6500 individuals, representing 248 species, 156 genera, and 58 families were recorded in the 13 samples (Supplementary Table 2). The number of species per sample of 500 individuals ranged from 47 to 110 (Table 2). The variation in species richness, proportions of rare and very infrequent species, and in the proportions of individuals and species in dispersal modes, were not related to fragments size (in all the regression analyses we found values of $r^2 \leq 0.165$, $F_{1,9} \leq 1.783$, and $p \geq 0.215$).

We found as many species in a sample of 500 individuals from a 12 ha fragment as in a same-sized sample from a 244.9 ha fragment (Table 2, Fig. 2). The highest numbers of species were observed in two medium fragments, in a large and in a small one: M3 (110 species), M2 (107), L1 (104), and S1 (103). The variation in species richness within small fragments was higher than within medium fragments, and among the samples from the very large forest. This can be seen by comparing the mean species richness ($\pm 95\%$ CI) between small (83.5 ± 40.6 species; $n = 4$), medium (103.0 ± 10.3 species; $n = 4$), and very large forest samples (95.0 ± 10.8 species; $n = 3$) (Fig. 2). Although the 95% confidence intervals overlapped in all cases, the range was much wider within small fragments.

The highest proportions of rare species occurred in two medium fragments and in a small one: M3 (80.0%), S4 (79.8%), and M2 (77.6%) (Table 2). The mean values ($\pm 95\%$ CI) of rare species in the small (74.4 ± 0.8 species; $n = 4$), medium (76.7 ± 0.4 species; $n = 4$), and very large reference forest (74.6 ± 0.1 species; $n = 3$) were similar (Fig. 3a).

The highest proportions of very infrequent species occurred in two medium fragments and in a small one: M3 (16.6%), S4 (15.2%), and M4 (14.4%) (Table 2). However, the highest mean value ($\pm 95\%$ CI) occurred in the small fragments (12.3 ± 0.3 species; $n = 4$), differing from the very large reference forest (7.3 ± 0.1 species; $n = 3$), but not from the medium fragments, which showed a wider 95% CI (10.0 ± 5.6 species; $n = 4$), which overlapped with the small and very large categories (Fig. 3b).

The proportion of species by dispersal syndrome varied little among fragments (Table 2). Small and medium fragments also did not differ from the very large forest with respect to the mean proportion of zoochoric and anemochoric species (Table 3). However, the mean proportion of autochoric species for the very large forest samples was significantly higher than in small- and medium-sized fragments (Table 3).

Table 2 – Characteristics of tree species composition in the 11 forest fragments studied in Campinas County, southeastern Brazil

	Forest fragments													Total
	S1	S2	S3	S4	M1	M2	M3	M4	L1	L2	VL1	VL2	VL3	
<i>Species richness</i>														
Number of species	103	85	47	99	98	107	110	97	104	65	97	98	90	248
<i>Species by abundance (number of individuals)^a</i>														
Rare (1–5)	76	65	32	79	70	83	88	75	77	50	78	72	67	100
Sparse (6–20)	23	15	12	12	23	21	18	18	24	8	15	23	19	72
Common (21–40)	3	3	1	7	4	1	2	3	2	4	3	2	2	38
Abundant (41–80)	1	2	1	1	1	2	2	0	1	3	1	1	2	20
Very abundant (≥81)	0	0	1	0	0	0	0	1	0	0	0	0	0	18
<i>Species by frequency (number of fragments)^b</i>														
Very infrequent (1–2)	11	11	5	15	1	15	18	14	7	3	7	8	6	87
Infrequent (3–6)	35	28	11	34	29	37	31	22	35	14	25	31	30	86
Frequent (7–10)	31	26	12	27	42	32	37	36	37	25	39	35	31	49
Very frequent (11–13)	26	20	19	23	26	23	24	25	25	23	26	24	23	26
<i>Species by dispersal modes (number of species)</i>														
Anemochoric	19	16	21	21	25	28	26	30	22	18	24	25	18	52
Autochoric	18	18	5	11	14	10	17	12	17	10	15	16	17	35
Zoochoric	66	50	21	67	59	68	66	55	65	37	57	57	55	157
<i>Species by dispersal modes (number of individuals)</i>														
Anemochoric	122	78	150	165	143	105	114	114	131	187	161	151	103	1724
Autochoric	106	250	6	95	156	157	126	166	146	125	145	118	216	1812
Zoochoric	272	171	344	240	201	237	259	220	223	188	193	231	181	2960

a This section refers to the number of species in each fragment that were represented by 1–5 individuals, 6–20 individuals, and so on.

b This section refers to the number of species in each fragment that were recorded in only one or two fragments – very infrequent, recorded in 3–6 fragments and so on.

The proportions of individuals in each dispersal mode varied widely among fragments (Table 2). The mean proportion of zoochoric individuals in the very large forest was significantly lower than in the small- and medium-sized fragments, and this proportion did not differ between the small and medium categories (Table 3).

3.2. Total species composition and similarity

The mean (±SE) similarity among small fragments was 41% (+3.8–3.9%), which was lower than the mean similarity between medium fragments, at 60.6% (+2.4–2.5%), and among

the samples from the very large forest, at 61.7% (±2.8%). The similarity among the large fragments was 61% (Supplementary Table 1).

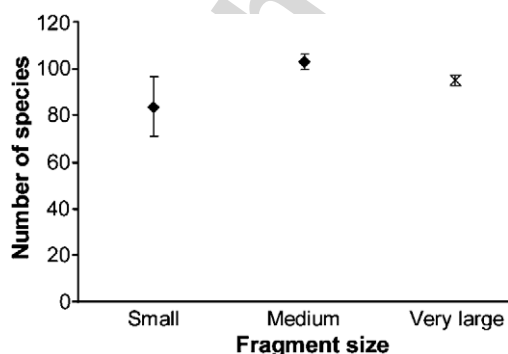


Fig. 2 – Mean number of tree species (±SE) per 500-tree sample for the small- and medium-sized fragments, and for the three samples from the very large forest in Campinas County, southeastern Brazil.

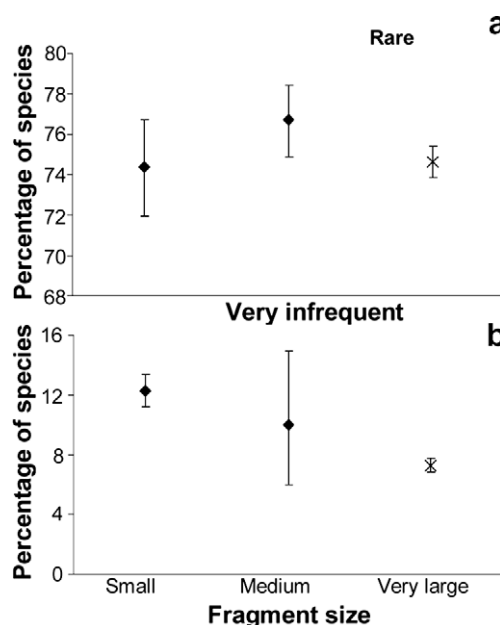


Fig. 3 – Mean proportion of (a) rare and (b) very infrequent species (±SE) per 500-tree sample for the small- and medium-sized fragments, and for the three samples from the very large forest in Campinas County, southeastern Brazil.

Table 3 – Mean proportion of anemochoric, autochoric, and zoochoric plant species (S) and individuals (N) ($\pm 95\%$ CI) for the small- and medium-sized fragments, and for the samples from the very large forest in Campinas County, southeastern Brazil

Fragment category ^a	Anemochoric		Autochoric		Zoochoric	
	S	N	S	N	S	N
Small (4)	25.3 (± 4.8)	25.5 (± 2.1)	14.9 (± 1.3)	19.4 (± 18.1)	59.1 (± 2.6)	51.5 (± 5.3)
Medium (4)	26.6 (± 0.3)	23.7 (± 0.4)	12.8 (± 0.4)	30.2 (± 0.4)	60.4 (± 0.2)	45.9 (± 0.6)
Very large (3)	23.5 (± 0.8)	27.5 (± 3.1)	16.9 (± 0.3)	31.7 (± 7.0)	59.6 (± 0.1)	40.3 (± 1.7)

^a Numbers in parenthesis indicate the number of fragments/samples in each fragment size category.

Fragments did not form groups according to their area, as shown in the two-dimensional NMS ordination plot (Fig. 4). Fragment S3 appeared quite isolated from the other fragments, and the samples taken within the very large forest (VL1, VL2, and VL3) appeared mixed with fragments from all size categories. These results suggest that variations in floristic composition among fragments are not related to their total area.

The NMS ordination (Fig. 4) represented 93% of the variation in the dataset, with 56% loaded on axis 1 and 37% on axis 2. The first strongest ordination axis was not related to fragment area ($r^2 = 0.045$; $F_{1,11} = 0.52$; $p = 0.486$), nor when area was combined with disturbance intensity in the multiple regression analysis (adjusted $r^2 = 0.048$; $F_{2,10} = 0.25$; $p = 0.783$). The second weaker axis showed a marginal significant relationship with area ($r^2 = 0.242$; $F_{1,11} = 3.51$; $p = 0.088$). In the multiple regression analysis, area and disturbance intensity together explained 64% of the variation in species composition related to axis 2, and the overall relationship was significant (adjusted $r^2 = 0.562$, $F_{2,10} = 8.7$; $p = 0.006$).

Geographical proximity seemed to be slightly reflected in the distance among fragments in the NMS plot (compare Figs. 1 and 4). Forest M1, which showed similarities above 50% with most fragments (Supplementary Table 1), is located equidistant to most of the fragments (Fig. 1). Geographical proximity may also be involved in the case of the samples from the very large forest (VL1, VL2, and VL3), several of which showed up to

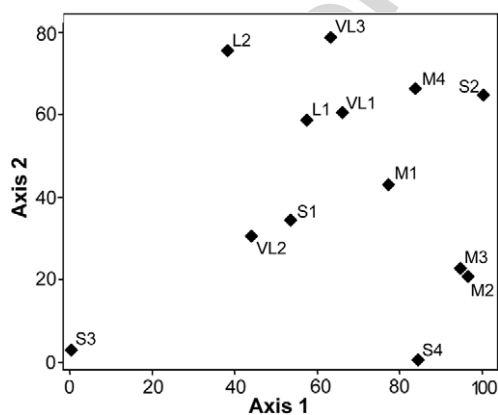


Fig. 4 – Two-dimensional NMS plot for the 11 forest fragments studied in Campinas County, southeastern Brazil. S1–S4: small fragments; M1–M4: medium fragments; L1–L2: large fragments; VL1–VL3: samples taken in the very large forest.

66% similarity. The Mantel test showed a negative correlation between geographical distance and the floristic similarity among fragments ($r_M = -0.372$, $p = 0.011$), indicating that, in spite of the variation, the closer the fragments are, the higher is their similarity.

4. Discussion

Most of the variation in species composition among the fragments was not related to fragment area. Contrary to our expectations, same-sized fragments were not more similar to each other than to fragments from another size category. In addition, most of the fragments showed nearly the same richness, proportions of rare and very infrequent species, and proportions of individuals and species in the three dispersal modes.

However, the range of variation, for most of the analyzed variables, was wider among the small fragments, than in the other categories. This is contrary to the prediction of Patterson (1987) that smaller fragments would converge in species composition. This result might be related to the greater variation among small fragments regarding site history, disturbance intensity, and environmental features, compared to other size categories. For instance, fires occur repeatedly on the edges of fragment S2, as attested by our personal observations, whereas fragment S1 has been protected against fires and liana infestation for many years. Small fragments were also located much farther from each other in the landscape than were the medium fragments for example, with mean distances of 11.2 km and 7.3 km respectively. This was consistent with our results showing that geographical proximity was a key factor, because the physical environment tends to be more uniform as fragments are closer together. It is also important to mention that, although soil and topography showed to play a minor role in our preliminary investigations, it is possible that they are having some influence in this case, since the small fragments are distributed among three different soil types and two topography types, whereas these features were much more uniform within the other size classes. Thus, the greater variation within the smaller fragments is not necessarily related to their size.

Vegetation patterns have long been associated with environmental heterogeneity (e.g., Cooper, 1926; Austin, 1985; Barberis et al., 2002). However, a number of factors can also influence species composition in forest patches, and some of them may be exacerbated as the area decreases. In our results, for example, the variations in the total species composition could not be explained solely by fragment area, but rather by

a combination of fragment area and disturbance intensity. This result is consistent with the studies of Honnay et al. (1999) and Ross et al. (2002), who found that disturbance was the major factor interacting with area to influence species richness and composition in forest fragments. This interaction can be explained by the increasing sensitivity to disturbance as fragments get smaller, which is possibly related to the increased edge:interior ratio; and by the assumption that anthropogenic disturbance promotes invasion of alien species in forest patches (Fox and Fox, 1986; Hobbs, 1988).

The numbers of species found in the fragments are well within the range reported for other semideciduous forests in São Paulo state (Torres et al., 1997; Metzger et al., 1997; Santos and Kinoshita, 2003). Only two samples contained relatively fewer species, one small fragment (S3) and one large one (L2). The absence of a relationship with area and species richness has been reported in many other studies (reviewed by Boecklen and Gotelli, 1984). One explanation proposed is that species respond differently to changes in habitat configuration (Grashof-Bokdam, 1997; Graae, 2000; Dupré and Ehrlén, 2002). For example, high survival rate in conjunction with vegetative reproduction is thought to be the way of escape from extinction for plants with low dispersal capacities, such as zoochoric species. This may explain why we did not find lower proportions of zoochoric species in smaller fragments, contrasting with observations by others that zoochoric species tend to decline with fragment area (Tabarelli and Mantovani, 1999; Dupré and Ehrlén, 2002; Grashof-Bokdam, 1997). In fact, we found the opposite: the highest proportions were observed in two small fragments (S1 and S4).

The species-specific response to environmental change might also explain the lack of a relationship between fragment size and the proportion of individuals in dispersal modes. However in this case, it should be added that the variations appear to be more an effect of differences in species dominance in each site, rather than a fragmentation effect. For example, the relatively higher proportion of zoochoric individuals in smaller fragments was highly influenced by the high dominance of a single zoochoric species (*Trichilia clauseni*) in fragment S3. On the other hand, the lower proportions of zoochoric individuals in the very large forest might be associated with the abundance of two autochoric species, *Croton floribundus* and *Esenbeckia leiocarpa*, which in turn could be limiting the occurrence of individuals from other species. The reasons for these differential dominances may be related to many different factors, such as soil, topography, site history, and forest dynamics (Burslem and Whitmore, 1999; Vormisto et al., 2004). Determination of these reasons will require more detailed and specific studies.

The existence of a time lag in the response of plant communities to changes in the habitat configuration, as demonstrated by Lindborg and Eriksson (2004), might also contribute to the inconsistent species-area effects observed in the fragments studied. As mentioned above, long-lived species may remain in some environments for many years, even if the conditions that determine their occurrence have changed (Inghe and Tamm, 1985; Turner and Corlett, 1996). In addition, the clonal growth of many of these species may hamper the occurrence of genetic drift (Honnay et al., 1999). It is possible that we did not find the expected relationship because of

the age of our fragments or the periods of time since their isolation. Hence, the observed patterns in the fragments studied may still reflect the landscape configuration of 100 years ago, and might be more related to the pre-existing heterogeneity than to the modifications caused by fragmentation (Kolb and Diekmann, 2004; Lindborg and Eriksson, 2004).

Nonetheless, it is important to mention that the delayed response creates an extinction debt, meaning that extinctions will occur in the future even in the absence of further perturbations (Tilman et al., 1994; Vellend et al., 2006). Thus, high species richness and the presence of rare and very infrequent species in a small forest patch is by no means a sign of health, or a guarantee of the conservation of species diversity. The time lag, however, may also provide an opportunity for threatened species to recover, which is an important issue for conservation biology.

Tree diversity in long-isolated fragments can also be maintained by other mechanisms (Brokaw, 1998). Dense second-growth vegetation might develop in the forest boundaries, buffering the forest interior from the altered microclimates and disturbance regimes. This mechanism might aid in the persistence of the diverse core species in fragments and ultimately in the conservation of diversity and composition (Matlack, 1994; Didham and Lawton, 1999). It is possible that this process is helping to maintain tree species in our fragments, but explicitly designed studies should be carried out to further investigate this hypothesis.

Our results suggest that the species composition within each forest fragment may be the result of a series of factors that vary and interact differently in space and time. For example, the small fragment (S3), which showed the lowest species richness and differed most from the others in the ordination plot, might be characterized as a single-dominant forest, since nearly 50% of the total individuals sampled belonged to a single species. Single-dominant forests might arise through a series of mechanisms (Connell and Lowman, 1989). However, its development is not easily attributable to a single trait, but rather appears to be a combination of environmental conditions and particular life-history attributes (Torti et al., 2001). On the other hand, site history could be related to both the higher number of species in the small fragment S1, which is maintained by the care of its landowner, and the low species number in the large fragment (L2), in which a large fire 10 years ago may have eliminated more-sensitive species. Moreover, differential dominances of species, possibly related to environmental heterogeneity, and the interactive effect of area and disturbance, are also influencing the composition of our fragments. Thus, it is important to bear in mind that the perception of the different effects of fragmentation on forest composition depends on the temporal scale adopted, because the community may never reach equilibrium in species composition on any given scale of time or space (Condit, 1996; Lindborg and Eriksson, 2004).

These examples may illustrate why it is so difficult to establish patterns, considering only size categories of these forests, but also indicate that each fragment has its own characteristics. These variations, however, enhance their conservation value. Fragment S3, for example, in spite of its low species number, possibly constitutes an important food source for the regional fauna because of the abundance of a zoochoric

species. The high proportions of very infrequent and rare species in small and in some medium fragments much enhance their conservation importance. In addition, we note that 12% of the species recorded have been found for the first time in the region of the study, and nearly 27% (63 species) are considered to be very infrequent in this region. Moreover, 14 taxa (5%) could not be identified to species level, and one of them remains entirely unidentified (Supplementary Table 2). These findings in a well-studied region like Campinas, which is located near several of the oldest Brazilian research institutes, indicate the great conservation value of these forests.

Our results lend support to the comments of Turner and Corlett (1996), that small fragments spread over an agricultural landscape are fundamental to the maintenance of biodiversity of a region, because they increase the likelihood of survival of many species and very often are homes for endangered species. In view of this, the question of the relevance of the current remnants to the maintenance of the original ecosystem composition seems of little practical or theoretical importance. It is practically impossible to know what the original composition of these forests was, given the long history of the fragmentation process. If we are to preserve something that represents this original composition, the only option left is to conserve these remnants, which, as shown here, can make important contributions.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.biocon.2006.10.027](https://doi.org/10.1016/j.biocon.2006.10.027).

REFERENCES

- Aizen, M.A., Feinsinger, P., 1994. Forest fragmentation, pollination, and plant reproduction in a chaco dry forest, Argentina. *Ecology* 75, 330–351.
- Austin, M.P., 1985. Continuum concept, ordination methods and niche theory. *Annual Review of Ecology and Systematics* 16, 39–61.
- Balasubramaniam, P., 2003. Floristic composition and patterns of regeneration of rainforest trees in the fragmented forests of the Anamalai Hills, southern Western Ghats. M.Sc. thesis, Saurashtra University, Rajkot.
- Barberis, I.M., Batista, W.B., Pire, E.F., Lewis, J.P., León, R.J.C., 2002. Wood population distribution and environmental heterogeneity in a Chaco forest, Argentina. *Journal of Vegetation Science* 13, 607–614.
- Benitez-Malvido, J., 1998. Impact of forest fragmentation on seedling abundance in a tropical rain forest. *Conservation Biology* 12, 380–389.
- Boecklen, W.J., Gotelli, N.J., 1984. Island biogeography theory and conservation practice: species-area or speciesous-area relationships? *Biological Conservation* 29, 63–80.
- Brokaw, N., 1998. Fragments past, present and future. *Trends in Ecology and Evolution* 13, 382–383.
- Burslem, D.F.R.P., Whitmore, T.C., 1999. Species diversity, susceptibility to disturbance and tree population dynamics in tropical rain forest. *Journal of Vegetation Science* 10, 767–776.
- Christofoletti, A., Federici, H., 1972. A terra campineira. *Indústrias Gráficas Mousinho*, Campinas.
- Condit, R., 1996. Defining and mapping vegetation types in mega-diverse tropical forests. *Trends in Ecology and Evolution* 11, 4–5.
- Connell, J.H., Lowman, M.D., 1989. Low-diversity tropical rain forests: some possible mechanisms for their existence. *The American Naturalist* 134, 88–119.
- Cooper, W.S., 1926. The fundamentals of vegetation change. *Ecology* 7, 391–413.
- Cottan, G., Curtis, J.T., 1956. The use of distance measures in phytosociological sampling. *Ecology* 37, 451–460.
- Cronquist, A., 1981. An Integrated System of Classification of Flowering Plants. Columbia University Press and The New York Botanical Garden, New York.
- Didham, R.K., Lawton, J.H., 1999. Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. *Biotropica* 31, 17–30.
- Dupré, C., Ehrlén, J., 2002. Habitat configuration, species traits and plant distributions. *Journal of Ecology* 90, 796–805.
- Durigan, G., Franco, G.A.D.C., Saito, M., Baitello, J.B., 2000. Estrutura e diversidade do componente arbóreo da floresta na Estação Ecológica dos Caetetus, Gália, SP. *Revista Brasileira de Botânica* 23, 371–383.
- Fox, B.J., Fox, M.D., 1986. The susceptibility of natural communities to invasion. In: Groves, R.H., Burdon, J.J. (Eds.), *Ecology of Biological Invasions an Australian Perspective*. Australian Academy of Science, Canberra, pp. 57–66.
- Goodman, D., 1987. The demography of chance extinction. In: Soule, M.E. (Ed.), *Viable Populations*. Cambridge University Press, Cambridge, pp. 11–34.
- Graae, B.J., 2000. The effect of landscape fragmentation and forest continuity on forest floor species in two regions of Denmark. *Journal of Vegetation Science* 11, 881–892.
- Grashof-Bokdam, C., 1997. Forest species in an agricultural landscape in the Netherlands: effects of habitat fragmentation. *Journal of Vegetation Science* 8, 21–28.
- Haig, A.R., Matthes, U., Larson, D.W., 2000. Effects of natural habitat fragmentation on the species richness, diversity, and composition of cliff vegetation. *Canadian Journal of Botany* 78, 786–797.
- Hill, J.L., Curran, P.J., 2001. Species composition in fragmented forests: conservation implications of changing forest area. *Applied Geography* 21, 157–174.
- Hobbs, E.R., 1988. Species richness of urban forests patches and implications for urban landscape diversity. *Landscape Ecology* 1, 141–152.
- Honnay, O., Endels, P., Vereecken, H., Hermy, M., 1999. The role of patch area and habitat diversity in explaining native plant

- species richness in disturbed suburban forest patches in northern Belgium. *Diversity and Distributions* 5, 129–141.
- Howe, H.F., Smallwood, J., 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13, 201–228.
- Inghe, O., Tamm, C.O., 1985. Survival and flowering of perennial herbs. IV. The behaviour of *Hepatica nobilis* and *Sanicula europaea* on permanent plots during 1943–81. *Oikos* 45, 400–420.
- Kapos, V., 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. *Journal of Tropical Ecology* 5, 173–185.
- Kapos, V., Wandelli, E., Camargo, J.L., Ganade, G., 1997. Edge-related changes in environment and plant responses due to forest fragmentation in Central Amazonia. In: Laurance, W.F., Bierregaard, R.O. (Eds.), *Tropical Forest Remnants: Ecology, Management, and Conservation of Forest Communities*. University of Chicago Press, Chicago, pp. 33–44.
- Kolb, A., Diekmann, M., 2004. Effects of environment, habitat configuration and forest continuity on the distribution of forest plant species. *Journal of Vegetation Science* 15, 199–208.
- Laurance, W.F., Yensen, E., 1991. Predicting the impacts of edge effects in fragmented habitats. *Biological Conservation* 55, 77–92.
- Laurance, W.F., Ferreira, L.V., Rankin-de-Merona, J.M., Laurance, S.G., Hutchings, R.W., Lovejoy, T.E., 1998. Effects of forest fragmentation on recruitment patterns in Amazonian tree communities. *Conservation Biology* 12, 460–464.
- Lindborg, R., Eriksson, O., 2004. Historical landscape connectivity affects present plant species diversity. *Ecology* 85, 1840–1845.
- MacArthur, R.H., Wilson, E.O., 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton.
- Matlack, G.R., 1994. Vegetation dynamics of the edge – trends in space and successional time. *Journal of Ecology* 82, 113–123.
- Mattos, C.O., 1996. Contribuição ao planejamento e gestão da Área de Proteção Ambiental de Souza e Joaquim Egídio, Campinas/SP. Dissertação de Mestrado. Universidade Estadual de São Paulo, São Paulo.
- McCune, B., Grace, J.B., 2002. *Analysis of ecological communities*. MjM Software Design, Gleneden Beach, Oregon.
- McCune, B., Mefford, M.J., 1999. *PC-ORD. Multivariate analysis of ecological data*. Version 4.34. MjM Software, Gleneden Beach, Oregon.
- Mello, M.H.A., Pedro Jr., M.J., Ortolani, A.A., Alfonsi, R.R., 1994. *Chuva e Temperatura: cem anos de observações em Campinas*. Boletim Técnico 154. Instituto Agrônomo Campinas, Campinas.
- Metzger, J.P., Bernacci, L.C., Goldemberg, R., 1997. Pattern of tree species diversity in riparian forest fragments of different widths (SE Brazil). *Plant Ecology* 133, 135–152.
- Miranda, Z.A.I., 1996. Plano de gestão da Área de Proteção Ambiental da região de Souza e Joaquim Egídio – APA Municipal. Relatório da Secretaria de Planejamento e Meio Ambiente – SEPLAMA. Prefeitura Municipal de Campinas, Campinas.
- Oliveira, J.B., Marcelo, N.C., Rossi, M., Calderano Filho, B., 1999. Mapa pedológico do estado de São Paulo. Legenda expandida, in: Oliveira, J.B. (Ed.), 1999. Boletim científico no. 45, Solos do estado de São Paulo. Embrapa and IAC, Campinas.
- Oliveira-Filho, A.T., Vilela, E.A., Carvalho, D.A., Gavilanes, M.L., 1994. Effects of soil and topography on the distribution of tree species in a tropical riverine forest in southeastern Brazil. *Journal of Tropical Ecology* 10, 483–508.
- Patterson, B.D., 1987. The principle of nested subsets and its implications for biological conservation. *Conservation Biology* 1, 321–334.
- Pimm, S.L., Jones, H.L., Diamond, J., 1988. On the risk of extinction. *The American Naturalist* 132, 757–785.
- Ross, K.A., Fox, B.J., Fox, M.D., 2002. Changes to plant species richness in forest fragments: fragment age, disturbance and fire history may be as important as area. *Journal of Biogeography* 29, 749–765.
- Santin, D.A., 1999. A vegetação remanescente do município de Campinas (SP): mapeamento, caracterização fisionômica e florística, visando a conservação. Tese de doutorado. Universidade Estadual de Campinas, Campinas.
- Santos, K., 1998. Flora arbustivo-arbórea do fragmento de floresta estacional semidecidual do Ribeirão Cachoeira, Campinas, SP. Dissertação de Mestrado. Universidade Estadual de Campinas, Campinas.
- Santos, K., Kinoshita, L.S., 2003. Flora arbustivo-arbórea do fragmento de floresta estacional semidecidual do Ribeirão Cachoeira, Município de Campinas – SP. *Acta Botanica Brasílica* 17, 325–341.
- Saunders, D.A., Hobbs, R.J., Margules, C.R., 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5, 18–32.
- Shafer, M.L., 1981. Minimum population sizes for species conservation. *Bioscience* 31, 131–134.
- Shepherd, G.J., 1988. FITOPAC – versão preliminar. Manual do usuário. Departamento de Botânica. Instituto de Biologia, Universidade Estadual de Campinas, Campinas.
- Tabanez, A.A.J., Viana, V.M., Dias, A.S., 1997. Consequências da fragmentação e do efeito de borda sobre estrutura, diversidade e sustentabilidade de um fragmento de floresta de planalto de Piracicaba, SP. *Revista Brasileira de Biologia* 57, 47–60.
- Tabarelli, M., Mantovani, W., 1999. A riqueza de espécies arbóreas na floresta atlântica de encosta no estado de São Paulo (Brasil). *Revista Brasileira de Botânica* 22, 217–223.
- Tilman, D., May, R.M., Lehman, C.L., Nowak, M.A., 1994. Habitat destruction and the extinction debt. *Nature* 371, 65–66.
- Torres, R.B., Martins, F.R., Kinoshita, L.S., 1997. Climate, soil and tree flora relationships in forests in the state of São Paulo, southeastern Brazil. *Revista Brasileira de Botânica* 20, 41–51.
- Torti, S.D., Coley, P.D., Kursar, T.A., 2001. Causes and consequences of monodominance in tropical lowland forests. *The American Naturalist* 157, 141–153.
- Turner, I.M., 1996. Species loss in fragments of tropical rain forest: a review of evidence. *Journal of Applied Ecology* 33, 200–209.
- Turner, I.M., Corlett, R.T., 1996. The conservation value of small, isolated fragments of lowland tropical rain forest. *Trends in Ecology and Evolution* 11, 330–333.
- Turner, I.M., Chua, K.S., Ong, J., Soong, B., Tan, H., 1996. A century of plant species loss from an isolated fragment of lowland tropical rainforest. *Conservation Biology* 10, 1229–1244.
- Van der Pijl, L., 1982. *Principles of Dispersal in Higher Plants*. Springer-Verlag, Berlin.
- Vellend, M., Verheyen, K., Jacquemyn, H., Kolb, A., van Calster, H., 2006. Extinction debt of forest plants persists for more than a century following habitat fragmentation. *Ecology* 87, 542–548.
- Veloso, H.P., Rangel Filho, A.L.R., Lima, J.C., 1991. Classificação da vegetação Brasileira adaptada a um sistema universal. Instituto Brasileiro de Geografia e Estatística (IBGE), Rio de Janeiro.
- Vormisto, J., Tuomisto, H., Oksanen, J., 2004. Palm distribution patterns in Amazonian rainforests: What is the role of topographic variation? *Journal of Vegetation Science* 15, 485–494.