



Variations in tree community composition and structure in a fragment of tropical semideciduous forest in southeastern Brazil related to different human disturbance histories[☆]

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Abstract

In an area of tropical seasonal semideciduous forest, the soil characteristics, floristic composition, physiognomic structure, and the distribution of three regeneration and three dispersal guilds were studied for four stands within the forest that had documented histories of varying degrees of human disturbance. The aim was to study forest regeneration in areas of preserved forest and secondary forest, with parts of both types of forest experiencing either 'intensive' or 'occasional' cattle trampling. The study was carried out in the Sebastião Aleixo da Silva Ecological Station, Bauru, São Paulo State, Brazil. Two stands were called 'secondary' because they corresponded to forest tracts that were felled and occupied by crops and pastures in the past and then abandoned to forest regeneration ca. 40 years before this study. The other two stands, called 'preserved', corresponded to areas of the fragment where the forest has been maintained with only minor human impacts. The arboreal component of the tree community (diameter at breast height or dbh ≥ 5 cm) was sampled in 20 plots of 40 m \times 40 m, and the subarboreal component (diameter at the base of the stem or dbb < 5 cm and height ≥ 0.5 m) in subplots of 40 m \times 2 m. Physiognomic features, such as canopy height and density of climbing plants, were registered all over a 5 m \times 5 m gridline laid on the sample plots. Soil bulk samples were collected for chemical and textural analyses. Most detected differences contrasted the secondary to the preserved forest stands. The soils of the secondary stands showed higher proportions of sand and lower levels of mineral nutrients and organic matter than those of the preserved stands, probably due to higher losses by leaching and erosion. Compared to the secondary stands, the preserved ones had higher proportions of tall trees, higher mean canopy height, lower species diversity, higher abundance of autochorous and shade-tolerant climax species, and lower abundance of pioneer and light-demanding climax species. Despite the high proportion of species shared by the preserved and secondary stands (108 out of 139), they differed consistently in terms of density of the most abundant species. On the other hand, the secondary and preserved stands held similar values for tree density and basal area, suggesting that 40 years were enough to restore these features. Effects of cattle trampling on the vegetation were detected for the frequency of trees of anemochorous and zoochorous species, which were higher in the stands under occasional and intensive cattle trampling, respectively. The density of thin climbers was lower in the stands with intensive trampling.

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1. Introduction

In the last decades, the area of disturbed forest has increased dramatically throughout the tropics as a result of human activities (Victor, 1975; Bushbacher, 1986; CONSEMA, 1985, Schmidt, 1987; Kronka et al., 1993). These forests are the result of either the continuous use of the primary forest for cattle grazing and wood harvesting or the abandonment of areas that were previously cleared for agricultural/cattle breeding activities, and are currently known as secondary forests (Brown and Lugo, 1990).

Disturbed forests can recover several of their features through the regeneration process (Saldarriaga and Uhl, 1991), depending upon the type of forest involved (Ewel, 1980); the intensity and frequency of disturbance rates (Uhl et al., 1982, 1988; Uhl and Bushbacher, 1985); the existence of appropriate microhabitats for plant regeneration through both establishment from seeds and sprouting of remaining stems and roots, the presence of a seed bank in the soil (Uhl, 1987; Young et al., 1987; Nepstad et al., 1996), the dispersion or seed rain inside the area (Guevara et al., 1986; Thomlinson et al., 1996; Otero-Arnaiz et al., 1999; Slocum and Horvitz, 2000), and the conditions of soil fertility and compacting (Buschbacher et al., 1988; Congdon and Herborn, 1993; Guariguata and Dupuy, 1997).

Some studies on the regeneration of tropical secondary forests after human interference have registered the changes taking place over several years, after disturbance ceased and the areas were abandoned (Uhl et al., 1982; Uhl, 1987). Research time is obviously the main limitation in these studies. Alternatively, other studies compare forest stands with different regeneration ages among themselves and with old-growth forest stands (Purata, 1986; Buschbacher et al., 1988; Saldarriaga et al., 1988; Aide et al., 1996; Vieira et al., 1996; Tabarelli and Mantovani, 1999; Zahawi and Augspurger, 1999). In both types of study, information on disturbance history and previous land use is essential.

Despite the high proportion of disturbed forest remnants in the present cover of the Brazilian Atlantic Forest (*sensu* Oliveira-Filho and Fontes, 2000), detailed studies on post-disturbance forest regeneration in southeastern Brazil are recent and scarce

(Oliveira-Filho et al., 1997; Tabarelli and Mantovani, 1999; Nunes et al., 2003). The current situation of the tropical semideciduous forests of São Paulo State represents a significant example of the drastic process of forest fragmentation and disturbance that took place in the region. Those forests used to cover an impressive proportion of the state's hinterlands (ca. 80%) before they were cut for wood exploitation, agricultural expansion, and industrial/urban growth (Victor, 1975; Leitão Filho and Morellato, 1995). Nowadays, the semideciduous forests of São Paulo State represent less than 5% of its original cover and occur discontinuously, in fragments of various sizes, protected either within state conservation units or as legally protected areas within private properties (Viana et al., 1997). The fragments are presently under protection of environmental legislation (Milaré, 1991), but are commonly surrounded by pasturelands, croplands and urban areas, which are potential sources of additional disturbance. Considering their critical situation, the protection of those fragments is of great urgency for biodiversity conservation in the region. An increased knowledge about their structure and organization, and their response to fragmentation and disturbance, is essential for the formulation of conservation policies and management plans aiming at both holding back the degradation process and promoting forest reclamation (Janzen, 1988; Viana et al., 1992; Leitão Filho and Morellato, 1995).

In the present contribution, we describe and compare the soils and tree communities of four stands of a fragment of tropical semideciduous forest in Bauru, São Paulo State, SE, Brazil, having a well documented history of disturbance. The four forest stands differed among themselves with respect to two main disturbance aspects: old-growth or second-growth and high or low intensity of cattle trampling and grazing.

We formulated two hypotheses: the forest stands that were felled and cultivated in the past (secondary stands) differ in soil chemical and textural properties and forest physiognomic structure, floristic composition, and species diversity from the stands that have been free from cutting (preserved stands); the forest stands that were under different intensities of trampling and grazing by cattle differ in tree community features, particular for the regeneration component (understory).

2. Materials and methods

2.1. Study area

The studied fragment of submontane seasonal semi-deciduous forest (*sensu* IBGE, 1992) covers an area of about 200 ha within the Sebastião Aleixo da Silva Ecological Station, Bauru municipality, São Paulo State, Brazil, situated at the coordinate 22°19'S and 49°04'W and at an altitude of 570 m (Fig. 1A). The area is currently surrounded by pasturelands. The predominant soils are reddish dystrophic Ferralsols (*sensu* FAO/UNESCO) or oxysols in VS Soil Taxonomy System. The climate is classified as sub-humid mesothermal with reduced rainfall during the winter, i.e. Thornthwaite's CB'cw type (Figueiredo and Sugahara, 1997). Data from the UNESP/Bauru Meteorological Research Institute (50 years of records) yield average monthly temperatures and rainfall rates of 26 °C and 250 mm, respectively, for the warmest months (December–January–February), and 20 °C and 50 mm, respectively, for the cooler months (May–June–July).

The area was privately owned until 1961, when it was disappropriated by the São Paulo State Forestry Institute and became a state conservation unit (Nogueira and Nogueira, 1991). According to information obtained from long-dwelling inhabitants and workers, the previous landowner preserved the forest at the more elevated sites, although selective logging took place occasionally. Adjacent forest areas were cleared and replaced by pastures and crops. After the change in ownership, these cultivated areas (ca. 100 ha) were abandoned and rapidly occupied by

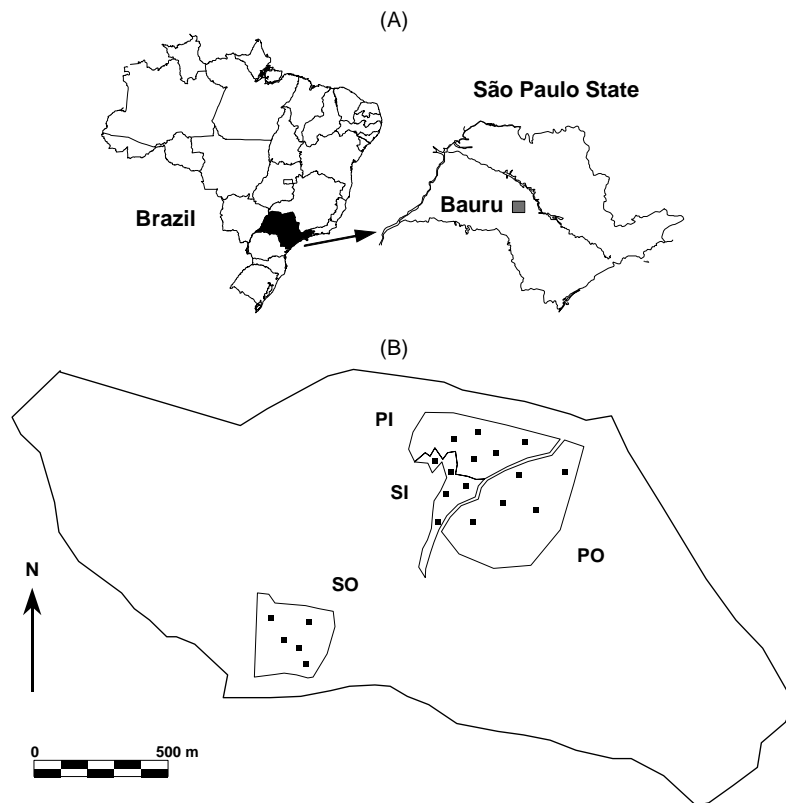


Fig. 1. (A) Geographical situation of the municipality of Bauru, São Paulo state, Brazil, and (B) outline of the Sebastião Aleixo da Silva Ecological Station showing the distribution of the 20 samples plots (40 m × 40 m of dimensions), shown as black squares, within the four studied stands of tropical semideciduous forest: PO—preserved forest with occasional cattle trampling; PI—preserved forest with intensive cattle trampling; SO—secondary forest with occasional cattle trampling; SI—secondary forest with intensive cattle trampling.

weeds, particularly the grass species *Panicum maximum* and *Melinis minutiflora*. In 1962, as a procedure to prevent the spreading of such weedy species and to reduce the risk of fire during the dry season, the local administration decided to introduce cattle into the area. Since then, cattle have been raised in the area, although the number of animals gradually reduced from ca. 50, in the 1960's, to ca. 15 at the time of this study (1998–1999). The animals have had full access to the whole forest area, although they usually concentrate their grazing and resting near water sources and adjacent pastures. According to Nogueira and Nogueira (1991), the cattle did promote the clearing of weedy grasses in the abandoned croplands and pastures, and also favored the dispersal of *Psidium guajava* (guava), which has been the main colonizing tree species in those areas. Nowadays, most of the area of the Ecological Station is occupied by forest physiognomies. With the help of maps, aerial photographs, and the knowledge of local people, we could easily discriminate in the field the second-growth areas from those covered by old-growth forest. Cavassan et al. (1984) produced the first description of the floristic composition and community structure of these forests.

2.2. Sampling design and surveys of the tree community and soils

We choose four forest stands for the purpose of this study, each of them combining a particular disturbance history. There were two stands of secondary forests, which had been cut and used for cattle grazing and plantations and then abandoned to forest regeneration 40 years before the present study, and two stands of preserved forests, corresponding to old-growth forest areas where only occasional selective logging took place in the distant past. In addition, we divided these two main categories into two classes of cattle grazing and trampling intensity, resulting in the four stands, defined as follows: (1) PO stand: preserved forest with occasional cattle trampling; (2) PI stand: preserved forest with intensive cattle trampling; (3) SO stand: secondary forest with occasional cattle trampling; (4) SI stand: secondary forest with intensive cattle trampling (Fig. 1B). We assessed the intensity of cattle usage of the forest with the help of local workers and by registering the density of cattle signs, such as

tracks, feces and vegetation clearings (herd resting spots).

We randomly located five sample plots of 40 m × 40 m (0.8 ha per stand) in each of the four forest stands (Fig. 1B) and also outlined a subplot of 40 m × 2 m along the central divide of each sample plot (0.04 ha per stand). We surveyed separately two components of the tree community: (a) the arboreal component comprised all individuals (including dead but still standing trees) with diameter ≥ 5.0 cm at breast height (dbh measured at 1.30 m) found within the 20 sample plots; (b) the subarboreal component included individuals ≥ 0.5 m high and with diameter at the base of the stem (dbs) < 5.0 cm found within the 20 subplots. We identified to species (dead trees excepted) and measured the height and circumference at breast height (cbh, for arboreal individuals) or at the base of the stem (cbs, for subarboreal individuals) of all recorded individuals. Voucher specimens are stored at the herbaria of the Universidade Estadual de Campinas (UEC) and Instituto Florestal (IFSP). Species were classified into the families recognized by the Angiosperm Phylogeny Group II (2003).

We collected 1.0 L soil samples from a depth of 0–20 cm at 16 spots randomly distributed within each sample plot. Then we mixed up the 16 soil samples to produce a single soil sample representative of the plot surface soil. Chemical and textural analyses were carried out at the Soil Laboratory of the Universidade Federal de Lavras following the standard procedures proposed by EMBRAPA (1997).

2.3. Description of forest physiognomic features

We described the physiognomic structure of the four forest stands through the following features: (a) number of individuals; (b) basal area; (c) mean and maximum height; (d) mean and maximum diameter; (e) abundance of climbing plants; (f) canopy height; (g) area of canopy gaps; (h) number of dead trees. We calculated all features for each of the 20 sample plots or their corresponding subplots. We extracted the first four features (a–d) from the data for live arboreal and subarboreal individuals, treated separately, and the number of dead trees (h) for arboreal individuals only. We obtained the other features (e–g) as follows:

According to Gentry (1991), ‘lianas’ are woody climbing plants, with thick stems, which are capable of growing in mature forests, while ‘vines’ are herbaceous or sub-woody climbing plants, with thinner stems, which commonly grow in disturbed places or at forest borders. The distinction between lianas and vines using these criteria requires a detailed knowledge of the species, which was absent in the present work, as we focused on trees. Therefore, we treated climbing plants as a growth-form and classified them into two categories based only on stem thickness. We assessed the abundance of climbing plants by counting the number of stems at eye height (about 1.60 m) of ‘thin’ (0.5–3.0 cm diameter) and ‘thick’ (>3.0 cm diameter) climbers found within each of the 64 subplots defined by a 5 m × 5 m grid laid on each sample plot. We recorded the number of stems at each of those subplots as abundance classes, defined as: (a) very abundant, 31–40 stems; (b) abundant, 21–30 stems; (c) intermediate, 11–20 stems; (d) few, 1–10 stems; (e) none; for thin climbers; and (f) very abundant, 10–16 stems; (g) abundant, 8–9 stems; (h) intermediate, 4–7 stems; (i) few, 1–3 stems; (j) none; for thick climbers. We used the class interval central values to obtain sample plot totals.

To assess the mean canopy height and area of canopy gaps of each sample plot, we measured the maximum height reached by the vegetation at the four corners of each of the same 64 subplots described above. We then produce a subplot mean for canopy height and an area of canopy gaps by counting the number of subplots with mean canopy height < 5 m. Both the procedure and criterion were based on Hubbel and Foster (1986) and Oliveira-Filho et al. (1997).

2.4. Species classification into regeneration and dispersion guilds

In order to search for ecologically meaningful differences between the forest stands for particular species groups, we classified all species into two guild systems: regeneration and dispersion (Denslow, 1980; Wheelwright, 1985; Wilson, 1989). The regeneration guilds, based on Swaine and Whitmore (1988) ecological species groups, were: (a) pioneer; (b) shade-tolerant climax species; (c) light-demanding climax species. Pioneer and climax species differ in the light environment required for establishment, the former

depending on direct sunlight. Light-demanding and shade-tolerant climax species are actually the halves of a continuum of solar radiation required by the plants for release from the bank of juveniles. The dispersion guilds were: (a) anemochorous, species with mechanisms to facilitate wind dispersion; (b) zoochorous, species with characteristics related to dispersal by animals; (c) autochorous, species dispersed by free fall or explosive mechanisms (van der Pijl, 1982). The classification of each species into the species guilds was based on a substantial body of scientific knowledge registered in the literature (Morellato and Leitão-Filho, 1992; Lorenzi, 1992, 1998; Gandolfi et al., 1995; Oliveira-Filho et al., 1997; Barroso et al., 1999; Nunes et al., 2003).

2.5. Data analysis

We used three parameters of species diversity to compare the four forest stands: species density per plot or subplot, Shannon diversity index (H') and Pielou evenness (J') (Krebs, 1989). We performed paired comparisons of the Shannon diversity indices of the four stands using the Hutcheson t -test for H' (Zar, 1996). After a graphical verification on data normality, we assessed differences among the four stands concerning species density per plot or subplot, soil chemical and textural properties and vegetation physiognomic features through analyses of variance, followed by Tukey tests, where appropriate. We tested the distribution of individuals into the species guilds for independence in the four forest stands using χ^2 -tests for contingency tables (Zar, 1996).

We performed a detrended correspondence analyses, DCA (Kent and Coker, 1992), using the program PC-ORD 3.0 (McCune and Mefford, 1997) in order to investigate the patterns emerging from species abundance in the light of differences among plots concerning environmental variables, disturbance history and species guilds (an a posteriori interpretation). We prepared two species abundance matrixes, for the arboreal and subarboreal components, which consisted of the number of individuals of each species across sample unit. The matrixes included only the 55 and 49 species with >10 arboreal and subarboreal individuals, respectively, in the total sample because of the negligible and irrelevant effects of rare species on ordination results. The abundance values were

log-transformed before analysis, as their distributions were skewed towards a few very large values (ter Braak, 1995).

3. Results

3.1. Soils

Using the interpretation criteria adopted by the Soil Laboratory of the Universidade Federal de Lavras, the soils of all forest stands were characterized by a sandy texture (>83% of sand), weak acidity, low amounts of P and high concentration of K^+ , but levels of Ca^{2+} , Mg^{2+} , total bases, saturation of bases and organic matter were high in the preserved stands, and intermediate to low in the secondary stands (Table 1). In fact, soil pH and levels of P, K^+ , Ca^{2+} , Mg^{2+} , total bases, saturation of bases and organic matter were significantly higher in the preserved than in the secondary stands, though PI and SO stands did not differ significantly for K^+ and Mg^{2+} . The percentage of sand was higher and the percentage of silt and clay were lower in soils of the secondary stands than in those of the preserved stands, though the PI and SO stands did not differ significantly for sand and silt, while the PI and SI stands did not differ significantly for clay.

Generally speaking, the soils of the secondary stands were coarser textured, more acidic and poorer in exchangeable bases and organic matter than those of the preserved stands. The overall 0.0 levels of Al^{3+} are probably related to the high soil pH that normally inhibits the formation of its exchangeable form.

3.2. Physiognomic features

For the mean density of arboreal individuals, the separate counts of dead trees, and the basal area of both arboreal and subarboreal individuals there were found no significant differences among the four forest stands, however, the mean density of subarboreal individuals differed significantly between the PO and SI stands, being nearly twice as high in the latter (Table 2). The preserved and secondary stands differed significantly for both the mean and maximum heights of arboreal individuals in the sample plots, with higher means in the preserved stands; for subarboreal individuals, there was no significant difference among the stands for maximum height and only the PO and SI stands differed for mean height, with higher means in the former. Most differences in both mean and maximum diameters among forest stands were non-significant and significant differences were found only

Table 1

Chemical and textural variables of the surface soil (0–20 cm of depth) in the four stands of tropical semideciduous forest surveyed in Bauru, SE, Brazil

Forest stands	pH in H ₂ O	P Mehlich (mg dm ⁻³)	K ⁺ (mg dm ⁻³)	Ca ²⁺ (cmol _c dm ⁻³)	Mg ²⁺ (cmol _c dm ⁻³)	Al ³⁺ (cmol _c dm ⁻³)
PO	6.8 ± 0.2 a**	4.4 ± 1.1 a**	139.8 ± 24.2 a*	10.0 ± 0.9 a**	1.5 ± 0.4 a*	0.0 ± 0.0 ns
PI	6.7 ± 0.4 a**	4.6 ± 1.3 a**	127.2 ± 34.8 ab*	7.6 ± 1.7 b**	1.5 ± 0.4 a*	0.0 ± 0.0 ns
SO	6.1 ± 0.1 b**	1.8 ± 0.4 b**	90.6 ± 13.4 b*	2.3 ± 1.1 c**	1.2 ± 0.1 ab*	0.0 ± 0.0 ns
SI	5.9 ± 0.2 b**	1.8 ± 0.4 b**	80.8 ± 15.2 b*	3.1 ± 0.2 c**	0.9 ± 0.3 b*	0.0 ± 0.0 ns
	Total bases (cmol _c dm ⁻³)	Saturation of bases (%)	Organic matter (%)	Sand (%)	Silt (%)	Clay (%)
PO	11.8 ± 1.1 a**	89.4 ± 1.8 a**	4.4 ± 1.8 a**	83.0 ± 1.8 c**	8.0 ± 1.6 a**	9.0 ± 1.0 a*
PI	9.5 ± 2.1 a**	86.3 ± 3.9 a**	3.1 ± 0.6 b**	86.6 ± 3.0 bc**	5.0 ± 1.9 b**	8.4 ± 2.7 ab*
SO	3.7 ± 1.2 b**	64.9 ± 9.0 b**	1.7 ± 0.6 c**	89.6 ± 2.1 ab**	4.6 ± 1.5 b**	5.8 ± 0.8 b*
SI	4.2 ± 0.5 b**	69.4 ± 3.6 b**	1.6 ± 0.2 c**	91.6 ± 1.8 a**	2.0 ± 1.2 b**	6.4 ± 0.9 ab*

Figures are mean ± S.D. of five soil samples. Where analyses of variance indicated significant differences among plots ($P < 0.05$), means followed by different letters indicate significant differences in Tukey tests ($P < 0.05$). Forest stands: PO—preserved forest with occasional cattle trampling; PI—preserved forest with intensive cattle trampling; SO—secondary forest with occasional cattle trampling; SI—secondary forest with intensive cattle trampling. Ns: not significant. cmol_c = centimoles of charge.

* $P < 0.05$.

** $P < 0.01$.

Table 2

Physiognomic variables of the four stands of tropical semideciduous forest surveyed in Bauru, SE, Brazil

Forest stands	Number of individuals, arboreal (ha ⁻¹)	Number of individuals, subarboreal (ha ⁻¹)	Basal area, arboreal (m ² ha ⁻¹)	Basal area, subarboreal (m ² ha ⁻¹)
PO	1330 ± 137 ns	9050 ± 4724 b*	26.12 ± 6.60 ns	4.58 ± 1.80 ns
PI	1165 ± 133 ns	12700 ± 4080 ab*	19.50 ± 10.60 ns	6.02 ± 1.56 ns
SO	1155 ± 344 ns	14650 ± 1708 ab*	14.88 ± 2.79 ns	6.17 ± 1.23 ns
SI	1229 ± 187 ns	19575 ± 7620 a*	19.51 ± 3.49 ns	3.90 ± 0.35 ns
	Mean height, arboreal (m)	Mean height, subarboreal (m)	Max. height, arboreal (m)	Max. height, subarboreal (m)
PO	9.4 ± 1.0 a**	1.8 ± 0.4 a*	27.2 ± 4.4 a**	6.4 ± 0.9 ns
PI	10.1 ± 0.4 a**	1.7 ± 0.3 ab*	30.8 ± 1.1 a**	7.7 ± 0.4 ns
SO	7.3 ± 0.2 b**	1.5 ± 0.3 ab*	17.4 ± 3.0 b**	6.9 ± 1.4 ns
SI	8.1 ± 0.8 b**	1.2 ± 0.2 b*	20.5 ± 3.5 b**	6.6 ± 0.9 ns
	Mean diameter, arboreal (cm)	Mean diameter, subarboreal (cm)	Max. diameter, arboreal (cm)	Max. diameter, subarboreal (cm)
PO	12.5 ± 1.18 ns	2.2 ± 0.4 a*	67.6 ± 16.5 a*	6.8 ± 1.5 ns
PI	12.9 ± 0.9 ns	1.9 ± 0.5 ab*	63.4 ± 16.4 ab*	8.6 ± 1.7 ns
SO	11.3 ± 1.3 ns	1.7 ± 0.1 ab*	41.8 ± 6.7 b*	9.7 ± 3.5 ns
SI	12.1 ± 0.4 ns	1.3 ± 0.2 b*	52.4 ± 14.6 ab*	6.3 ± 1.5 ns
	Mean canopy height (m)	Number of dead trees (ha ⁻¹)	Number of thick climbers (ha ⁻¹)	Number of thin climbers (ha ⁻¹)
PO	12.1 ± 3.3 a**	74 ± 27 ns	1911 ± 319 a*	8428 ± 2033 a*
PI	13.9 ± 2.2 a**	74 ± 27 ns	1783 ± 731 a*	5228 ± 3076 ab*
SO	7.4 ± 1.6 b**	114 ± 66 ns	975 ± 109 b*	8438 ± 1000 a*
SI	9.3 ± 0.7 b**	71 ± 22 ns	1281 ± 308 ab*	4636 ± 1408 b*

Figures are mean ± S.D. of five sample units (1600 m² for arboreal and 80 m² for subarboreal). Where analyses of variance indicated significant differences among plots ($P < 0.05$), means followed by different letters indicate significant differences in Tukey tests ($P < 0.05$). Forest stands: PO—preserved forest with occasional cattle trampling; PI—preserved forest with intensive cattle trampling; SO—secondary forest with occasional cattle trampling; SI—secondary forest with intensive cattle trampling. ns: not significant.

* $P < 0.05$.

** $P < 0.01$.

for mean diameter of subarboreal individuals, higher in the PO than in the SI stands, and maximum diameter of arboreal individuals, higher in the PO than in the SO stands. In short, the preserved stands differed from the secondary mainly in a greater number of larger individuals and lower density of smaller and thinner subarboreal individuals. Indeed, the largest sampled individuals (height > 20 m and diameter > 40 cm), though not abundant (1.2% of total), occurred almost exclusively in the preserved stands (117 out of 122).

The higher abundance of taller individuals in the preserved stands is consistent with both the mean canopy heights (Table 2) and frequency distributions of canopy heights in the four forest stands (Fig. 2),

both with higher values in the preserved than in the secondary stands. In fact, in the secondary stands, more than 50% of canopy height records were below 10 m and none were above 20 m whereas, in the preserved stands, more than 50% were between 10 and 20 m and ca. 10% were above 20 m. The largest area of canopy gaps (canopy height < 5 m) was found for the SO stand (63 out of 320 records), with very low values in the other stands.

The mean density of thick climbers was higher in the preserved than in the secondary stands, while the density of thin climbers was higher in the stands with occasional cattle trampling than in those with intensive trampling, PO and SO (Table 2). Nevertheless, these differences were not significant for the SI and PI

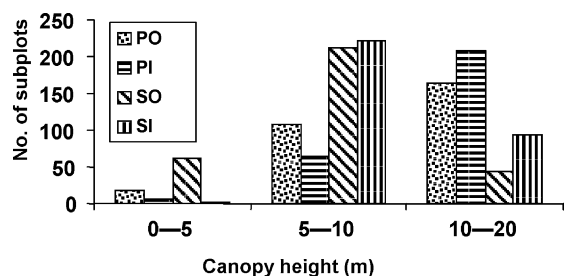


Fig. 2. Frequency distribution of mean canopy heights at the 320 subplots (5 m × 5 m of dimensions) laid on the five sample plots (40 m × 40 m of dimensions) used to survey each of the four stands of tropical semideciduous forest in Bauru, SE, Brazil. Forest stands: PO—preserved forest with occasional cattle trampling; PI—preserved forest with intensive cattle trampling; SO—secondary forest with occasional cattle trampling; SI—secondary forest with intensive cattle trampling.

Table 3

Species sampled in the fragment of tropical semideciduous forest surveyed in Bauru, SE, Brazil, with their number of arboreal and subarboreal individuals registered in the four forest stands (PO—preserved forest with occasional cattle trampling; PI—preserved forest with intensive cattle trampling; SO—secondary forest with occasional cattle trampling; SI—secondary forest with intensive cattle trampling) and their classification into guilds of regeneration (Reg) and dispersion (Disp)

Families and species	Arboreal				Subarboreal				Guilds	
	PO	PI	SO	SI	PO	PI	SO	SI	Reg	Disp
Anacardiaceae										
<i>Astronium graveolens</i> Jacquin	7	1	11	6	12	33	4	25	Stc	Ane
<i>Tapirira guianensis</i> Aublet	–	–	5	–	–	–	1	5	Ldc	Zoo
Annonaceae										
<i>Annona cacans</i> Warm.	–	3	5	3	–	–	–	–	Ldc	Zoo
<i>Unonopsis lindmanii</i> R.E.Fries	3	5	2	–	6	7	3	8	Stc	Zoo
<i>Xylopia aromatica</i> (Lam.) Mart.	–	–	1	–	–	–	–	–	Ldc	Zoo
Apocynaceae										
<i>Aspidosperma parvifolium</i> A.DC.	2	–	–	–	–	–	–	–	Ldc	Ane
<i>Aspidosperma polyneuron</i> Müll.Arg.	254	43	–	–	42	17	–	1	Ldc	Ane
<i>Tabernaemontana catharinensis</i> A.DC.	4	144	88	180	–	13	20	26	Ldc	Zoo
Araliaceae										
<i>Aralia warmingiana</i> (E.Marchal) Harms	–	2	–	1	–	–	–	–	Ldc	Zoo
Arecaceae										
<i>Acrocomia aculeata</i> (Jacquin) Lodd.	–	–	2	–	–	–	–	–	Pio	Zoo
<i>Syagrus oleracea</i> (Mart.) Becc.	7	1	–	–	–	–	–	–	Ldc	Zoo
<i>Syagrus romanzoffiana</i> (Cham.) Glassman	–	–	3	1	–	–	–	–	Ldc	Zoo
Asteraceae										
<i>Gochnatia polymorpha</i> (Less.) Cabrera	–	–	159	5	–	–	38	4	Pio	Ane
Bignoniaceae										
<i>Jacaranda micrantha</i> Mart.	2	–	1	–	–	–	–	–	Ldc	Ane
<i>Tabebuia alba</i> (Cham.) Sandw.	–	–	7	–	–	–	5	–	Ldc	Ane
<i>Tabebuia heptaphylla</i> (Vell.) Toledo	–	2	–	2	–	–	–	–	Stc	Ane
<i>Tabebuia impetiginosa</i> (Mart.) Standley	–	–	–	13	–	–	–	–	Ldc	Ane
<i>Zyheria tuberculosa</i> (Vell.) Bureau	–	2	4	–	–	–	2	–	Ldc	Ane

stands, concerning thick climbers and thin climbers, respectively.

In conclusion, most physiognomic features with significant differences among stands were related to the preserved–secondary comparisons, and the sole feature that could be associated with cattle trampling intensity was the density of thin climbers, though this was significantly lower only for the SI stand.

3.3. Tree community structure and species diversity

The surveys totaled 3903 arboreal individuals in 3.2 ha of plots and 2239 subarboreal individuals in 0.16 ha of corresponding subplots, which were identified as belonging to 139 species and 45 botanical families. The species list and their number of arboreal

Table 3 (Continued)

Families and species	Arboreal				Subarboreal				Guilds	
	PO	PI	SO	SI	PO	PI	SO	SI	Reg	Disp
Boraginaceae										
<i>Cordia ecalyculata</i> Vell.	–	2	–	–	–	1	2	6	Ldc	Zoo
<i>Cordia superba</i> Cham.	1	–	–	–	–	–	–	–	Stc	Zoo
<i>Cordia trichotoma</i> (Vell.) Arrab.	1	2	10	7	–	1	2	4	Ldc	Ane
<i>Patagonula americana</i> L.	12	11	3	2	–	4	16	4	Stc	Ane
Burseraceae										
<i>Protium heptaphyllum</i> (Aublet) Marchand	–	–	1	–	–	–	1	1	Ldc	Zoo
Cannabaceae										
<i>Celtis pubescens</i> Sprengel	3	10	1	38	–	2	1	14	Pio	Zoo
Caricaceae										
<i>Jacaratia spinosa</i> (Aublet) A.DC.	–	3	–	–	–	–	–	–	Pio	Zoo
Celastraceae										
<i>Maytenus ilicifolia</i> Mart.	–	–	–	–	1	–	2	–	Stc	Zoo
Combretaceae										
<i>Terminalia triflora</i> (Griseb.) Lillo	–	–	13	3	–	–	13	–	Ldc	Ane
Ebenaceae										
<i>Diospyros inconstans</i> Jacquin	2	1	4	–	–	3	4	–	Stc	Zoo
Erythroxylaceae										
<i>Erythroxylum pelleterianum</i> A.St.-Hil.	–	–	–	–	–	–	2	–	Stc	Zoo
Euphorbiaceae										
<i>Actinostemon klotzschii</i> (Didrichs) Pax	7	3	–	–	53	58	1	–	Stc	Aut
<i>Alchornea glandulosa</i> Poepp. & Endl.	–	2	4	30	–	–	–	13	Pio	Zoo
<i>Croton floribundus</i> Sprengel	–	12	29	121	–	7	12	12	Pio	Aut
<i>Gymnanthes concolor</i> (Sprengel) Muell.Arg.	1	–	–	–	12	–	–	4	Stc	Aut
<i>Sapium glandulosum</i> (L.) Morong	–	–	–	2	–	–	–	–	Ldc	Zoo
Fabaceae										
<i>Acacia polyphylla</i> DC.	19	17	3	6	21	25	2	14	Pio	Ane
<i>Albizia niopoides</i> (Spruce) Burkart	–	–	–	1	–	–	–	–	Ldc	Ane
<i>Albizia polycephala</i> (Benth.) Killip	5	20	7	33	–	1	4	13	Ldc	Ane
<i>Bauhinia longifolia</i> (Bongard) Steudel	–	3	25	34	3	–	19	4	Ldc	Ane
<i>Caesalpinia ferrea</i> Benth.	–	–	–	2	–	–	–	2	Ldc	Zoo
<i>Calliandra foliolosa</i> Benth.	20	8	6	–	15	10	–	–	Stc	Ane
<i>Centrolobium tomentosum</i> Guillem.	22	24	30	–	1	1	6	–	Stc	Ane
<i>Copaifera langsdorffii</i> Desf.	–	–	–	1	–	–	–	–	Ldc	Zoo
<i>Enterolobium contortisiliquum</i> (Vell.) Morong	–	–	2	–	–	–	–	–	Ldc	Zoo
<i>Holocalyx balansae</i> Mich.	123	56	–	–	–	4	–	–	Stc	Zoo
<i>Hymenaea courbaril</i> L.	–	1	–	–	–	–	–	–	Ldc	Zoo
<i>Inga striata</i> Benth.	–	–	–	1	–	–	4	–	Ldc	Zoo
<i>Lonchocarpus cultratus</i> (Vell.) Az.Tozzi & H.C.Lima	2	18	1	11	1	13	2	2	Ldc	Ane
<i>Machaerium brasiliense</i> Vogel	–	–	18	–	–	1	1	–	Ldc	Ane
<i>Machaerium hirtum</i> (Vell.) Stellfeld	–	1	70	24	–	–	12	4	Ldc	Ane
<i>Machaerium nictitans</i> (Vell.) Benth.	5	–	–	–	–	–	–	–	Ldc	Ane
<i>Machaerium stipitatum</i> (DC.) Vogel	43	82	43	39	4	7	25	8	Ldc	Ane
<i>Machaerium villosum</i> Vogel	–	–	1	–	–	–	–	–	Ldc	Ane
<i>Myroxylon peruiferum</i> L.f.	2	–	–	3	–	–	–	–	Stc	Ane

Table 3 (Continued)

Families and species	Arboreal				Subarboreal				Guilds	
	PO	PI	SO	SI	PO	PI	SO	SI	Reg	Disp
Fabaceae (cont.)										
<i>Parapiptadenia rigida</i> (Benth.) Brenan	19	16	10	79	1	9	15	153	Ldc	Ane
<i>Peltophorum dubium</i> (Sprengel) Taub.	4	3	22	31	–	–	–	1	Ldc	Ane
<i>Piptadenia gonoacantha</i> (Mart.) Macbr.	1	23	13	8	–	7	2	10	Pio	Ane
<i>Platypodium elegans</i> Vogel	–	–	–	9	–	–	–	3	Ldc	Ane
<i>Pterogyne nitens</i> Tul.	–	1	2	15	–	–	1	3	Ldc	Ane
<i>Senna obtusifolia</i> (L.) Irwin & Barneby	–	–	–	–	–	–	1	–	Pio	Zoo
<i>Senna splendida</i> (Vogel) Irwin & Barneby	–	–	–	–	–	–	3	–	Pio	Zoo
<i>Stryphnodendron obovatum</i> Benth.	–	–	9	–	–	–	–	–	Ldc	Aut
<i>Sweetia fruticosa</i> Sprengel	4	3	6	–	2	–	–	–	Ldc	Ane
Lauraceae										
<i>Endlicheria paniculata</i> (Sprengel) Macbr.	–	–	3	2	–	–	1	–	Stc	Zoo
<i>Nectandra megapotamica</i> (Sprengel) Mez	–	20	4	12	–	6	3	–	Ldc	Zoo
<i>Ocotea corymbosa</i> (Meisner) Mez	–	–	2	–	–	–	–	–	Ldc	Zoo
<i>Ocotea indecora</i> (Schott) Mez	4	3	–	–	–	–	–	–	Ldc	Zoo
<i>Ocotea velutina</i> (Nees) Rohwer	2	–	1	3	–	–	–	16	Ldc	Zoo
Lecythidaceae										
<i>Cariniana estrellensis</i> (Raddi) Kuntze	1	2	23	1	–	–	8	–	Ldc	Ane
Loganiaceae										
<i>Strychnos brasiliensis</i> (Sprengel) Mart.	–	–	–	–	–	2	2	–	Stc	Zoo
Malvaceae										
<i>Ceiba speciosa</i> (A.St.-Hil.) Gibbs & Semir	22	2	2	2	2	1	–	1	Ldc	Ane
<i>Christiana macrodon</i> Toledo	–	4	–	–	9	2	–	–	Stc	Ane
<i>Guazuma ulmifolia</i> Lam.	–	4	32	58	1	–	–	4	Ldc	Zoo
<i>Luehea divaricata</i> Mart. & Zucc.	–	–	6	1	–	–	10	–	Ldc	Ane
Meliaceae										
<i>Cedrela fissilis</i> Vell.	–	–	2	3	–	1	2	1	Ldc	Ane
<i>Guarea guidonia</i> (L.) Sleumer	–	–	–	1	–	–	–	2	Stc	Zoo
<i>Guarea kunthiana</i> A.Juss.	0	1	–	2	–	–	1	3	Stc	Zoo
<i>Guarea macrophylla</i> Vahl.	–	–	2	–	–	–	–	–	Stc	Zoo
<i>Melia azedarach</i> L.	–	–	–	1	–	–	–	–	Ldc	Zoo
<i>Trichilia catigua</i> A.Juss.	29	17	–	–	24	11	1	–	Stc	Zoo
<i>Trichilia clausenii</i> C.DC.	6	86	4	0	0	74	6	3	Stc	Zoo
<i>Trichilia elegans</i> A.Juss.	10	2	2	–	14	12	11	5	Stc	Zoo
<i>Trichilia pallida</i> Swartz	–	1	6	–	–	–	16	5	Stc	Zoo
Monimiaceae										
<i>Mollinedia widgrenii</i> A.DC.	–	1	–	1	–	1	–	10	Stc	Zoo
Moraceae										
<i>Ficus glabra</i> Vell.	1	2	1	–	–	–	–	–	Ldc	Zoo
<i>Maclura tinctoria</i> (L.) D.Don.	8	7	2	–	–	–	–	–	Ldc	Zoo
Myrsinaceae										
<i>Myrsine umbellata</i> Mart.	–	3	39	9	–	–	41	6	Ldc	Zoo
Myrtaceae										
<i>Campomanesia guazumifolia</i> (Cambess.) O.Berg	8	1	1	1	4	3	6	2	Stc	Zoo
<i>Campomanesia xanthocarpa</i> O.Berg	6	4	–	1	–	–	–	–	Ldc	Zoo
<i>Eugenia blatantha</i> (O.Berg) D.Legrand	–	–	–	–	–	–	–	1	Ldc	Zoo
<i>Eugenia florida</i> DC.	–	2	16	–	–	–	10	1	Stc	Zoo

Table 3 (Continued)

Families and species	Arboreal				Subarboreal				Guilds	
	PO	PI	SO	SI	PO	PI	SO	SI	Reg	Disp
<i>Eugenia stictosepala</i> Kiaersk.	2	–	1	–	–	1	2	–	Stc	Zoo
<i>Myrcia albo-tomentosa</i> O.Berg	–	–	–	–	–	–	1	–	Ldc	Zoo
<i>Myrcia laruotteana</i> Cambess.	–	–	–	–	–	–	1	–	Ldc	Zoo
<i>Myrcia multiflora</i> (Lam.) DC.	4	–	–	–	3	3	–	–	Stc	Zoo
<i>Myrcianthes pungens</i> (O.Berg) D.Legrand	5	–	–	–	–	3	–	–	Stc	Zoo
<i>Myrciaria floribunda</i> (West) O.Berg	1	–	1	–	–	–	–	–	Stc	Zoo
<i>Plinia cauliflora</i> (Mart.) Kausel	–	–	–	–	–	–	1	–	Stc	Zoo
<i>Plinia rivularis</i> (Cambess.) Rotman	–	–	–	–	–	1	–	–	Stc	Zoo
<i>Psidium guajava</i> L.	–	–	3	60	–	–	10	4	Ldc	Zoo
<i>Syzygium jambos</i> (L.) Alston	–	–	–	2	–	–	–	2	Stc	Zoo
Nyctaginaceae										
<i>Guapira opposita</i> (Vell.) Reitz	11	3	6	–	7	3	4	–	Stc	Zoo
Opiliaceae										
<i>Agonandra excelsa</i> Griseb.	–	2	–	–	–	1	–	–	Ldc	Zoo
Phyllanthaceae										
<i>Margaritaria nobilis</i> L.f.	–	–	2	–	–	–	–	–	Ldc	Aut
<i>Phyllanthus acuminatus</i> Vahl	–	1	–	–	–	–	–	–	Stc	Aut
Phytolaccaceae										
<i>Gallesia integrifolia</i> (Sprengel) Harms	1	7	–	–	–	–	–	1	Ldc	Zoo
Piperaceae										
<i>Piper aduncum</i> L.	–	–	–	–	–	–	–	23	Ldc	Zoo
<i>Piper amalago</i> L.	–	–	–	–	2	74	1	44	Stc	Zoo
Polygonaceae										
<i>Ruprechtia laxiflora</i> Meisner	6	–	–	–	32	–	–	–	Stc	Ane
Proteaceae										
<i>Roupala brasiliensis</i> Klotzsch	–	–	4	–	–	–	11	–	Ldc	Ane
Rhamnaceae										
<i>Colubrina glandulosa</i> Perkins	–	4	–	–	–	–	–	–	Ldc	Zoo
<i>Rhamnidium elaeocarpum</i> Reissek	5	10	42	2	7	11	24	28	Ldc	Zoo
Rosaceae										
<i>Prunus myrtifolia</i> (L.) Urban	–	–	1	1	2	–	2	–	Ldc	Zoo
Rubiaceae										
<i>Chomelia catharinae</i> (Smith & Downs) Steyerl.	–	–	–	–	2	–	–	–	Stc	Zoo
<i>Chomelia obtusa</i> Cham. & Schtdl.	–	–	–	–	–	–	1	–	Stc	Zoo
<i>Coutarea hexandra</i> (Jacquin) K.Schum.	6	3	5	1	–	–	4	–	Stc	Ane
<i>Ixora venulosa</i> Benth.	–	–	–	–	–	–	–	1	Stc	Zoo
<i>Psychotria carthagenensis</i> Jacquin	–	–	–	–	–	5	23	36	Stc	Zoo
<i>Psychotria pubigera</i> Schtdl.	–	–	–	–	–	–	1	–	Stc	Zoo
<i>Randia nitida</i> (Kunth) DC.	–	–	–	–	–	–	5	1	Stc	Zoo
<i>Rudgea jasminoides</i> (Cham.) Müll.Arg.	–	–	–	–	–	–	–	1	Stc	Zoo
Rutaceae										
<i>Balfourendron riedelianum</i> (Engler) Engler	16	11	2	–	1	2	–	1	Stc	Ane
<i>Citrus aurantium</i> L.	–	–	1	21	–	1	4	33	Stc	Zoo
<i>Metrodorea nigra</i> A.St.-Hil.	273	148	–	–	73	24	–	–	Stc	Aut
<i>Zanthoxylum caribaeum</i> Lam.	–	1	4	1	–	2	4	–	Ldc	Zoo
<i>Zanthoxylum fagara</i> (L.) Sargent	–	–	5	1	–	2	–	–	Ldc	Zoo
<i>Zanthoxylum riedelianum</i> Engler	–	–	–	–	–	–	1	–	Ldc	Zoo

Table 3 (Continued)

Families and species	Arboreal				Subarboreal				Guilds	
	PO	PI	SO	SI	PO	PI	SO	SI	Reg	Disp
Salicaceae										
<i>Casearia gossypiosperma</i> Briquet	5	9	14	4	–	5	13	9	Ldc	Zoo
<i>Casearia sylvestris</i> Swartz	1	4	9	30	–	2	3	5	Ldc	Zoo
<i>Prockia crucis</i> P.Browne	–	2	–	–	–	–	–	–	Stc	Zoo
Sapindaceae										
<i>Allophylus edulis</i> (A.St.-Hil.) Radlk.	–	–	25	–	–	–	24	1	Stc	Zoo
<i>Cupania vernalis</i> Cambess.	–	9	27	25	2	23	19	71	Ldc	Zoo
<i>Diatenopteryx sorbifolia</i> Radlk.	1	6	–	–	–	1	–	–	Ldc	Ane
Sapotaceae										
<i>Chrysophyllum gonocarpum</i> (Mart. & Eichler) Engler	22	9	1	–	1	7	9	–	Stc	Zoo
Solanaceae										
<i>Cestrum laevigatum</i> Schtdl.	–	–	–	–	2	–	53	95	Stc	Zoo
<i>Cestrum strigillatum</i> Ruiz & Pavón	–	–	–	–	–	–	20	21	Stc	Zoo
Urticaceae										
<i>Cecropia pachystachya</i> Trécul	–	–	–	7	–	–	–	–	Pio	Zoo
<i>Urera baccifera</i> (L.) Gaud.	16	10	–	–	–	–	–	–	Stc	Zoo
Verbenaceae										
<i>Aloysia virgata</i> (Ruiz & Pavón) A.Juss.	17	6	1	19	–	–	–	2	Pio	Ane
Vochysiaceae										
<i>Qualea jundiahy</i> Warm.	–	–	1	–	–	–	–	–	Ldc	Ane

Pio = pioneer; Ldc = light-demanding climax; Stc = shade-tolerant climax; Ane = anemochorous; Aut = autochorous; Zoo = zoochorous.

and subarboreal individuals in each forest stand are given in Table 3, together with their classification into the regeneration and dispersion guilds. Of the species total, 72 (52%) occurred in both the preserved and secondary stands, 21 (15%) were exclusive to the preserved stands and 46 (33%) to the secondary stands. Therefore, the preserved and secondary stands shared 108 out of 139 species (78%). Although there was a high number of species in common among the forest stands, they did differ substantially in terms of most abundant species. More details on the species' quantitative data in each tree community component and forest stand are given in Toniato (2001).

The mean number of species of the arboreal component per sample plot (species density) ranged from 31 to 36 in the four forest stands, but there was no significant difference among them (Table 4). Significant differences among the stands were found, however, for the species density of the subarboreal component, which was lower in the PO stand than in both secondary stands (SO and SI); the PI stand did

not differ significantly. The PO and SO stands also registered, respectively, the significantly lowest and highest Shannon diversity (H') for both the arboreal and subarboreal components. The PI and SI stands yielded intermediate H' values for both components, but did not differ significantly between themselves. Pielou' evenness indices (J') followed similar patterns.

3.4. Multivariate analyses of tree community structure

The ordination of sample units and species through detrended corresponded analysis (DCA) of the species' abundances yielded high eigenvalues for the first ordination axes for both the arboreal and subarboreal matrixes: 0.765 and 0.752, respectively, representing 30.0 and 21.4% of the total variance. This indicates that a 'long' species gradient is summarized by the first axis. On the other hand, the second axis yielded much lower eigenvalues, 0.217 and 0.228, for the arboreal and subarboreal matrixes, respectively, adding only

Table 4

Species diversity variables of the four stands of tropical semideciduous forest surveyed in Bauru, SE, Brazil

Vegetation component	Forest stands	Number of individuals sampled	Number of species sampled	Species density ^a	H ^b (nats indiv. ⁻¹)	J
Arboreal	PO	1064	55	31.4 ± 2.1 ns	2.66 c	0.67
Arboreal	PI	932	69	32.8 ± 3.8 ns	3.18 b	0.75
Arboreal	SO	924	75	36.0 ± 11.7 ns	3.41 a	0.79
Arboreal	SI	983	59	31.0 ± 9.2 ns	3.10 b	0.76
Arboreal	Total	3903	117			
Subarboreal	PO	362	32	14.4 ± 5.8 b ^{***}	2.70 c	0.78
Subarboreal	PI	508	50	21.8 ± 5.6 ab ^{***}	3.10 b	0.79
Subarboreal	SO	586	72	31.6 ± 6.3 a ^{***}	3.69 a	0.86
Subarboreal	SI	783	59	31.2 ± 6.7 a ^{***}	3.16 b	0.78
Subarboreal	Total	2239	103			

ns: not significant.

^a Figures are mean ± S.D. of five sample units (1600 m² for arboreal and 80 m² for subarboreal) and where analyses of variance indicated significant differences among plots ($P < 0.05$), means followed by different letters indicate significant differences in Tukey tests ($P < 0.05$).^b Different letters indicate significant differences in Hutcheson t -tests ($P < 0.001$). Forest stands: PO—preserved forest with occasional cattle trampling; PI—preserved forest with intensive cattle trampling; SO—secondary forest with occasional cattle trampling; SI—secondary forest with intensive cattle trampling.^{***} $P < 0.001$.

8.5 and 6.5% to the explained variance. Therefore, it summarizes much 'shorter' species gradients. Longer gradients are those with many species replacements throughout, while shorter gradients consist mostly of changes in species abundances (ter Braak, 1995).

The ordination of sample units by DCA is given in the diagrams of Figs. 3A and 4A, for the arboreal and subarboreal components, respectively. In both cases, the first ordination axis strongly discriminated the sample units of the preserved and secondary stands to either the left or right side of the diagrams, although arboreal and subarboreal diagrams show opposing ordination directions. There was no clear separation of sample units according to the intensity of cattle trampling, except in the case of the arboreal component of the secondary stands by the second (and much weaker) ordination axis.

The species ordination by DCA is given in Figs. 3B and 4B, for the arboreal and subarboreal components, respectively. Species that were characteristically more abundant in either the preserved or the secondary stands appeared on either extremes of the diagrams. For example, *Metrodorea nigra*, *Aspidosperma polyneuron*, *Holocalyx balansae*, *Actinostemon klotschii*, *Trichilia catigua*, *Trichilia elegans*, *Chrysophyllum gonocarpum* and *Balfourodendron riedelianum* predominated in the arboreal component of the preserved

stands. *Rhamnidium elaeocarpus*, *Annona cacans*, *Machaerium brasiliensis*, *Gochnatia polymorpha*, *Terminalia triflora* and *Cupania vernalis* were more abundant in the arboreal component of the SO stand, whereas *Psidium guajava*, *Croton floribundus*, *Tabernaemontana catharinensis*, *Guazuma ulmifolia*, *Alchornea glandulosa*, *Bauhinia longifolia* and *Celtis pubescens* were more abundant in the arboreal component of the SI stand. It must be pointed out that shade-tolerant species are also concentrated towards the preserved stands extreme.

Similar trends hold true for the subarboreal component (Fig. 4B). In the secondary stands, typical shade-tolerant understory species, such as *Piper aduncum*, *Cestrum laevigatum*, *C. strigillatum*, *Mollinedia widgrenii*, *Trichilia pallida* and *Psychotria carthagenensis*, occurred along with juvenile individuals of arboreal species, such as *Croton floribundus*, *Gochnatia polymorpha*, *Patagonula americana*, *Alchornea glandulosa*, *Myrsine umbellata*, *Cupania vernalis* and *Psidium guajava*. The preserved stands concentrated juvenile individuals of shade-tolerant canopy and subcanopy species, such as *Astronium graveolens*, *Trichilia clausenii*, *T. elegans*, *T. catigua*, *Ruprechtia laxiflora*, *Metrodorea nigra*, *Chrysophyllum gonocarpum*, *Guapira opposita*, *Gymnanthes concolor* and *Campomanesia guazumifolia*, together with individuals of a few light-demanding and pioneer

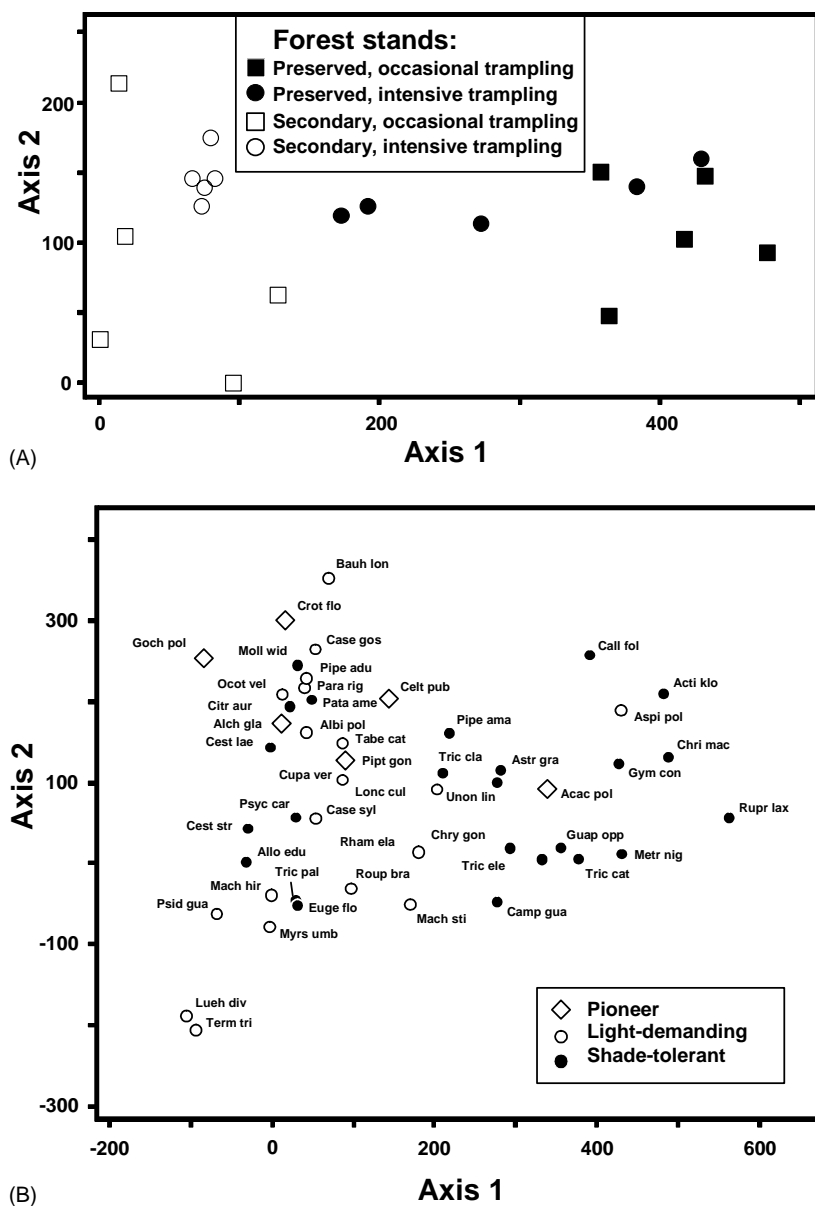


Fig. 4. Detrended correspondence analysis (DCA): ordination of (A) 20 sample subplots used to survey four stands of tropical semideciduous forest in Bauru, SE, Brazil, and (B) 49 species of the subarborescent component. Ordination based on the number of individuals per sample plot. Symbols discriminate forest stands (A) and species regeneration guilds (B).

and less frequent in the two secondary stands. Similar trends were observed for the frequency of trees of subarborescent species per regeneration guild, but differences were not significant for pioneer species.

In the case of dispersion guilds, individuals of anemochorous species, of both the arboreal and sub-

arborescent components, appeared at significantly higher frequencies than expected in the two stands with occasional cattle trampling, PO and SO, and at lower frequencies than expected in the two stands with intensive trampling, PI and SI. The opposite trend was observed for individuals of zoochorous species of

Table 5

Number of individuals per species guild in the four stands of tropical semideciduous forest surveyed in Bauru, SE, Brazil, given in contingency tables with χ^2 -tests (expected values within parenthesis) prepared for each tree community component and guild system

Component (guilds)	Forest stands				χ^2
	PO	PI	SO	SI	
Arboreal (regeneration)					
Pioneer	40 (152.4)	73 (133.5)	212 (132.3)	234 (140.8)	220.0***
Light-demanding climax	409 (583.4)	446 (511.0)	580 (506.6)	705 (539.0)	122.2***
Shade-tolerant climax	615 (328.2)	413 (287.5)	132 (285.0)	44 (303.2)	609.1***
χ^2	385.6***	90.5***	140.7***	334.5***	951.3***
Subarboreal (regeneration)					
Pioneers	21 (30.9)	41 (42.5)	59 (50.0)	69 (66.6)	4.9 ns
Light-demanding climax	67 (142.1)	118 (195.5)	283 (230.1)	406 (306.3)	115.1***
Shade-tolerant climax	274 (189.0)	339 (260.0)	244 (305.9)	305 (407.2)	100.5***
χ^2	81.1***	54.8***	26.3***	58.2***	220.5***
Arboreal (dispersion)					
Anemochorous	493 (456.9)	314 (400.2)	511 (396.8)	358 (422.1)	64.0***
Autochorous	281 (165.2)	164 (144.7)	40 (143.5)	121 (152.6)	164.9***
Zoocchorous	290 (441.9)	454 (387.1)	373 (383.8)	504 (408.3)	86.5***
χ^2	136.2***	32.7***	107.8***	38.7***	315.5***
Subarboreal (dispersion)					
Anemochorous	146 (119.9)	136 (170.9)	204 (194.0)	258 (259.3)	13.3**
Autochorous	138 (42.5)	97 (60.6)	13 (68.8)	16 (92.0)	344.2***
Zoocchorous	78 (199.6)	283 (284.5)	369 (323.1)	509 (431.7)	94.4***
χ^2	294.1***	28.9***	52.3***	76.6***	452.0***

Forest stands: PO—preserved forest with occasional cattle trampling; PI—preserved forest with intensive cattle trampling; SO—secondary forest with occasional cattle trampling; SI—secondary forest with intensive cattle trampling. ns: not significant.

** $P < 0.005$.

*** $P < 0.001$.

the arboreal component, i.e. they were either more or less frequent than expected in stands with either intensive or occasional cattle trampling, respectively. A similar trend was registered for the subarboreal component, excepting the SO stand, where zoochorous individuals showed higher than expected individual's frequency. Individuals of autochorous species occurred at higher than expected frequencies in the preserved stands and lower than expected frequencies in the secondary stands.

4. Discussion

4.1. Soils

The differences registered between the soils of the secondary and preserved stands strongly suggest that

there was a significant depletion of mineral nutrients, organic matter and finer sediments from the soils of the secondary stands, quite probably as a consequence of increased erosion and leaching after the forest cover was removed. These changes have already been registered in cleared forest areas throughout the tropics, particularly for coarse-textured soils (e.g. Uhl et al., 1982; Buschbacher et al., 1988; Eden et al., 1991). The sandy oxysols of the study region are already known for being particularly sensitive to both surface and sub-surface erosion (Ross et al., 1997). The progression of forest regeneration in an area is often accompanied by the improvement of soil fertility and water storage capacity (Aweto, 1981; Toky and Ramakrishnan, 1983). However, in the present case, it is important to stress that the 40-year regeneration period was not long enough to restore the primitive soil features.

4.2. Physiognomic structure

Differences in mean canopy height and in mean and maximum tree height demonstrated that the preserved stands had a more developed physiognomic structure than the secondary stands, as already observed for other forests in SE, Brazil (Oliveira-Filho et al., 1997; Tabarelli and Mantovani, 1999; Nunes et al., 2003). However, this was not reflected by tree density and basal area, and was only weakly reflected by some parameters related to tree diameter, suggesting that 40 years were sufficient for the secondary stands to approach the preserved stands in terms of tree density, basal area and average diameter, but not in terms of canopy height and density of high-stature trees. Several studies have suggested different timings for the restoration of physiognomic features in tropical secondary forests. As in the present case, Aide et al. (1996) have observed that 40-year-old secondary forests in Puerto Rico do not distinguish themselves from non-disturbed forests in relation to density and basal area. Studies in Brazilian Atlantic rainforests, by Tabarelli and Mantovani (1999), and in Amazonian rainforests, by Uhl et al. (1982, 1988) and Saldarriaga et al. (1988), all suggest longer periods for the restoration of tree basal area, volume and biomass. This difference may be related to the seasonal (semideciduous) character of the forest studied in Bauru. According to Ewel (1980), the growth of tropical forest vegetation occurs more rapidly in certain environments than in others, and forests occurring under warmer and rainier climates grow a higher amount of biomass than those occurring in drier and cooler climates. Therefore, moist tropical forests show a lower post-disturbance resiliency than do tropical montane and seasonal forests, which require a comparatively shorter span of time to regenerate.

The largest area of canopy gaps was registered in the SO stand, where there was a larger number of broken trees and a more open canopy than in the other three stands. We believe that this was probably due to the stand's location near the fragment edges. As stated by Murcia (1995), wind-throwing of trees is a more likely event near the edges of forest fragments than in their core areas.

The abundance of climbing plants in tropical forests is considered an important physiognomic feature when assessing their succession stages and distur-

bance regimes (Gentry, 1991). Tangles of climbing plants are generally considered as strong indicators of either past or ongoing disturbance processes (Hergaty and Caballé, 1991). On the other hand, the presence of thick-stemmed climbing plants (lianas) hanging from tall trees is often a reliable indicator of forest maturity (Budowski, 1970). This is consistent with the higher mean abundances of thick climbing plants in the preserved stands. Although this difference was not significant for the SI stand, we believe that this may be partially due to its location near the two preserved stands, which could have operated as sources of lianas.

The lower mean abundances of thin climbing plants in the stands with intensive cattle trampling (PI and SI) strongly suggests a constraint on the establishment and growth of slender vines through the mechanical damage caused by the animals as they roam the forest understory. Thicker and more resistant climbers, such as lianas, would be little affected. This difference, however, was not significant for the PI stand, possibly because of its location near the forest edges, where the growth of climbing plants is commonly favored by increased light radiation (Oliveira-Filho et al., 1997; Viana et al., 1997), and, to some extent, this could have compensated the cattle damage.

4.3. Tree species composition and diversity

The most remarkable difference in floristic composition among the studied stands was the absence of *Aspidosperma polyneuron*, *Metrodorea nigra* and *Holocalyx balansae* from both the arboreal and sub-arboreal components of the secondary stands. According to Lorenzi (1992), these species are generally found in later succession stages of forests situated on more fertile soils, as were the preserved stands, in which the same species were important constituents of the forest canopy. This reinforces the fact that the successful establishment of mature forest species in secondary forests may involve very long time spans. On the other hand, the preserved and secondary stands shared ca. 78% of the total number of species, showing that a considerable part of the floristic composition was restored during the 40-year regeneration. As stated by Tabarelli and Mantovani (1999), floristic composition is often restored long before the patterns of abundance.

Species richness and diversity of tropical forests are frequently lower in mature forests than during regeneration phases (Saldarriaga et al., 1988; Brown and Lugo, 1990; Aide et al., 1996; Tabarelli and Mantovani, 1999). According to Horn (1976), this is because the highest species diversity is reached at intermediate succession stages, when the changing environmental condition allows the simultaneous occurrence of species typical of both early and late succession stages. Likewise, in the present case, the secondary stands showed species diversity indices and species density per sample unit equal to or higher than those registered in the preserved stands, consistent with their intermediate succession phase.

In the particular case of the SO stand, its highest species richness and diversity is probably due to the high environmental heterogeneity of this area, which bears the largest area of canopy gaps and is located near the fragment edges. Natural moderate disturbance processes and edge effects are sources of environmental heterogeneity and may be important to the maintenance of species diversity in tropical forests (Denslow, 1980; Hartshorn, 1980; Murcia, 1995; Laska, 1997). On the other hand, the lowest species diversity registered in the PO stand, for both the arboreal and subarboreal components, is probably related to the numerical dominance of a few species. In fact, late succession stages and low disturbance regimes may favor the dominance of a few species by gradually eliminating those settled in the wake of past disturbance events (Hubbel and Foster, 1990; Oliveira-Filho et al., 1997).

4.4. *Species regeneration and dispersion guilds*

The relative abundance of individuals of different species regeneration and dispersion guilds was the tree community feature that most strongly reflected the man-made disturbance history of the four forest stands.

The significantly higher abundance of shade-tolerant species in the preserved stands and of pioneer and light-demanding species in the secondary stands is highly consistent with the results obtained for other Brazilian tropical forests, where the progress of regeneration was followed by increasing relative abundance of shade-tolerant species at the expense of pioneer and light-demanding ones (Oliveira-Filho et al., 1997;

Tabarelli and Mantovani, 1999; Nunes et al., 2003). The classification of species into regeneration guilds may be questionable when several tropical forest species can survive and grow under relatively wide gradients of light intensity (e.g. Augspurger, 1984; Sork, 1987; Popma and Bongers, 1991). Nevertheless, such a classification has proved to be a useful tool for assessing forest integrity regarding disturbances as forest regeneration status (e.g. Manokaran and Kochumen, 1987; Felfili, 1995; Oliveira-Filho et al., 1997; Tabarelli and Mantovani, 1999; Nunes et al., 2003).

With regards to dispersion guilds, individuals of autochorous species occurred at higher frequencies in the preserved than in the secondary stands. This is probably related to the shorter dispersion distances of autochorous propagules compared to the generally longer distances reached by those dispersed by wind and animals (Willson, 1992). Combined data from the preserved stands do not confirm the predominance of zoochorous over anemochorous species in mature tropical forests, as observed in other studies (e.g. Howe and Smallwood, 1982; Tabarelli and Mantovani, 1999). Quite unexpectedly, the number of trees of zoochorous species was significantly higher than that of anemochorous species in the stands with intensive cattle trampling (PI and SI), while anemochorous predominated over zoochorous species in the stands with occasional trampling (PO and SO). In fact, the predominance of zoochorous species in tropical forests may be related to many other factors besides regeneration phase. Indeed, in the early stages of forest regeneration, cattle may possibly contribute by dispersing the seeds of zoochorous species.

According to Nogueira and Nogueira (1991), in addition to restricting the growth of some weedy species, the cattle also promoted forest regeneration in the study area through the dispersal of guava seeds. The spread of guava (*Psidium guajava*) in tropical pastures with the help of cattle has already been registered elsewhere in the tropics and associated with the species' high germination rates and resistance to trampling (Somarriba, 1985, 1995; Zahawi and Augspurger, 1999). After some time, guava trees may turn grazing areas useless because of the increasing shade and their attractiveness to other disperser animals. Therefore, once established during the regeneration process, zoochorous trees and shrubs may operate as "regeneration cores" which bring in additional

zoochorous species (Connel and Slatyer, 1977; Guevara et al., 1986; Vieira et al., 1994; Otero-Arnaiz et al., 1999; Slocum and Horvitz, 2000). However, as guava trees were registered only in the secondary stands, they are not part of the predominance of zoochorous species in the PI stand. We can only speculate that the cattle may have dispersed other species that were able to establish themselves in the PI stand, or, alternatively, that the high abundance of guava trees in the nearby SI stand would have increased the activity of disperser animals in the PI stand.

The anemochorous mode of dispersion predominated among the trees of the two forest stands with occasional cattle trampling, PO and SO. In the case of the preserved one (PO), this was clearly related to the abundance of anemochorous large-sized tree species (*Aspidosperma polyneuron*, *Ceiba speciosa*, *Machaerium stipitatum*, *Acacia polyphylla*, *Centrolobium tomentosum*, *Balfourodendron riedelianum*, among others). It is important to consider that the anemochorous mode of dispersion is more abundant in the canopy and emergent layers of seasonal forests, than it is in moist forests (Howe and Smallwood, 1982; Willson, 1992). Therefore, this is probably the usual pattern for this forest type, so that it reproduced itself in the secondary stand with occasional cattle trampling (SO). This gives additional evidence for the important role played by the cattle in influencing the tree species composition of the studied forest stands.

5. Conclusions

Results from this study have partially confirmed the hypothesis that the forest stands with different anthropogenic disturbance histories still show differences in the soil conditions and vegetation features. Most differences detected among stands arose in comparisons between preserved forests and secondary forests regenerated on abandoned crop and grazing lands. The soils of the secondary forests still reflect the past losses of mineral nutrients and finer sediments caused by forest cover removal. Some vegetation features of the secondary forests, such as tree density and basal area and a significant part of the floristic composition, are currently similar to those observed in the preserved forests. Many other features, however, have not been restored after a 40-year regeneration time. Among

these, are the greater proportions of trees of higher stature and of shade-tolerant and autochorous species that are typical of the preserved forest.

The impact of cattle in the forests of the study area was less marked than the consequences of the major impact of deforestation and cultivation despite this latter ceasing 40 years ago. One of the most evident effects was actually the facilitation of forest regeneration through the dispersion of guava trees by the cattle. This does not mean, however, that there were no adverse impacts to forest regeneration caused by cattle, not least that cattle breeding should be a recommended practice to promote tropical forest regeneration.

However, there was evidence that higher cattle activity reduced the density of vines and increased the proportion of trees of zoochorous species in both secondary and preserved forest stands.

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