TREE STRUCTURE AND SPECIES COMPOSITION CHANGES IN AN URBAN TROPICAL FOREST FRAGMENT (SÃO PAULO, BRAZIL) DURING A FIVE-YEAR INTERVAL

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Abstract – [Tree structure and species composition changes in an urban tropical forest fragment (São Paulo, Brazil) during a five-year interval]. The management of remnant forest patches requires a comprehensive understanding of their functioning and evolution, which can be achieved by monitoring the main community components in the medium and long terms. We analysed structural and compositional changes in a forest fragment at the University of São Paulo (USP) (23°33'44"-23°34'02"S; 46°43'38"-46°43'49"W) from 1992 to 1997. Surveys were performed within a 100 x 50 m plot, and included trees with diameter at breast height (dbh) ≥ 15.9 cm in 1992 and trees with dbh ≥ 10 cm in 1997. Tree species were identified and classified according to successional stages. Structural and dynamic variables were compared for the most abundant species, for successional groups, and for the whole community. Density and basal area of the community increased considerably in the period; species diversity and evenness remained almost the same. For native species, both diversity and evenness decreased. *Archontophoenix cunninghamiana*, an exotic palm, showed the highest growth and recruitment rates of all species, indicating a process of biological invasion. Pioneers decreased in density and showed the lowest recruitment and the highest mortality among ecological groups, while late successional species increased in density and had low mortality. Compared to another 62 neotropical forests, the USP forest shows low stability, typical of immature or regenerating forests. Potential recruitment and regeneration problems of native species, especially the late successional ones, were detected and may be explained by *A. cunninghamiana* outcompeting native species. These results illustrate the need to manage fragments of native vegetation to maintain biodiversity.

Resumo – [Alterações na estrutura e composição arbórea de um fragmento urbano de floresta Atlântica (São Paulo, Brasil) num intervalo de cinco anos]. O manejo de fragmentos florestais remanescentes necessita do entendimento abrangente de seus processos evolutivos e funcionais, que pode ser alcançado por meio de monitoramento, a médio e longo prazos, dos componentes-chave da comunidade. Foram aqui analisadas mudanças na estrutura e composição de um fragmento florestal, localizado na Universidade de São Paulo (USP) (23°33'44"-23°34'02"S; 46°43'38"-46°43'49"W), ocorridas entre 1992 e 1997. Os levantamentos foram feitos numa área de 100 x 50 m, incluindo árvores com diâmetro na altura do peito (dap) ≥ 15,9 cm; o levantamento de 1997 também incluiu árvores com dap ≥ 10 cm. Variáveis estruturais e dinâmicas foram comparadas para as espécies mais abundantes, para grupos sucessionais e para a comunidade. Densidade e área basal da comunidade aumentaram consideravelmente no período; diversidade e equabilidade permaneceram praticamente as mesmas. Para as espécies nativas, diminuíram tanto diversidade como equabilidade. A palmeira exótica *Archontophoenix cunninghamiana* teve maiores taxas de recrutamento e crescimento dentre todas as espécies, indicando um processo de invasão biológica. Dentre os grupos ecológicos, as espécies pioneiras decresceram em densidade e tiveram menor recrutamento e maior mortalidade, ao passo que o contrário se deu para as climáxicas. Comparada a outras 62 florestas neotropicais, a floresta estudada demonstrou menor estabilidade, tipicamente encontrada em florestas imaturas ou em regeneração. Potenciais problemas no recrutamento e na regeneração das espécies nativas, especialmente as tardias, foram detectados, podendo ser explicados pela competição de *A. cunninghamiana* com as espécies nativas. Os resultados apresentados demonstram a necessidade de se manejar fragmentos de vegetação nativa para se conservar sua biodiversidade.

Key words: Atlantic tropical forest, forest dynamics, biological invasion, succession.

Introduction

In most cities that have experienced recent and rapid development, urban expansion has not always been properly planned, leading to the destruction of almost all natural environments. Remnants of native ecosystems in urban landscapes are therefore precious because of their capacity to ameliorate problems caused by overurbanisation, such as air pollution, soil impermeabilization, climatic warming, and others, besides the amenity value provided by vegetation and fauna, especially birds. The São Paulo metropolis exemplifies such an under-planned urban process, and the original vegetation is nowadays represented by tiny forest fragments in public parks or biological reserves.

Small remaining fragments of tropical forests tend to be highly fragile (according to Nilsson & Grelsson's 1996 definition of fragility) once the complex net of biological interactions that support their communities is weakened. The removal of original species from the system, especially key species, and the establishment of aliens, may be responsible for extensive changes in the community structure, in the microclimate, in trophic associations and all other inter-specific relationships such as pollination, dispersion and competition, and result in biodiversity deterioration, both in terms of species and processes.

Because of their high susceptibility to disturbance, small forest fragments must be constantly monitored and managed in order to direct successional processes towards maintaining species and habitat diversity (Fiedler & Jain 1992, Sharitz *et al.* 1992, Slocombe 1993).

Successful ecological management requires a comprehensive understanding of the structure and dynamics of remnant forest patches and knowledge of past and present processes. This shows what changes have occurred and provides information on possible problems and how to achieve forest conservation. In this sense, studies based on growth, recruitment, mortality or surviving rates related to ecological groups which follow the community dynamics in the medium and long terms, enable the general tendencies in the community to be elucidated, facilitating predictions and decision-making. These types of studies, especially those based on permanent plots, have been recognised as essential for the ecological management of tropical forests, even though data are collected in small fragments or over short time scales (Hubbell & Foster 1992, Milton *et al.* 1994, Condit 1995, Guariguata *et al.* 1997, Oliveira-Filho *et al.* 1997, Terborgh *et al.* 1997).

The present study analyses the dynamics of trees in a small urban forest fragment (about 10 ha) in the city of São Paulo over a five-year interval in order to supply basic information for management actions. Therefore, both dynamic (mortality, recruitment, and growth) and structural variables (related to size) were analysed at several different levels: the whole community, exotic species, the native community, ecological groups, and the most abundant populations.

Material and Methods

Study Area – This study was carried out in the Forest Reserve of the University of São Paulo (USP), campus "Armando de Salles Oliveira" (23°33'44"-23°34'02"; 46°43'38"-46°43'49"W). The campus is on the west side of São Paulo urban area, and the Reserve occupies 102.100 m^2, at 730 to 775 m elevation. It is crossed by a stream, which starts inside the Reserve and drains into an artificial lake at the Reserve boundary (Fig. 1).

The substrate is formed by Tertiary and Quaternary deposits of the São Paulo basin (Joly 1950). The soil is clayey, acid, nutrient-poor and aluminium-rich (Varanda 1977). Mean annual temperature is about 19.2°C and mean annual rainfall 1,207 mm. Mean monthly temperatures go from 14°C (June) to 23°C (February) and mean monthly rainfall varies from 230 mm (January) to 40 mm (August), when the soil suffers a water deficit (Gorresio-Roizman 1993). Air relative humidity is around 80% and SE winds, coming from the ocean, prevail all year round (Varanda 1977).

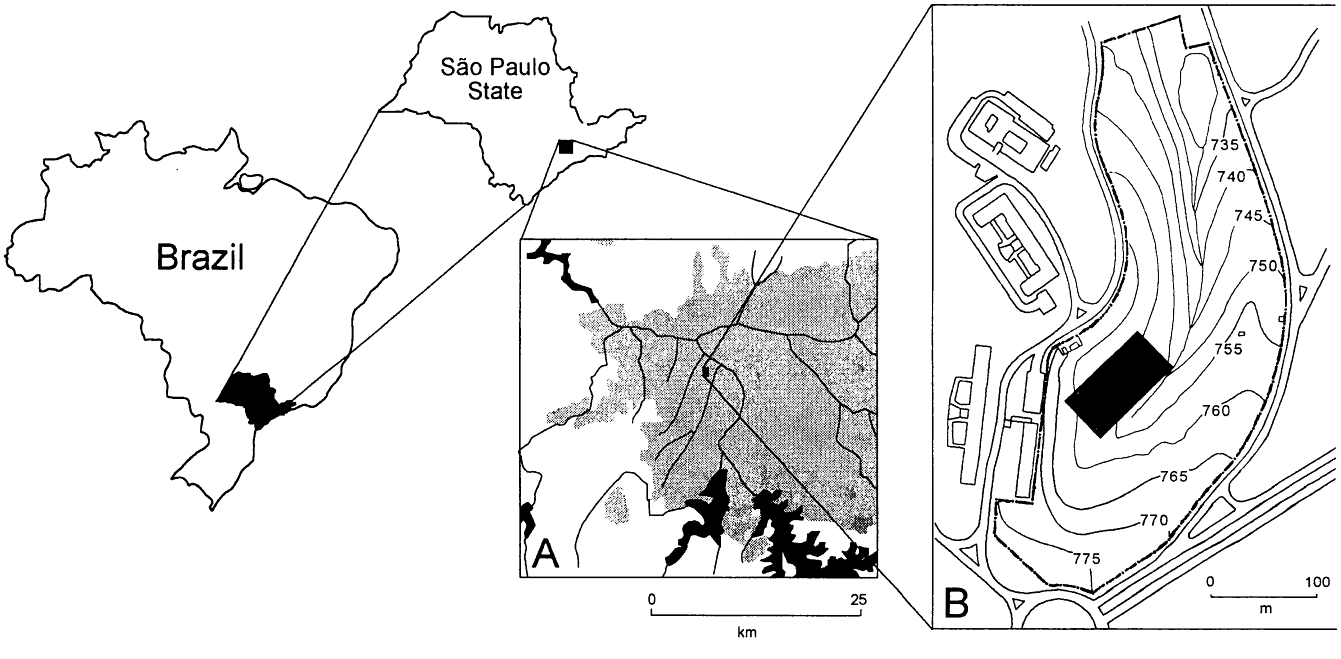

Fig. 1: Location of the studied plot, in the USP Forest Reserve, São Paulo, Brazil (modified from Rossi 1994) (grey area in A = São Paulo urban zone; black rectangle in B = studied plot).

The USP Forest Reserve comprises a patch of secondary forest (Cersósimo 1993) estimated by Rossi (1994) to be at least 90 years old (based on the species present in its intermediate stratum). At least since the 1930s, the forest has been isolated from other patches, initially surrounded by pastures and later by the campus of the USP, which was installed in the 1940s. This forest went through some major disturbances during the construction of the surrounding roads in the 1940s, 50s and 60s. After that time, people started to use the forest for recreational purposes until 1979, when the area was fenced to stop the disturbances associated with that kind of activity (Rossi 1994).

The forest belongs to the domain of dense ombrophilous forests and maintains floristic relationships with the Atlantic Dense Ombrophilous Forest and the Semideciduous Seasonal Forest (*sensu* Veloso *et al.* 1991). More than 120 native woody species have been identified in this patch (Rossi 1994) and it represents one of the few fragments of the regional native vegetation in São Paulo city.

Data Collection and Analysis – A 100 m x 50 m (0.5 hectare) area was delimited in the Reserve (Fig. 1), where the living trees were surveyed twice, in June 1992 and September 1997 (5.25 year interval). The first survey included all trees with diameter at breast height (dbh, measured at 1.30 m height) ≥ 15.9 cm (calculated from girth at breast height ≥ 50 cm). In the second survey (September 1997), the dbh qualification was reduced and all trees ≥ 10 cm dbh were included.

Following measurement of dbh, the trees were marked with numbered aluminium tags for subsequent identification. Botanical material was collected and voucher specimens of the newly-registered species were deposited in the herbarium Botânica, Instituto de Biociências, Universidade de São Paulo (São Paulo, SP, Brazil) (SPF).

Literature descriptions of the species found in our study area (Gorresio-Roizman 1993, Mantovani 1993, Tabarelli 1994, Knobel 1995) were used to classify the native species into ecological groups according to the successional stages where they appear most frequently, as: a) "late successional" – the species usually cited in the literature as "late secondary"; b) "secondary" – those cited as "early secondary" or simply "secondary"; and c) "pioneer" – those cited as such. The exotic species were analysed as a separate group.

Density and basal area were determined according to Mueller-Dombois and Ellenberg (1974), for both 1992 and 1997 surveys. Species diversity was calculated according to Shannon's and Wiener's (H') index using natural logarithms (Magurran 1988), and evenness, by the Pielou (J') index (Pielou 1975).

As a measure of quantitative similarity between the surveys of 1992 and 1997, we used the Czekanowski coefficient (Kent & Coker 1992):

$$S_c = 2 \,.\, \Sigma\min(X_i, Y_i) \,/\, (\Sigma X_i + \Sigma Y_i)$$

where X_i and Y_i = the number of individuals of species i in each of the two surveys;
$\Sigma\min(X_i, Y_i)$ = the sum of the lesser scores of species i.

Mortality, recruitment and population growth were calculated following the model proposed by Korning and Balslev (1994a):

$$r=(C_t/C_0)^{1/t} - 1$$

where r is the mean annual mortality rate ($r < 0$), mean annual recruitment rate ($r > 0$) or mean annual population growth rate;
t is time (in years); C_0 and C_t are population sizes (number of individuals or basal area) at time 0 and after t years, respectively.

Diagrams of dbh frequency distribution were made for the three most abundant native species (species with more than 15 individuals both in 1992 and 1997), the exotic species, the ecological groups and for the whole community (all species combined). The diagrams were constructed according to 2.5 cm-wide classes, starting at 15 cm dbh (1992 data) or 10 cm dbh (1997 data)[1].

Dbh increment was estimated for the three most abundant species and for the community as a whole and it was expressed as change in dbh per unit time (mm.year^{-1}). The relationship between dbh increment (mm.year^{-1}) and dbh in 1992 (mm) was analysed by simple linear regression analysis (Zar 1999), for the community as a whole and for the three most abundant species.

The two surveys (1992 and 1997) could not be compared statistically as they are not random samples, but whole censuses of the studied area.

Results

Analysis of the community – In 1992, 156 individuals with dbh ≥ 15.9 cm were found in the 0.5 ha area, belonging to 45 species, 35 genera and 22 families (Table 1). Total basal area was $19.21\ \text{m}^2.\text{ha}^{-1}$. In 1997, 167 individuals with the same dbh were found, belonging to 46 species, 36 genera and 23 families, and total basal area was $21.17\ \text{m}^2.\text{ha}^{-1}$ (Table 1).

From 1992 to 1997, total density and basal area increased considerably, 7.1% ($1.31\%.\text{year}^{-1}$) and 10.2% ($1.87\%.\text{year}^{-1}$) respectively (Table 2). The median dbh changed from 24.03 in 1992 to 23.87 in 1997. Seven individuals died (4.49% of the total, mortality rate = $0.87\%.\text{year}^{-1}$) and 18 were recruited (11.54%, recruitment rate = $2.10\%.\ \text{year}^{-1}$) so that, in 1997, the commu-

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[1] The 1992 survey was based on a minimum dbh of 15.9 cm. Therefore, in the respective dbh frequency distribution diagrams, the first class is actually smaller, including individuals of 15.9-17.5 cm.

Table 1. Species sampled (dbh ≥ 15.9 cm) in 0.5 hectare of the USP Forest Reserve (São Paulo, SP) and some of their structural and dynamic variables. N=number of individuals; BA=basal area. (* Ecological groups according to Gorresio-Roizman 1993, Mantovani 1993, Tabarelli 1994 and Knobel 1995.)

Species	Family	Ecological	1992		1997		Deaths	Recruits
		group *	N	BA ($m^2.ha^{-1}$)	N	BA ($m^2.ha^{-1}$)		
Alchornea sidifolia Müll. Arg.	Euphorbiaceae	pioneer	32	4.52	32	4.74	2	2
Croton floribundus Spreng.	Euphorbiaceae	pioneer	22	2.22	21	2.35	2	1
Cordia ecalyculata Vell.	Boraginaceae	late succes.	18	1.18	20	1.58	1	3
Maytenus evonymoides Reiss.	Celastraceae	late succes.	6	0.45	6	0.47	0	0
Casearia sylvestris Sw.	Flacourtiaceae	secondary	5	0.35	5	0.39	0	0
Eugenia cerasiflora Miq.	Myrtaceae	late succes.	5	0.29	7	0.40	0	2
*Cecropia glaziou*i Snethl.	Cecropiaceae	pioneer	4	0.38	4	0.43	0	0
Cedrela fissilis Vell.	Meliaceae	late succes.	4	1.21	5	1.33	0	1
Archontophoenix cunninghamiana H.Wendl. & Drude	Arecaceae	exotic	3	0.22	9	0.59	0	6
Machaerium nictitans (Vell.) Benth.	Leguminosae	secondary	3	1.29	3	1.22	0	0
Machaerium villosum Vog.	Leguminosae	late succes.	3	1.01	3	1.02	0	0
Prunus sellowii Koehne	Rosaceae	secondary	3	0.31	3	0.33	0	0
Rollinia sylvatica (A.St.-Hil.) Mart.	Annonaceae	late succes.	3	0.44	3	0.46	0	0
Sorocea bonplandii (Baill.) Burg. Lanj. & Boer	Moraceae	late succes.	3	0.21	3	0.22	0	0
Alchornea triplinervia (Spreng.) Müll. Arg.	Euphorbiaceae	secondary	2	0.42	2	0.53	0	0
Andira anthelmia (Vell.) Macbr.	Leguminosae	secondary	2	0.21	2	0.20	0	0
Cabralea canjerana (Vel.) Mart.	Meliaceae	secondary	2	0.15	2	0.17	0	0
Cordia sellowiana Cham.	Boraginaceae	secondary	2	0.19	2	0.20	0	0
Cupania oblongifolia Mart.	Sapindaceae	late succes.	2	0.14	2	0.15	0	0
Machaerium stipitatum (DC.) Vog.	Leguminosae	secondary	2	0.26	3	0.32	0	1
Nectandra grandiflora Nees	Lauraceae	late succes.	2	0.30	2	0.31	0	0
Nectandra puberula Nees	Lauraceae	late succes.	2	0.16	2	0.17	0	0
Cinnamomum triplinervea (Ruiz & Pav.) Kosterm.	Lauraceae	late succes.	2	0.30	2	0.29	0	0
Rollinia sericea R.E.Fr.	Annonaceae	late succes.	2	0.19	2	0.24	0	0
Solanum erianthum D.Don	Solanaceae	pioneer	2	0.14	1	0.05	1	0
Campomanesia guaviroba (DC.) Kiaerskov	Myrtaceae	late succes.	1	0.04	1	0.04	0	0
Cecropia hololeuca Miq.	Cecropiaceae	pioneer	1	0.11	1	0.16	0	0
Chorisia speciosa A.St.-Hil.	Bombacaceae	secondary	1	0.17	1	0.20	0	0
Dalbergia myriantha (Mart.) Benth.	Leguminosae	late succes.	1	0.07	0	0.00	1	0
Endlicheria paniculata (Spreng.) Macbride	Lauraceae	late succes.	1	0.06	1	0.07	0	0
Ficus insipida Willd.	Moraceae	late succes.	1	0.97	1	1.05	0	0
Guettarda viburnoides Cham. & Schlecht	Rubiaceae	late succes.	1	0.13	1	0.13	0	0
Inga sessilis (Vell.) Mart.	Leguminosae	late succes.	1	0.11	1	0.11	0	0
Linociera arborea Eichl.	Oleaceae	late succes.	1	0.05	1	0.05	0	0
Maytenus robusta Reiss.	Celastraceae	secondary	1	0.05	1	0.07	0	0
Myrcia multiflora (Lam.) DC.	Myrtaceae	late succes.	1	0.07	1	0.07	0	0
Ocotea laxa (Nees) Mez	Lauraceae	late succes.	1	0.06	1	0.06	0	0
Ocotea odorifera (Vell.) Rohwer	Lauraceae	late succes.	1	0.04	1	0.04	0	0
Ocotea puberula (Rich.) Nees	Lauraceae	late succes.	1	0.17	1	0.18	0	0
Sloanea monosperma Vell.	Elaeocarpaceae	late succes.	1	0.10	1	0.10	0	0
Syagrus romanzoffiana (Cham.) Glassm.	Arecaceae	secondary	1	0.08	1	0.08	0	0
Tapirira guianensis Aubl.	Anacardiaceae	late succes.	1	0.07	1	0.08	0	0
Tibouchina granulosa Cogn.	Melastomataceae	pioneer	1	0.08	1	0.11	0	0
Vitex polygama Cham.	Verbenaceae	late succes.	1	0.09	1	0.09	0	0
Zollernia ilicifolia Vog.	Leguminosae	late succes.	1	0.14	1	0.17	0	0
Cyathea delgadii Sternb.	Cyatheaceae	late succes.	0	0.00	1	0.08	0	1
Piptadenia gonoacantha (Mart.) Macbr.	Leguminosae	secondary	0	0.00	1	0.06	0	1
Total			156	19.21	167	21.17	7	18

Table 2. Structural and dynamic variables of the three ecological groups, exotic, native and total community (dbh ≥ 15.9 cm) in 0.5 hectare of the USP Forest Reserve (São Paulo. SP). N = number of individuals; BA = basal area.

	1992		1997		Deaths	Recruits	N growth	BA growth
	N	BA ($m^2.ha^{-1}$)	N	BA ($m^2.ha^{-1}$)			(%.year^{-1})	(%.year^{-1})
Pioneers	62	7.45	60	7.84	5	3	-0.62	0.98
Secondaries	24	3.48	26	3.76	0	2	1.54	1.45
Late successional	67	8.05	72	8.98	2	7	1.38	2.11
Exotic	3	0.22	9	0.59	0	6	23.28	20.10
Natives	153	18.98	158	20.58	7	12	0.61	1.55
Total	156	19.21	167	21.17	7	18	1.31	1.87

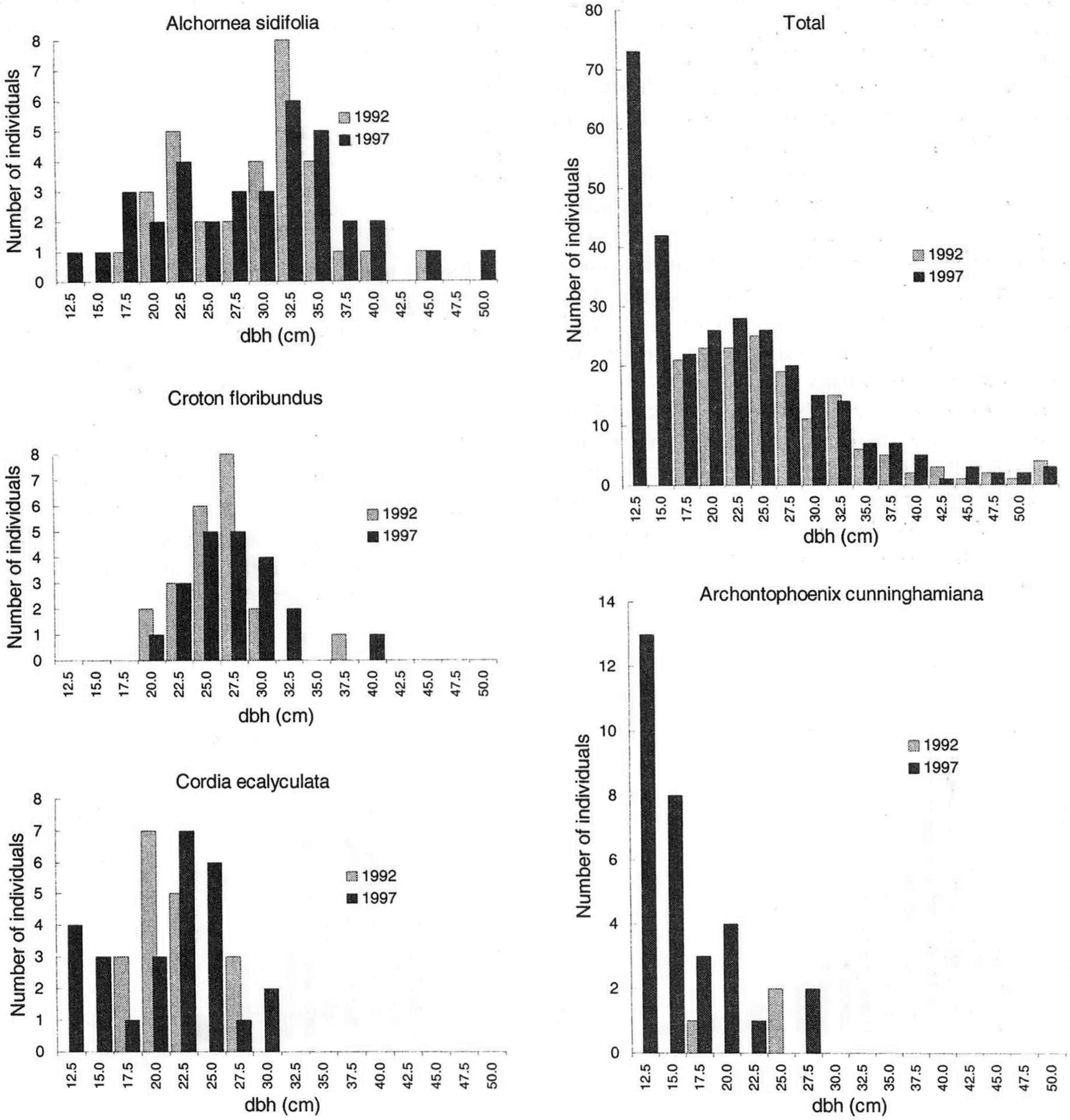

Fig. 2: Frequency distribution of diameter at breast height (dbh) of the exotic *Archontophoenix cunninghamiana*, of the three most abundant species in the studied plot, and of the total community, in 1992 (dbh ≥ 15.9 cm) and 1997 (dbh ≥ 10 cm). Numbers on the x-axis indicate upper class limits.

nity of large trees comprised 167 individuals and 46 species (Tables 1 and 2).

The calculated Czekanowski coefficient (S_c) between 1992 and 1997 was 94.74%. The ranking of species based on density and basal area changed little in 5 years. The first three species – *Alchornea sidifolia, Croton floribundus* and *Cordia ecalyculata*, respectively – maintained their positions in the density rank (Table 1), although the absolute density of *C. floribundus* decreased and of *C. ecalyculata* increased. However, the species in the fourth and fifth positions of the density rank in 1992 – *Maytenus evonymoides* and *Casearia sylvestris* – were outranked by *Archontophoenix cunninghamiana* and *Eugenia cerasiflora*, respectively, in 1997. Basal areas of most species increased, even though some species, such as *C. floribundus*, decreased in number of individuals. *Cordia ecalyculata, Eugenia cerasiflora, Cedrela fissilis, Machaerium stipitatum* and especially *Archontophoenix cunninghamiana* showed increased densities and basal areas (Table 1).

During the studied period, one species – *Dalbergia myriantha* (represented by one individual in 1992) –

disappeared from the community and two new species – *Cyathea delgadii* and *Piptadenia gonoacantha* – were found, totalizing 46 species in 1997 (Table 1). Species diversity (H') and evenness (J') remained almost the same, changing respectively from 3.10 nats.ind^{-1} to 3.13 nats.ind^{-1} and from 81.48% to 81.63%.

The mode of the dbh distribution curve (dbh ≥ 15.9 cm) for the whole community in 1992 (Fig. 2), was within the intermediate class 22.5-25.0 cm. In 1997, the dbh frequency distribution curve showed two peaks, one in the lowest dbh class (10 to 12.5 cm) and another in the 20 to 25 cm dbh classes. The number of individuals increased in almost all dbh classes, in agreement with the general increase in density.

Dbh increment of all trees between 1992 and 1997 was not correlated with the dbh in 1992 (regression analysis: n=168; F=0.02; p=0.887). The average dbh increment was 2.10 mm.year^{-1} (n= 168; st. error = 0.231; median = 1.213) (Table 3). The highest dbh increment recorded was that of one individual of *Cordia ecalyculata*, 11.5 mm.year^{-1}.

Table 3. Mean dbh increment (mm.year^{-1}) of the three most abundant species, of other species except those three, and of the total species surveyed.

Species	Mean (95% confidence interval)
Alchornea sidifolia	1.55 (±0.79)
Croton floribundus	2.77 (±1.09)
Cordia ecalyculata	4.67 (±2.42)
Other species	1.63 (±0.98)
Total	2.10 (±0.65)

Exotic species – The only exotic species found was *Archontophoenix cunninghamiana* (Table 1), an Australian palm introduced to São Paulo gardens and squares as an ornamental. It was first introduced in the campus of the University of São Paulo about 2-3 decades ago, and continues to be planted in the campus gardens.

The population of *A. cunninghamiana* showed the highest increment both in number of individuals (3 to 9) and in basal area (0.22 to 0.59 m^2.ha^{-1}) among all species in the area (Table 1). It showed no mortality in the studied period (Table 1), and was responsible for one third of the community's recruitment, as well as

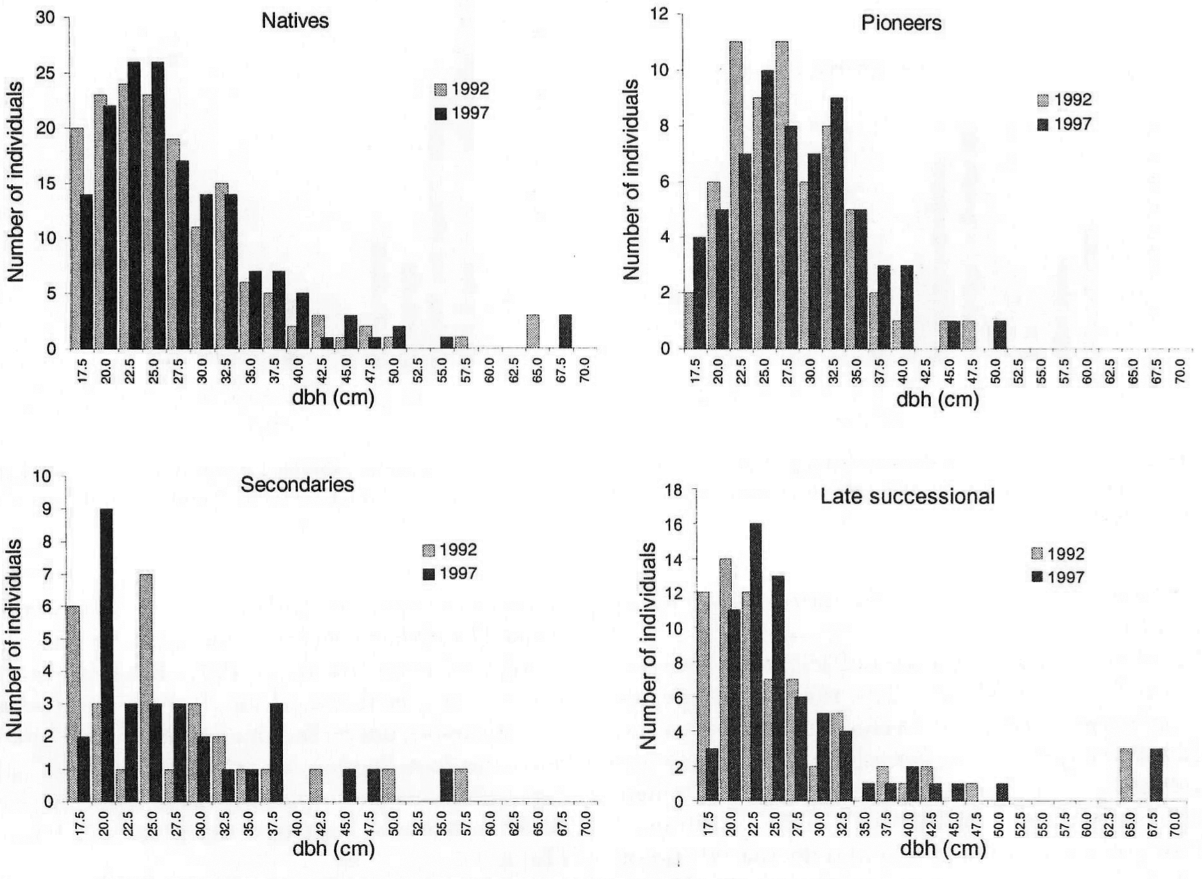

Fig. 3: Frequency distribution of diameter at breast height (dbh) of late successional, secondary, and pioneer species, and of the total native community in the studied plot, in 1992 and 1997 (dbh ≥ 15.9 cm). Numbers on the x-axis indicate upper class limits.

for almost half of the community's growth in number of individuals (Table 2). As a consequence of its high population growth (23.28%.year^{-1}), *A. cunninghamiana* rose from the 9th position in the number of individuals rank in 1992, to 4th in 1997 (Table 1). It also rose ten positions in the basal area rank (Table 1).

The small sample of *A. cunninghamiana* in 1992 did not permit a meaningful analysis of its dbh frequency distribution (dbh ≥ 15.9 cm), but data from 1997 (dbh > 10 cm) show high numbers of individuals in the lower (10-15 cm) dbh classes in comparison with the higher (>15 cm) dbh classes (Fig. 2).

Native community – The total density and basal area increased for the community of native species (i.e., excluding *A. cunninghamiana*) – 3.27% and 8.42%, respectively (Table 2) – although less than for the whole community. However, its diversity decreased from 3.03 to 2.97 nats.ind^{-1} although species richness increased, revealing an evenness decline (79.96% to 77.96%).

The dbh distribution of native trees shows a decrease in the number of individuals within lower classes (dbh < 20 cm) from 1992 to 1997 (Fig. 3), even though there was an overall increase in the number of native individuals in the community in the same period (Table 2).

Ecological groups – When species are viewed as successional groups we notice that between 1992 and 1997 the community received one more secondary species, ending up with 13 secondary species. The number of late successional species (27) and pioneers (6 species) remained the same. However, the number of late successional and secondary individuals increased, while the pioneer group decreased (Table 2). The pioneers showed low recruitment and high mortality, which resulted in a decline in the number of individuals. The late successional group, on the other hand, exhibited low mortality and high recruitment, with an increase in the number of individuals (Table 2). Although the density of pioneers decreased in the period, they still accounted for 36% of the total individuals in 1997 (against 40% in 1992). As a result of increased number of individuals and dbh increment, the increase in basal area of the community was highest for late successional species and lowest for the pioneers (Table 2).

The dbh distribution of the late successional group (Fig. 3) shows a remarkable decrease of lower dbh classes (<20 cm) from 1992 to 1997, and an increase of the intermediate classes (20-25 cm), resulting in an increase in all measures of central tendency (mode, median and mean) and a change in the overall shape of the curve (Fig. 3). Pioneers show, in both surveys, higher numbers of individuals in the intermediate dbh classes; the secondary species did not show a regular pattern.

Most abundant native species – The three most abundant species in 1992, *Alchornea sidifolia*, *Croton floribundus* and *Cordia ecalyculata*, kept their positions in the rank of density, from 1992 to 1997 (Table 1). Both *A. sidifolia* and *C. floribundus* (pioneer species) increased their basal areas (4.52 to 4.74 m^2.ha^{-1}, and 2.22 to 2.35 m^2.ha^{-1}, respectively), while maintaining their density (*A. sidifolia*) or having it decreased (*C. floribundus*); *C. ecalyculata*, a late successional species, showed an increase in both density (36 to 40 ind.ha^{-1}) and basal area (1.18 to 1.58 m^2.ha^{-1}) (Table 1), and consequently an increased relative basal area (6.14 to 7.54%).

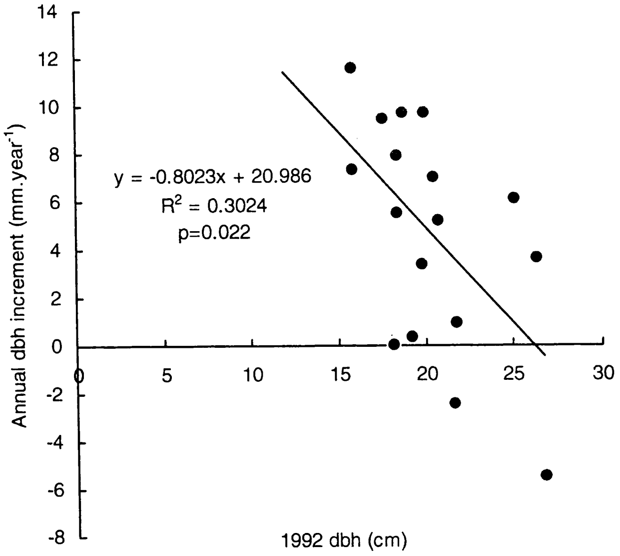

Fig. 4: Relationship between the increment (in the period 1992-1997) of diameter at breast height (dbh) and the dbh in 1992, for *Cordia ecalyculata*.

The prevailing dbh of *A. sidifolia*, *C. floribundus* and *C. ecalyculata* in 1992 fell within the intermediate classes (Fig. 2). The distribution of *A. sidifolia* did not change considerably from 1992 to 1997, which may be related to its low growth rate (see below). In the case of *C. floribundus*, the maximum dbh increased from 1992 to 1997, but no individuals were recorded in the lowest dbh classes (10.0-17.5 cm dbh); still, all the four dbh classes between 17.5 and 27.5 cm had fewer or the same number of individuals in 1997 than in 1992. *Cordia ecalyculata* showed a decrease in density in the 15.9 to 20 cm dbh classes from 1992 to 1997, but the number of individuals with dbh > 20 cm increased in the period (Fig. 2). This species showed a rather irregular pattern of dbh distribution, peaking in the 10-12.5 cm dbh class and in the 20-22.5 cm dbh class.

In contrast to the overall community, *C. ecalyculata* showed a negative correlation between initial dbh and dbh increment (n=17; R^2=0.30; F=6.50; p=0.022), which means that smaller individuals tended to grow faster in dbh than the bigger ones (Fig. 4). The same correlation was not significant for either *Alchornea sidifolia* (n=31; F=0.003; p=0.96) or *Croton floribundus* (n=20; F=4.05; p=0.059). Among these three species, *A. sidifolia* showed the lowest average dbh increment, followed by *C. floribundus* and *C. ecalyculata* (Table 3), although *A. sidifolia* and *C. floribundus* are considered pioneer species, while *C. ecalyculata* is considered a late successional species. Average dbh increment of all the other species summed together was slightly higher than that of *A. sidifolia* (Table 3).

Discussion

The data presented here are restricted due to the rather small sampled area and the relatively high minimum dbh adopted, and have to be analysed carefully taking these restrictions into account. Nevertheless, we consider that important and useful information can be extracted from them.

The analysed area in the USP forest showed a number of structural changes pointed out by Clark (1996) as being expected for tropical forests undergoing ecological succession. For example, the total basal area should increase during the process, as well as the number of large-trunked trees. The contribution of shade-tolerant species in the community is also expected to increase, while the abundance of pioneers should decline. In the USP forest, an increment in the total basal area was noticed, although the number of large trees did not increase. It is possible, however, that for an area of the size analysed here, the latter process could only be detected over a larger time scale. This highlights the importance of repeating such surveys regularly. Pioneer species, an important group of total trees in the studied area, decreased in density, while the opposite happened to secondary and, especially, to late successional species, as would be expected during the successional process.

Alchornea sidifolia and *Croton floribundus*, both pioneer species and the two most frequent in the community, presented small numbers of individuals in the lower dbh classes and high numbers in the intermediate dbh classes in both surveys. This pattern of "mound-shaped" dbh frequency distribution is very similar to those related by Finegan (1996) for long-lived pioneer species in a secondary forest in Barro Colorado Island. The author interpreted this pattern as being the consequence of lack of recruitment, mortality of smaller individuals and the outgrowth into higher-diameter classes. The same interpretation could be made for *A. sidifolia* and *C. floribundus* in the USP forest. We may infer that both species may have had a massive establishment in the area at the beginning of the successional process and now, after some decades, are leaving the community. Following this reasoning, we expect the populations of both species to decline in the near future.

Assuming that *A. sidifolia* and *C. floribundus* populations established in the study area early in the successional process, and postulating a constant rate of dbh increment, it is possible to calculate the age of this forest patch by dividing the mean dbh for each species in 1997 by the corresponding mean dbh increment. For *C. floribundus*, the estimated age would be 263 mm/ 2.77 mm.year^{-1} = 95 years, a value very close to Rossi's (1994) estimate, of about 90 years. The estimated forest age based on *A. sidifolia* alone would be 287 mm/ 1.55 mm.year^{-1} = 185 years. This latter estimate is considerably higher, since *A. sidifolia* attains a bigger size and has a lower dbh increment rate compared to *C. floribundus*.

Some other data might explain this discrepancy between the two estimates. Analysing another forest fragment in São Paulo, Gomes (1998) found much higher dbh increment rates for *A. sidifolia* (9.71 mm.year^{-1}; n = 16; SD = 5.55) than we did. He sampled smaller trees (8.0-21.5 cm dbh) in a more open and disturbed forest than the USP site. These data indicate that, for this particular species, the assumption of constant dbh increment is not valid, and that smaller trees of this species grow faster in dbh than bigger ones. Taking this into account, the estimated age of the *A. sidifolia* population in the USP forest would decrease, getting closer to the estimate derived from the data of *C. floribundus*.

The tendency of higher dbh increment for larger trees, found by many authors (Connell *et al.* 1984, Felfili 1995, Oliveira-Filho *et al.* 1997, Gomes 1998), was not verified in this study for *A. sidifolia* and *C. floribundus*.

The increase in both density and basal area of some late successional species in the USP forest, such as *Cordia ecalyculata*, *Eugenia cerasiflora* and *Cedrela fissilis*, may indicate that the community is reaching maturity. However, the same happened to *Archontophoenix cunninghamiana*, the exotic palm (Table 1), as discussed later.

The community as a whole was very dynamic (high growth rate according to the number of individuals), compared to 63 other studies in neotropical forest sites (trees with dbh ≥ 10 cm) (Table 4). This reflects a relatively low stability, typical of immature or regenerating forests. The recruitment rate in the USP forest was amongst the highest 30% of the compared forests; the mortality rate was amongst the lowest 20% (Table 4).

One possible explanation for the low mortality measured in the USP forest is the minimum dbh adopted for the survey, which was relatively high (considered relatively large trees). Some authors relate the highest mortality rates in the lowest dbh classes (5 to 10 cm) (e.g., Oliveira-Filho *et al.* 1997). However, several other

Table 4. Dynamic variables of some neotropical forest plots, arranged by N growth (dbh = minimum diameter at breast height; N growth = growth in number of individuals). All values transformed to the model of Korning & Balslev (1994a) (modified from Gomes 1998).

Site	dbh (cm)	period (years)	mortality (%.year^{-1})	recruitment (%.year^{-1})	N growth (%.year^{-1})	Reference
Lavras, Brazil	15.0	5.00	1.30	3.97	2.86	Oliveira-Filho *et al.* (1997)
Cuyabeno, Ecuador	10.0	2.15	1.04	3.08	2.08	Korning & Balslev (1994a, b)
Caño Rosalba, Venezuela	10.0	2.00	0.66	2.32	1.68	Veillon (1985) *apud* Phillips (1996)
São Paulo, Brazil	16.0	5.59	0.92	2.40	1.58	Gomes (1998)
Tambopata, Peru	10.0	7.75	1.82	2.86	1.37	Phillips & Gentry (1994)
São Paulo, Brazil	15.9	5.25	0.87	2.10	1.31	This study
Venezuela	10.0	11.00	1.42	2.29	1.18	Carey *et al.* (1994)
Mucuy, Venezuela	10.0	14.10	0.63	1.61	1.10	Veillon (1985) *apud* Phillips (1996)
Cuzco Amazónico, Peru	10.0	5.20	1.79	2.56	0.96	Phillips (1996)
Venezuela	10.0	16.00	1.40	1.89	0.86	Carey *et al.* (1994)
San Carlos de Río Negro, Venezuela	10.0	10.33	1.14	1.81	0.85	Uhl & Murphy (1981), Uhl *et al.* (1988)
Barro Colorado, Panama	10.0	8.00	2.01	2.50	0.83	Hubbell & Foster (1990)
Venezuela	10.0	16.00	0.68	1.26	0.70	Carey *et al.* (1994)
Venezuela	10.0	16.00	1.36	1.72	0.69	Carey *et al.* (1994)
Manú, Peru	10.0	15.00	2.75	2.35	0.48	Gentry & Terborgh (1990)
Mucuy, Venezuela	10.0	11.90	0.54	0.96	0.47	Veillon (1985) *apud* Phillips (1996)
Manaus, Brazil	25.0	5.00	1.44	1.80	0.46	Jardim (1990)
Allpahuayo, Peru	10.0	5.30	1.43	1.77	0.45	Phillips (1996)
Tambopata, Peru	10.0	11.67	1.94	1.98	0.44	Phillips & Gentry (1994)
Linhares, Brazil	10.0	15.00	1.51	1.60	0.42	Rolim (1997)
Venezuela	10.0	10.00	2.96	2.65	0.39	Carey *et al.* (1994)
Venezuela	10.0	14.00	2.10	1.92	0.34	Carey *et al.* (1994)
Manaus, Brazil	25.0	5.00	1.44	1.65	0.30	Jardim (1990)
Manaus, Brazil	10.0	5.17	0.88	1.12	0.28	Rankin-de-Merona *et al.* (1990)
Tambopata, Peru	10.0	7.00	0.70	0.94	0.28	Phillips & Gentry (1994)
Venezuela	10.0	11.00	0.43	0.68	0.28	Carey *et al.* (1994)
Jatum Sacha, Ecuador	10.0	5.00	1.45	1.63	0.27	Phillips & Gentry (1994)
Venezuela	10.0	29.00	1.58	1.23	0.19	Carey *et al.* (1994)
Sucusari, Peru	10.0	4.00	2.10	2.13	0.16	Phillips (1996)
Manú, Peru	10.0	15.50	2.26	1.82	0.15	Gentry & Terborgh (1990)
Yanamono, Peru	10.0	9.75	2.78	2.35	0.14	Phillips & Gentry (1994)
Venezuela	10.0	10.00	2.21	1.96	0.14	Carey *et al.* (1994)
Manaus, Brazil	10.0	5.17	0.83	0.89	0.09	Rankin-de-Merona *et al.* (1990)
Tambopata, Peru	10.0	7.75	2.80	2.40	0.05	Phillips & Gentry (1994)
Tambopata, Peru	10.0	7.75	2.66	2.28	0.03	Phillips & Gentry (1994)
Allpahuayo, Peru	10.0	5.30	2.03	1.87	0.00	Phillips (1996)
Venezuela	10.0	11.00	1.42	1.24	0.00	Carey *et al.* (1994)
La Selva, Costa Rica	10.0	13.00	2.16	1.67	-0.05	Lieberman *et al.* (1990)
La Selva, Costa Rica	10.0	13.00	2.40	1.80	-0.08	Lieberman *et al.* (1990)
Añangu, Ecuador	10.0	4.92	1.87	1.66	-0.09	Korning & Balslev (1994a, b)
Venezuela	10.0	17.00	1.52	1.13	-0.11	Carey *et al.* (1994)
Caño Rosalba, Venezuela	10.0	2.00	1.71	1.49	-0.19	Veillon (1985) *apud* Phillips (1996)
Brasília, Brazil	10.0	6.00	3.44	2.74	-0.22	Felfili (1994, 1995)
Venezuela	10.0	11.00	0.95	0.66	-0.23	Carey *et al.* (1994)
Mishana, Peru	10.0	7.58	1.60	1.24	-0.23	Phillips & Gentry (1994)
La Selva, Costa Rica	10.0	13.00	1.88	1.33	-0.24	Lieberman *et al.* (1990)
Cuzco Amazónico, Peru	10.0	5.20	2.22	1.77	-0.28	Phillips (1996)
Venezuela	10.0	29.00	2.05	1.08	-0.31	Carey *et al.* (1994)
Venezuela	10.0	18.00	1.70	1.04	-0.35	Carey *et al.* (1994)
Manaus, Brazil	10.0	5.17	1.14	0.74	-0.36	Rankin-de-Merona *et al.* (1990)
Venezuela	10.0	19.00	2.06	1.20	-0.39	Carey *et al.* (1994)
Manaus, Brazil	10.0	5.17	1.32	0.69	-0.59	Rankin-de-Merona *et al.* (1990)
Manaus, Brazil	10.0	5.17	1.40	0.75	-0.61	Rankin-de-Merona *et al.* (1990)
Manaus, Brazil	25.0	5.00	1.52	0.86	-0.61	Jardim (1990)
Venezuela	10.0	17.00	2.28	1.10	-0.75	Carey *et al.* (1994)
Venezuela	10.0	18.00	1.70	0.62	-0.89	Carey *et al.* (1994)
Pakitiza, Peru	10.0	4.00	2.65	1.60	-0.92	Dallmeier *et al.* (1992) *apud* Phillips (1996)
Pakitiza, Peru	10.0	4.00	2.25	1.17	-1.00	Dallmeier *et al.* (1992) *apud* Phillips (1996)
Añangu, Ecuador	10.0	8.50	3.03	-	-	Korning & Balslev (1994a, b)
Monte Verde, Costa Rica	30.0	3.31	2.50	-	-	Matelson *et al.* (1995)
Barro Colorado, Panama	19.0	13.60	1.97	-	-	Milton *et al.* (1994)
Añangu, Ecuador	10.0	8.50	1.87	-	-	Korning & Balslev (1994a, b)
Manaus, Brazil	10.0	4.00	1.13	-	-	Jardim (1990)
Mean			1.71	1.69	0.27	
Median			1.70	1.67	0.16	
Lower Quartile			1.30	1.13	-0.23	
Upper Quartile			2.16	2.13	0.48	
Std. Dev.			0.68	0.69	0.74	

studies found no correlation between mortality and the individual size when dbh was higher than 5-10 cm (Swaine *et al.* 1987, Lieberman *et al.* 1985, Manokaran & Kochummen 1987), while Hubbell and Foster (1992) and Milton *et al.* (1994) registered higher mortality for the biggest trees in Barro Colorado Island. In any case, even if compared only to those sites with a minimum dbh of 15 cm or higher (Table 4), the USP forest shows the lowest mortality.

The growth rate (number of individuals) of the USP forest ranked sixth of 58 forest sites (Table 4). Interestingly, two of the five sites which showed growth rates higher than that of USP forest were also isolated secondary and/or disturbed patches in SE Brazil (Oliveira-Filho *et al.* 1997, Gomes 1998). The fact that these forests at present are more dynamic could be a result of major disturbances experienced by each one of them in the past. It could also be due to pronounced edge effects that act in small fragments, which have been shown to affect various processes important to the dynamics of trees, including increased recruitment rate (Laurance *et al.* 1998). It is important to stress, however, that a large contribution to the measured growth in number of individuals is due to the exotic palm *Archontophoenix cunninghamiana*. This species showed a very high increment in density and basal area, and its dbh distribution in 1992 and 1997 suggests a process of biological invasion in the fragment (according to Pysek's [1995] definition). It is possible that the growth of *A. cunninghamiana* population is associated with the measured density decline of young individuals of native species (represented by the lower dbh classes), especially those of late successional species, this pattern being an indication of inadequate regeneration in this group. *A. cunninghamiana*, apparently a shade-tolerant species, may be outcompeting the native late successional species. This assumption is supported by observing this species *in situ:* below a reproductive individual of *A. cunninghamiana* one can find dozens of its seedlings and saplings but none of other species.

Although the overall community showed a growth in number of individuals for almost all dbh classes, its curve of dbh distribution does not show the usual shape recorded for well-balanced tropical forests, where the previous dbh class has more individuals than the subsequent dbh class (e. g., Nadkarni *et al.* 1995, Guariguata *et al.* 1997, Oliveira-Filho *et al.* 1997, Werneck *et al.* 2000). This reinforces the possibility of a generalized regeneration problem in the fragment. Excluding *A. cunninghamiana* from the community, the number of small individuals (dbh < 20 cm) decreased from 1992 to 1997, indicating that individuals of *A. cunninghamiana* are taking the place of other species in the community.

Conclusions

The composition of the studied forest in terms of ecological groups, where the abundance of pioneer species is relatively high, although declining, and the group of late successional species is increasing, indicates that the USP forest is still undergoing successional changes. Even being probably at least 90 years old, this forest is still very dynamic and pioneer species are abundant in the community, indicating that this kind of tropical forest takes more than a century to reach maturity, as highlighted by Finegan (1996) for some tropical forests. The distribution of dbh frequencies, especially of late successional species and of the community as a whole, shows that native species in general are facing regeneration problems. We believe the most important reason for this is the invasion of the forest fragment by *A. cunninghamiana*. The very high growth and recruitment rates found for this species, with no mortality, show its potential to dominate the community in a few years. Still, the isolation of the fragment, its small size and frequent (direct and indirect) man-caused disturbances – such as the entry of people in the forest (especially students and researchers), air pollution and noise due to the traffic of vehicles in the neighbouring roads which drive the animals away, among others – probably contribute to the unbalance of smaller individuals of native species.

We want to stress the need to manage small fragments of native vegetation – as the USP Forest Reserve – aiming at maintaining their natural diversity, including the control of invasive species. The present study indicates *A. cunninghamiana* as a potential problem in the studied forest and that management actions are necessary towards its control. Therefore, further studies concerning the behaviour of *A. cunninghamiana* in the USP Forest Reserve are being conducted, in order to gather more detailed information about the species.

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