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Diversity and structure of the tree community of a fragment of tropical secondary forest of the Brazilian Atlantic Forest domain 15 and 40 years after logging

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ABSTRACT – (Diversity and structure of the tree community of a fragment of tropical secondary forest of the Brazilian Atlantic Forest domain 15 and 40 years after logging). Two adjacent tracts of tropical secondary forest, situated in Itambé do Mato Dentro, south-eastern Brazil, which had been regenerating for 15 and 40 years after clearing, were compared with the purpose of detecting differences in species diversity and composition, species guild composition (regeneration, stratification and dispersion), and stand structure. Four and three 1,125 m^2 plots laid on the 15- and 40-year-old stands, respectively, sampled 2,430 trees with diameter at the base of the stem ≥ 5 cm. The number of species (S = 199) was high for this forest type and significantly higher for the older stand. Tree density was significantly higher in the younger stand, particularly for smaller trees, whereas the two stands did not differ in both basal area and volume per hectare. Trees of shade-tolerant and understory species were significantly more abundant in the older stand. Though sharing a large proportion of species (49%), the two stands differed significantly in the abundance of many species. Live stumps probably contributed to the relatively quick restoration of some forest characteristics, particularly species diversity, basal area and volume.

Key words - Brazilian Atlantic forest, forest regeneration, succession, tropical secondary forest

RESUMO – (Diversidade e estrutura da comunidade arbórea de um fragmento de floresta tropical secundária do domínio da Floresta Atlântica 15 e 40 anos após o corte). Dois trechos adjacentes de floresta secundária, situados em Itambé do Mato Dentro, MG, e que estiveram em regeneração por 15 e 40 anos depois do corte foram comparados com o propósito de detectar diferenças em diversidade e composição de espécies, composição de guildas (regeneração, estratificação e dispersão) e estrutura do povoamento. Quatro e três parcelas de 1.125 m^2 foram distribuídas nos povoamentos de 15 e 40 anos de idade, respectivamente, e amostraram 2.430 árvores com diâmetro na base do tronco ≥ 5 cm. O número de espécies (S = 199) foi alto para essa tipologia florestal e significativamente maior para o povoamento mais velho. A densidade de árvores foi significativamente mais alta no povoamento mais jovem, particularmente para árvores menores, ao passo que os dois povoamentos não diferiram em área basal e volume por hectare. Árvores de espécies tolerantes à sombra e de espécies de sub-bosque foram significativamente mais abundantes no povoamento mais velho. Apesar de compartilharem uma grande proporção de espécies (49%) os dois povoamentos diferiram significativamente quanto à abundância de muitas espécies. As cepas das árvores provavelmente contribuíram para a relativamente rápida restauração de algumas características da floresta, particularmente diversidade de espécies, área basal e volume.

Palavras-chave - Floresta Atlântica, floresta secundária tropical, regeneração florestal, sucessão

Introduction

The Brazilian Atlantic forests, which once covered an area of about 1.1 million km^2 along the eastern Brazilian coast, are among the most threatened tropical forests of the world, as their range largely coincides with the most populated areas of the country (SOS Mata Atlântica & INPE 1993). These forests are now reduced to only about 5% of their original cover and most remnants are in either small (< 10 ha) disturbed fragments or larger areas sheltered on steep mountain slopes (Viana & Tabanez 1996, SOS Mata Atlântica 1998).

During the last decades, the increasing pressure on authorities to halt indiscriminate deforestation has achieved results and fragments of secondary forests are thriving all over the region. However, the ‘complete’ restoration of many characteristics of the original mature forest is dependent upon many factors, particularly regeneration time, distribution and size of forest fragments, the history of land use and disturbance, and the existence of preserved mature forests on the

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landscape (Whitmore 1990, Saldarriaga & Uhl 1991, Guariguata & Dupuy 1997, Parthasarathy 1999). Important forest characteristics, such as species richness and diversity, species composition, and tree density and biomass, are affected differently by these factors and are restored at different rates (Uhl *et al*. 1982, Saldarriaga *et al*. 1988, Saldarriaga & Uhl 1991, Tabarelli & Mantovani 1999).

A detailed knowledge of the mechanisms of tree community organization that take place during forest regeneration is necessary to provide a solid foundation for an efficient management and conservation of tropical secondary forests remnants. There are, however, few studies of forest regeneration in the Brazilian Atlantic Forest domain and most that have been done are in the coastal rainforests (*e.g*. Klein 1980, Mendonça *et al*. 1992, Pessoa *et al*. 1997, Tabarelli & Mantovani 1999). In the present contribution we compared a number of characteristics of two adjacent tracts of hinterland semideciduous forest of the Atlantic Forest Domain. By the time of the study, these forest stands had been regenerating for 15 and 40 years after clearing, respectively. We posed the following central question: were there clear differences between the two stands in their tree community features, and, if so, could these differences be related to regeneration time? To this goal, we compared the two stands for their species richness and evenness, species composition, proportion of trees per species guild (regeneration, stratification and dispersion), and stand structure (tree density, basal area, volume and size class distribution).

Material and methods

Study area – Our study was carried out in a ca. 9.8 ha forest fragment located at 19°26'S and 43°14'W, and at 610-630 m of altitude, in Fazenda Camarinha, municipality of Itambé do Mato Dentro, state of Minas Gerais, Brazil. The area lies on the margin of the Dona Rita Hydroelectric Reservoir, formed by a dam built across the Rio Tanque in 1960. The climate of the region is characterised by warm temperatures throughout the year with a rainy summer and a dry winter. The tree flora of this area is characteristic of the semideciduous forests of the Rio Doce basin, in eastern Minas Gerais (Carvalho *et al*. 2000, Oliveira-Filho & Fontes 2000). Small forest fragments at different regeneration phases are abundant in the region and the five nearest fragments are found within a 1 km distance from the studied forest.

Different areas of the forest fragment were logged on three occasions, as indicated in Figure 1. The first harvest was in 1957 during the construction of the dam. All trees on the valley bottom (now under water) and on part of the surrounding slopes (western side) were felled and used for props by the builders. After the reservoir was formed, the forest regenerated on the felled slope and there was little disturbance by humans in the fragment for more than 20 years. After this period, the fragment was harvested twice more and the remaining areas of mature forest were logged to produce charcoal. The first logging, in 1982, cleared the eastern side of the slope and the second, in 1996, the hilltop. Therefore,

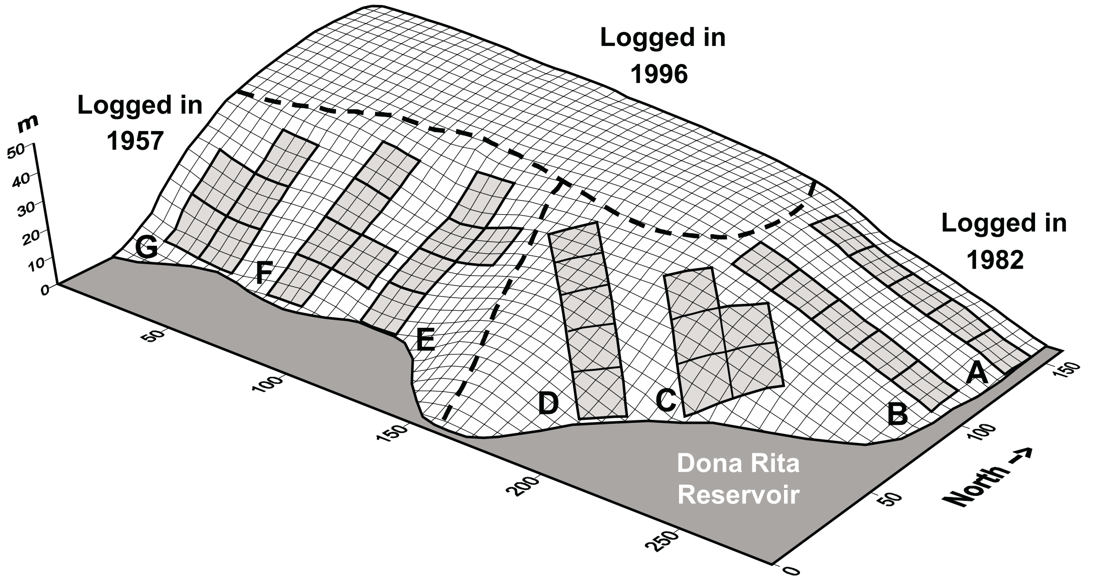

Figure 1. Surface grid of the area of secondary forest surveyed in Itambé do Mato Dentro, south-eastern Brazil, showing the distribution of the seven sample plots (A-G) and the three sectors (dashed lines) where trees were felled in different years. Plots are made up of five adjacent 15 × 15 m subplots; lines on surface grid are spaced at 5 m intervals.

when we surveyed the forest in 1997, there were three sectors corresponding to different regeneration ages. The stands on the western (ca. 2.1 ha) and eastern (ca. 3.2 ha) slopes were 40 and 15 years old, respectively, and forest physiognomy was characterised in both stands by a canopy of irregular height (12-20 m), dense understory and low deciduousness. During the dry season < 15% of trees are totally leafless while the others only reduce their foliage. The hilltop vegetation (ca. 4.5 ha) was only one-year old and consisted of a dense mix of saplings, sprouting stumps and vine tangles.

Forest and soil surveys – Sampling procedure followed the protocol of our previous studies (*e.g.* Botrel *et al*. 2002) devised to capture the maximum variation in both species abundance distributions and environmental variables. We sampled soils and trees in seven 1,125 m^2 plots located in the forest fragment, four plots in the 15-year-old sector and three in the 40-year-old (Figure 1), in order to use a similar sampling intensity for both stands (ca. 15% of their areas). The hilltop sector was not included because logging was too recent and there was no tree above the minimum sampling size established. The area was also divided for sampling into three slopes, according to their aspect: east (plots A and B), southeast (plots C and D) and south (plots E, F and G). On each slope, plots were aligned perpendicularly to the reservoir margin and 20 m apart. Each plot was made up of five 15 × 15 m adjacent subplots arranged in a row starting at the margin of the reservoir and ending at the forest edge adjacent to the hilltop. In four of the plot areas this distance was < 75 m, therefore some subplots were placed to the side of the main rows, at a randomly assigned position along the row.

All trees occurring in the subplots with a circumference at the base of the stem (CBS) ≥ 15.7 cm (5 cm diameter) were identified and their CBS and total height were measured. For the few buttressed trees, the CBS was recorded above the buttresses. Voucher specimens are stored at the Herbarium of the Universidade Federal de Lavras (ESAL). The species of flowering plants (all but Cyatheaceae) were classified into families following the Angiosperm Phylogeny Group II (APG II 2003).

In order to assess differences in soil properties between the two stands, four 0.5-litre soil samples were collected from a depth of 0-20 cm at the midpoints between the corners and the centre of each subplot. The four soil samples were mixed up to produce a single soil sample representative of the subplot surface soil. Chemical and granulometric analyses were carried out at the Soil Laboratory of the Universidade Federal de Lavras following standard procedures (Embrapa 1997).

Data analysis – Plot means were calculated for each of the following soil variables: pH, P, K^+, Ca^{++}, Mg^{++}, Al^{+++}, total exchangeable bases, saturation of bases, organic matter, and percentage sand, silt and clay. Above ground tree volume estimates were calculated for each plot using the formula 'volume = basal area*height*0.6', following Korning & Balslev (1994). Tree frequency distributions into classes of diameter and height were prepared for each separated sample plot using class intervals with exponentially increasing ranges to make up for the normally steep decrease in tree density toward larger diameters and heights (see Oliveira Filho *et al*. 2001). Then each soil variable and tree community physiognomic variable was compared between the two stands, in a 3 × 4 plots design, using two-sample *t* tests. Independent, normal populations with equal variances were deliberately assumed to perform the tests. As stated by Zar (1996), "the biological researcher cannot (…) always be assured that these assumptions are correct. Fortunately numerous studies have shown that the *t* test is robust enough to stand considerable departures from its theoretical assumptions, especially if sample sizes are equal or nearly equal, and especially when two-tailed hypotheses are considered".

Three parameters of species diversity were used to compare the 15- and 40-year-old stands: species richness, Shannon diversity index (*H*') and Pielou evenness (*J*') (Krebs 1989). These parameters were plotted on sample area for each of the two stands using the 15 × 15 m subplots as sample units in order to refine the effects of increasing area. The means and their 95% confidence intervals of each diversity parameter were calculated for each sample size from sub-sampling all possible combinations of subplots. The second-order jackknife estimator (Palmer 1991) of the total number of species in each stand was also calculated. The Shannon diversity indices of the two stands were compared with Hutcheson's *t* test (Zar 1996).

A detrended correspondence analysis, DCA (Hill & Gauch 1980), was performed using the program Canoco 4 (ter Braak & Šmilauer 1998) in order to investigate whether the emerging patterns of species abundance distribution were related to the two stand ages. The 35 subplots were used, instead of the seven plots, in order to assess both intra-plot and inter-plot variations. The species abundance matrix consisted of the relative importance values (RIVs) of each species across subplot. RIVs were obtained from the sum of species density and volume, both standardised to the site total (van Tongeren 1995). As recommended by ter Braak (1995), rare species were eliminated (including only the 47 species with RIV ≥ 5 in the total sample) and RIVs were log-transformed before analysis. The seven stands were graphically discriminated on the subplot ordination diagram in order to assess, *a posteriori*, the relationship between the overall species distribution pattern and the two stand ages.

For each of the 47 species used in DCA, their abundances expressed as both number of trees and total volume were compared between the 15- and 40-year-old stands. Chi-square statistics was used to test the species frequency of trees in each stand against the expected frequencies obtained from the total number of trees of each stand, and the *t* test to compare the distribution of the species volume in each stand in a 4 × 3 plots design (see assumptions of the *t* test above).

In order to search for ecologically meaningful differences between the two forest communities for particular species groups, all 201 species were classified into three guild systems: regeneration, stratification and dispersion. The regeneration guilds, based on Swaine & Whitmore's (1988) ecological species groups, were: (a) pioneer, (b) shade-tolerant climax species, and (c) light-demanding climax species. Pioneer and climax species differ on 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 stratification guilds were based on the stature commonly reached by the adult individuals: (a) small, 2-8 m; (b) medium, > 8-17.5 m; and (c) large, ≥ 17.5 m tall (see Oliveira-Filho *et al.* 1994). The dispersion guilds were: (a) anemochorous, species with mechanisms to facilitate dispersal by wind; (b) zoochorous, species with characteristics related to dispersal by animals; and (c) autochorous, species dispersed by free fall or ballistic mechanisms (van der Pijl 1982). The classification of each species into the species guilds was based on scientific knowledge registered in the literature (Morellato & Leitão-Filho 1992, Lorenzi 1992, 1998, Gandolfi *et al.* 1995, Oliveira-Filho *et al.* 1997, Barroso *et al.* 1999, Nunes *et al.* 2003). The distribution of trees into the species guilds in the two forest communities were tested for independence with chi-square tests for contingency tables (Zar 1996).

Results

The soils of the two stands did not differ significantly for all chemical and textural variables but organic matter (table 1). The proportions of organic matter were significantly higher in the soils of the 15-year-old forest stand than in those of the 40-year old stand.

Tree density was significantly higher in the younger stand than in older one; no significant difference was found between the stands for basal area and volume per hectare (table 2). The distribution of the number of trees per plot differed significantly between the two stands for particular classes of diameters and heights (figure 2). The younger stand had significantly higher numbers of trees of the 5-9 cm diameter class and > 5-10 m height class.

A total of 2.430 individual trees and 199 species were registered (table 3). The numbers of species sampled for each stand age were similar, 152 and 145 for the younger and older stands, respectively (table 2), and 98 species (*i.e.* 49%) were shared by the two stands. Despite these figures, the shapes of the two species-area curves (figure 3A) indicate that the 15-year old subplots accumulated significantly more species at smaller areas (≤ 7 subplots) but were surpassed by the 40-year old subplots over larger sample areas (≥ 12 subplots), suggesting that total species richness was probably higher in the older stand. In fact, at the sample size of 14 subplots, the 95% confidence intervals obtained from all possible subplot series were 135.9-136.1 and 140.2-142.0 species for the younger and older stands, respectively. This was reinforced by the second-order jackknife estimators, which projected a total of 227.2 species for the older stand in contrast to 215.8 species for the younger stand (table 2).

The evenness-area curves in figure 3B show a steeper decrease of *J'* values with increasing sample size for the younger stand. However, this difference

Table 1. Soil variables in the two stands of secondary forest in Itambé do Mato Dentro, south-eastern Brazil. Figures are means ± standard deviations of the four and three 1,125 m^2 plots used to survey the 15- and 40-year-old stands, respectively. Each variable is compared between plots using two-sample *t* tests. (ns = non-significant).

	15-year-old stand $N = 4$	40-year-old stand $N = 3$	*t* tests
pH in H_2O	4.44 ±0.02	4.37 ± 0.19	0.62 ns
P Mehlich (mg.dm^{-3})	1.4 ±0.00	1.5 ± 0.1	2.00 ns
K+ (mg.dm^{-3})	46.0 ±5.2	41.5 ± 10.8	0.62 ns
Ca++ (cmolc.dm^{-3})	0.36 ±0.04	0.57 ± 0.27	1.37 ns
Mg++ (cmolc.dm^{-3})	0.12 ±0.03	0.28 ± 0.23	1.21 ns
Al+++ (cmolc.dm^{-3})	1.94 ±0.08	1.71 ± 0.38	1.00 ns
Total bases (cmolc.dm^{-3})	0.60 ±0.07	0.96 ± 0.50	1.24 ns
Saturation of bases (%)	5.68 ±0.88	11.00 ± 6.74	1.35 ns
Organic matter (%)	3.06 ±0.14	2.32 ± 0.06	7.17 p<0.01
Sand (%)	50.2 ±1.2	50.9 ± 5.4	0.20 ns
Silt (%)	18.3 ±2.7	17.8 ± 1.2	0.25 ns
Clay (%)	32.2 ±3.1	31.3 ± 5.5	0.23 ns

Table 2. Variables of tree community physiognomy and diversity in the two stands of secondary forest in Itambé do Mato Dentro, south-eastern Brazil. Figures with ranges are means ± standard deviations of the four and three 1,125 m^2 plots used to survey the 15- and 40-year-old stands, respectively. Each variable is compared between plots using two-sample *t* tests (Hutcheson's *t* is used for Shannon's diversity, *H*').

	Total Sample *N* = 7	15-year-old stand *N* = 4	40-year-old stand *N* = 3	*t* statistics
Number of trees per plot	347 ± 78	401 ± 42	276 ± 49	3.07 *
Basal area per plot (m^2)	4.256 ± 0.182	4.318 ± 0.088	4.174 ± 0.264	0.87 ns
Volume per plot (m^3)	32.02 ± 3.76	30.03 ± 2.31	34.67 ± 3.98	1.65 ns
Total number of trees	2430	1603	827	
Total number of species	199	152	145	
Shannon's *H*' (nats.individual^{-1})	4.317	4.123	4.105	0.31 ns
Pielou's evenness, *J*'	0.816	0.821	0.825	
Second-order jackknife estimate	268	216	227	

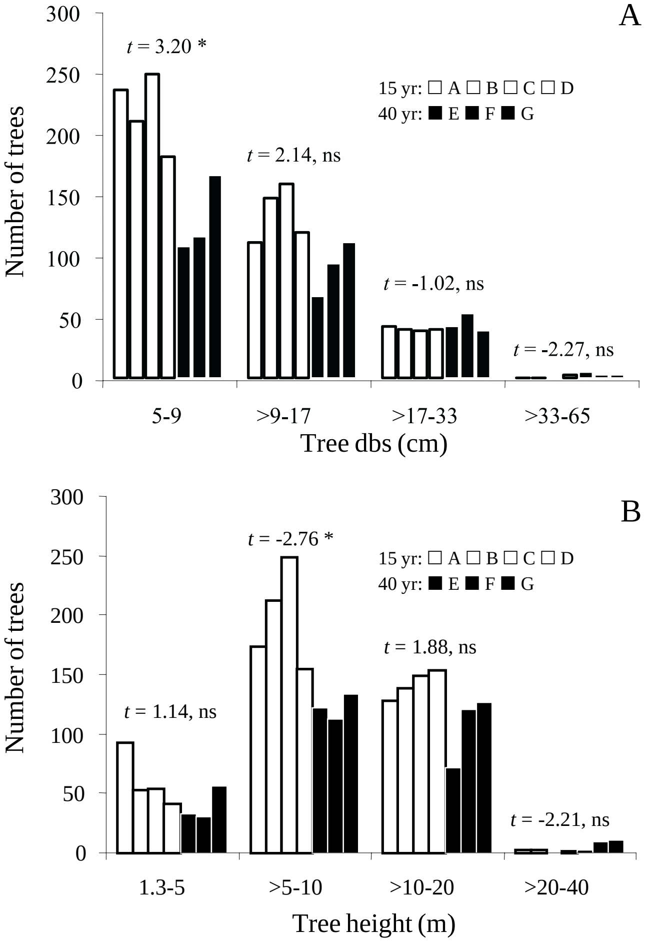

Figure 2. Distribution of the number of trees per diameter (A) and height (B) classes in the seven 1,125 m^2 sample plots of secondary forest (A-G) in Itambé do Mato Dentro, south-eastern Brazil. For each class of diameter and height, the distributions of the number of trees per plot are compared between the two stand ages (15- and 40-year-old) with two-sample *t* test.

was not significant because the 95% confidence intervals for mean *J*' of the two series overlap throughout the distribution (0.825-0.826 and 0.823-0.833 at 14 subplots for the younger and older stands, respectively). As the Shannon diversity index is influenced by both the number of species and species evenness, the *H*'- area curves (figure 3C) naturally compromised the richness- and *J*'-area curves. The younger stand had significantly higher *H*' values at smaller areas (≤ 8 subplots) but were surpassed by the older stand at the sample size of 14 subplots, where *H*' had 95% confidence intervals of 4.04-4.05 and 4.06-4.13 for the younger and older stands, respectively. Despite this, the Hutcheson's *t* test did not yield a significant difference between the stands's *H*' (table 2).

The eigenvalues produced by DCA (axis 1 = 0.305, axis 2 = 0.157) were small, indicating 'short' gradients, *i.e.* most species occurred throughout the gradients, varying essentially in their abundances (ter Braak 1995). The two stand ages appeared as two very distinct subplot clusters in the DCA biplot (figure 4A). In addition, subplots of different plots were generally mixed within their respective age cluster, denoting little to none inter-plot discrimination. Plot D was the only exception, as its subplots were more discriminated from those of plots A, B and C.

The DCA ordination of species (figure 4A) strongly agrees with the differences found between stand ages for tree frequency and volume of particular species (table 4). Of the 47 species used in the DCA, 24 were significantly more frequent in either the younger or the older stand, and 11 out of these 24 species also differed in the distribution of volumes in the 15- and 40-year-old plots. The same 24 species are placed accordingly on

Table 3. Tree species sampled on seven 1,125 m^2 plots of secondary forest in Itambé do Mato Dentro, south-eastern Brazil, followed by brackets containing their classification into species guilds and the number of individuals recorded in the 15- and 40-year-old plots (N_{15} and N_{40}), respectively. Regeneration guilds: PI = pioneer, LD = light-demanding, ST = shade-tolerant. Stratification guilds: L = large, M, medium, S = small. Dispersion guilds: Ane = anemochorous, Aut = autochorous, Zoo = zoochorous. Species are given per family and listed in alphabetical order.

Families/Species	Guilds	N_{15}	N_{40}
ACHARIACEAE			
Carpotroche brasiliensis (Raddi) A.Gray	ST-L-Zoo	3	8
ANACARDIACEAE			
Astronium fraxinifolium Schott	LD-L-Ane	96	3
Astronium graveolens Jacquin	ST-L-Ane	3	7
Tapirira obtusa (Benth.) Mitchell	LD-L-Zoo	2	0
Thyrsodium spruceanum Salzm.	LD-L-Zoo	13	10
ANNONACEAE			
Anaxagorea phaeocarpa Mart.	ST-L-Zoo	16	12
Duguetia lanceolata A. St.-Hil.	ST-L-Zoo	9	2
Guatteria nigrescens Mart.	ST-M-Zoo	1	0
Guatteria pogonopus Mart.	LD-L-Zoo	1	4
Guatteria villosissima A. St.-Hil.	LD-L-Zoo	34	5
Rollinia laurifolia Schltdl.	LD-L-Zoo	2	0
Xylopia brasiliensis Sprengel	ST-L-Zoo	9	0
Xylopia sericea A. St.-Hil.	LD-M-Zoo	39	14
APOCYNACEAE			
Aspidosperma parvifolium A. DC.	LD-L-Ane	1	1
Aspidosperma ramiflorum Müll. Arg.	LD-L-Ane	0	1
Aspidosperma spruceanum Benth.	LD-L-Ane	2	0
Himatanthus lancifolius (Müll. Arg.) Woodson	LD-M-Ane	2	1
Malouetia arborea (Vell.) Miers	LD-L-Ane	1	1
Tabernaemontana hystrix (Steud.) A. DC.	LD-M-Zoo	1	0
AQUIFOLIACEAE			
Ilex cerasifolia Reissek	ST-M-Zoo	6	13
ARALIACEAE			
Dendropanax cuneatus (DC.) Decne & Planchon	ST-M-Zoo	0	4
Schefflera morototoni (Aublet) Maguire *et al.*	LD-L-Zoo	9	2
ARECACEAE			
Bactris acanthocarpa Mart.	ST-S-Zoo	0	1
Polyandrococos caudescens (Mart.) Barb. Rodr.	LD-L-Zoo	1	0
Syagrus romanzoffiana (Cham.) Glassman	LD-L-Zoo	13	2
ASTERACEAE			
Eremanthus incanus (Less.) Less.	PI-M-Ane	6	0
Piptocarpha macropoda Baker	LD-M-Ane	9	0
BIGNONIACEAE			
Jacaranda macrantha Cham.	LD-L-Ane	3	0
Jacaranda puberula Cham.	LD-L-Ane	5	3
Sparattosperma leucanthum (Vell.) K. Schum.	LD-L-Ane	10	1
Tabebuia vellosoi Toledo	ST-L-Ane	1	1
Zeyheria tuberculosa (Vell.) Bureau	LD-L-Ane	1	1
BORAGINACEAE			
Cordia ecalyculata Vell.	LD-L-Zoo	1	0
Cordia magnoliifolia Cham.	ST-M-Zoo	0	1
Cordia sellowiana Cham.	LD-L-Zoo	1	0
BURSERACEAE			
Protium brasiliense (Sprengel) Engler	ST-M-Zoo	1	0
Protium heptaphyllum (Aublet) Marchand	LD-L-Zoo	15	10

continue

continuation

Families/Species	Guilds	N_{15}	N_{40}
BURSERACEAE			
Protium spruceanum (Benth.) Engler	ST-L-Zoo	9	8
Protium warmingianum March.	ST-L-Zoo	0	7
CELASTRACEAE			
Maytenus glazioviana Loes.	ST-M-Zoo	0	1
Maytenus robusta Reissek	ST-M-Zoo	4	0
Maytenus salicifolia Reissek	ST-M-Zoo	1	2
CHRYSOBALANACEAE			
Couepia meridionalis Prance	LD-L-Zoo	3	1
CHRYSOBALANACEAE			
Licania hypoleuca Benth.	LD-L-Zoo	71	30
Licania octandra (Hoffmgg.) Kuntze	LD-L-Zoo	3	0
CLETHRACEAE			
Clethra scabra Pers.	LD-M-Ane	1	0
CLUSIACEAE			
Calophyllum brasiliense Cambess.	ST-L-Zoo	4	3
Kielmeyera lathrophyton Saddi	LD-M-Ane	2	0
Tovomitopsis saldanhae Engler	ST-L-Zoo	0	3
Vismia guianensis (Aublet) Pers.	PI-M-Zoo	2	0
COMBRETACEAE			
Terminalia glabrescens Mart.	LD-L-Ane	1	1
CYATHEACEAE			
Cyathea corcovadensis (Raddi) Domin	ST-M-Ane	0	1
Cyathea delgadii Sternb.	ST-S-Ane	0	2
Cyathea leucofolis Domin	ST-S-Ane	0	1
DICHAPETALACEAE			
Stephanopodium engleri Baillon	ST-M-Zoo	2	0
EBENACEAE			
Diospyros hispida A.DC.	LD-L-Zoo	1	0
ERYTHROXYLACEAE			
Erythroxylum citrifolium A. St.-Hil.	ST-M-Zoo	1	0
Erythroxylum pelleterianum A. St.-Hil.	ST-S-Zoo	10	3
EUPHORBIACEAE			
Actinostemon klotzschii (Didrichs) Pax	ST-S-Aut	1	0
Aparisthmium cordatum (Juss.) Baillon	LD-L-Aut	0	2
Chaetocarpus echinocarpus (Baillon) Ducke	LD-M-Aut	26	6
Croton floribundus Sprengel	PI-L-Aut	1	0
Gymnanthes concolor (Sprengel) Müll. Arg.	LD-M-Aut	0	17
Mabea fistulifera Mart.	PI-M-Aut	69	39
Maprounea guianensis Aublet	LD-M-Aut	1	0
Pera glabrata (Schott) Poepp.	LD-L-Zoo	99	18
Pogonophora schomburgkiana Miers	ST-L-Aut	52	16
Sapium glandulosum (L.) Morong	LD-L-Zoo	0	2
FABACEAE			
Acacia polyphylla DC.	LD-L-Ane	0	1
Albizia polycephala (Benth.) Killip	LD-L-Ane	0	4
Anadenanthera colubrina (Vell.) Brenan	PI-L-Ane	2	2
Andira fraxinifolia Benth.	ST-L-Zoo	0	2
Apuleia leiocarpa (Vogel) Macbr.	LD-L-Ane	90	99
Cassia ferruginea (Schrad.) Schrad.	LD-L-Zoo	3	3
Copaifera langsdorffii Desf.	LD-L-Zoo	18	5
Dalbergia frutescens (Vell.) Britton	LD-L-Ane	1	2

continue

continuation

Families/Species	Guilds	N_{15}	N_{40}
FABACEAE			
Dalbergia nigra (Vell.) Fr. Allem.	LD-L-Ane	37	13
Dalbergia villosa (Benth.) Benth.	LD-L-Ane	20	2
Hymenolobium janeirense Kuhlman	LD-L-Ane	2	2
Inga marginata Willd.	ST-M-Zoo	2	0
Inga striata Benth.	LD-L-Zoo	2	6
Inga vera Willd.	LD-L-Zoo	0	1
Machaerium acutifolium Vogel	LD-L-Ane	2	1
Machaerium brasiliense Vogel	LD-L-Ane	5	0
Machaerium dimorphandrum Hoehne	LD-L-Ane	3	0
Machaerium lanceolatum (Vell.) Macbr.	LD-L-Ane	0	1
Machaerium stipitatum (DC.) Vogel	LD-L-Ane	3	1
Melanoxylon brauna Schott	ST-L-Ane	8	11
Piptadenia gonoacantha (Mart.) Macbr.	PI-L-Ane	0	2
Plathymenia reticulata Benth.	LD-L-Ane	8	3
Platypodium elegans Vogel	LD-L-Ane	17	5
Pseudopiptadenia contorta (DC.) Lewis & H.C. Lima	LD-L-Ane	1	0
Sclerolobium rugosum Mart.	LD-L-Ane	5	2
Senna multijuga (L.C. Rich.) Irwin & Barneby	LD-L-Zoo	2	0
Swartzia acutifolia Vogel	ST-L-Zoo	6	0
Swartzia apetala Raddi	ST-L-Zoo	2	0
Swartzia flaemingii Vogel	LD-L-Zoo	0	1
Swartzia macrostachya Benth.	LD-L-Zoo	16	0
Swartzia multijuga Hayne	LD-L-Zoo	1	1
Swartzia myrtifolia (Schott) Cowan	LD-L-Zoo	0	1
Swartzia polyphylla DC.	LD-L-Zoo	7	1
Sweetia fruticosa Sprengel	LD-L-Ane	0	3
Tachigali paratyensis (Vell.) H.C. Lima	ST-L-Ane	1	1
Zygia latifolia (L.) Fawc. & Rendle	ST-L-Aut	15	2
LAURACEAE			
Aniba firmula (Nees & Mart.) Mez	LD-L-Zoo	4	1
Endlicheria glomerata Mez	ST-M-Zoo	5	4
Nectandra megapotamica (Sprengel) Mez	LD-L-Zoo	3	0
Nectandra oppositifolia Nees	ST-L-Zoo	1	1
Nectandra reticulata (Ruiz & Pavón) Mez	ST-L-Zoo	1	0
Nectandra warmingii Meisner	ST-L-Zoo	0	3
Ocotea corymbosa (Meisner) Mez	LD-L-Zoo	7	6
Ocotea dispersa (Nees) Mez	LD-L-Zoo	3	0
Ocotea divaricata (Nees) Mez	ST-L-Zoo	1	1
Ocotea laxa (Nees) Mez	ST-M-Zoo	0	1
Ocotea odorifera (Vell.) Rohwer	ST-L-Zoo	0	2
Ocotea velutina (Nees) Rohwer	LD-L-Zoo	4	6
Urbanodendron verrucosum (Nees) Mez	ST-L-Zoo	3	3
LECYTHIDACEAE			
Cariniana estrellensis (Raddi) Kuntze	LD-L-Ane	0	1
Lecythis lanceolata Poiret	ST-M-Zoo	0	1
MALPIGHIACEAE			
Byrsonima sericea DC.	LD-L-Zoo	32	1
Heteropterys byrsonimifolia A. Juss.	LD-M-Ane	2	0
MALVACEAE			
Eriotheca candolleana (K. Schum.) A. Robyns	LD-L-Ane	1	1
Luehea divaricata Mart. & Zucc.	LD-L-Ane	4	4

continue

continuation

Families/Species	Guilds	N_{15}	N_{40}
MALVACEAE			
Luehea grandiflora Mart. & Zucc.	LD-L-Ane	0	5
MELASTOMATACEAE			
Miconia calvescens DC.	ST-M-Zoo	0	4
Miconia fasciculata Gardner	ST-M-Zoo	0	1
Miconia trianae Cogn.	LD-M-Zoo	4	0
Tibouchina granulosa Cogn.	LD-M-Ane	0	2
MELIACEAE			
Guarea guidonia (L.) Sleumer	ST-M-Zoo	1	1
Guarea kunthiana A. Juss.	ST-L-Zoo	2	0
Trichilia hirta L.	LD-L-Zoo	2	0
Trichilia pallens C.DC.	ST-M-Zoo	2	0
Trichilia pallida Swartz	ST-M-Zoo	6	24
MORACEAE			
Brosimum guianense (Aublet) Huber	LD-L-Zoo	4	2
Brosimum lactescens (S. Moore) C.C. Berg.	LD-L-Zoo	7	11
Ficus gomelleira Kunth & Bouché	ST-L-Zoo	1	0
Sorocea guilleminiana Gaud.	ST-M-Zoo	4	1
MYRTACEAE			
Calyptranthes clusiifolia (Miq.) O. Berg	ST-M-Zoo	7	3
Campomanesia dichotoma (O. Berg) Mattos	LD-M-Zoo	17	9
Campomanesia xanthocarpa O. Berg	LD-M-Zoo	0	1
Eugenia cuprea (O. Berg) Nied.	LD-L-Zoo	0	1
Eugenia florida DC.	ST-M-Zoo	13	17
Eugenia neoglomerata Sobral	ST-L-Zoo	0	4
Eugenia neolanceolata Sobral	ST-L-Zoo	32	13
Gomidesia anacardiifolia (Gardner) O. Berg	ST-M-Zoo	10	9
Marlierea warmingiana Kiaersk.	ST-L-Zoo	16	1
Myrcia detergens Miq.	LD-L-Zoo	12	5
Myrcia eriopus DC.	ST-M-Zoo	0	1
Myrcia rufula Miq.	LD-M-Zoo	0	2
Myrciaria glomerata O. Berg	ST-S-Zoo	4	1
Myrciaria tenella (DC.) O. Berg	ST-M-Zoo	0	7
Pimenta pseudocaryophyllus (Gomes) Landrum	LD-M-Zoo	88	1
Plinia cauliflora (Mart.) Kausel	ST-L-Zoo	6	1
Psidium cattleianum Sabine	ST-L-Zoo	1	0
Psidium robustum O. Berg	LD-M-Zoo	3	0
Psidium rufum Mart.	LD-M-Zoo	1	7
NYCTAGINACEAE			
Guapira hirsuta (Choisy) Lundell	ST-M-Zoo	3	1
Guapira opposita (Vell.) Reitz	ST-M-Zoo	9	3
OCHNACEAE			
Ouratea parviflora Baillon	ST-M-Zoo	2	0
OLACACEAE			
Schoepfia brasiliensis A. DC.	ST-M-Zoo	2	4
PHYLLANTHACEAE			
Savia dictyocarpa Müll. Arg.	ST-L-Aut	6	7
PICRAMNIACEAE			
Picramnia parvifolia Engler	ST-M-Zoo	1	0
POACEAE			
Guadua angustifolia Kunth	LD-L-Ane	1	0

continue

continuation

Families/Species	Guilds	N_{15}	N_{40}
PROTEACEAE			
Euplassa incana (Klotzsch) Johnston	LD-L-Zoo	0	1
Euplassa legalis (Vell.) Johnston	LD-L-Zoo	0	1
RUBIACEAE			
Amaioua guianensis Aublet	ST-M-Zoo	12	7
Bathysa nicholsonii K. Schum.	ST-M-Ane	8	54
Chomelia catharinae (Smith & Downs) Steyerm.	ST-M-Zoo	0	2
Genipa infundibuliformis Zappi & Semir	LD-L-Zoo	1	1
Guettarda uruguensis Cham. & Schltdl.	LD-L-Zoo	3	2
Ixora warmingii Müll. Arg.	ST-M-Zoo	4	0
Psychotria carthagenensis Jacquin	ST-S-Zoo	0	1
Psychotria vellosiana Benth.	LD-M-Zoo	0	1
Rudgea jasminoides (Cham.) Müll. Arg.	ST-M-Zoo	1	1
Tocoyena sellowiana (Cham. & Schltdl.) K. Schum.	ST-M-Zoo	1	1
Warszewiczia longistaminea K. Schum.	LD-L-Ane	1	0
RUTACEAE			
Esenbeckia febrifuga (A. St.-Hil.) A. Juss.	ST-M-Aut	0	2
Pilocarpus giganteus Engler	ST-L-Aut	23	6
Zanthoxylum rhoifolium Lam.	LD-L-Zoo	0	1
Zanthoxylum tingoassuiba A. St.-Hil.	LD-L-Zoo	0	1
SALICACEAE			
Casearia decandra Jacquin	ST-M-Zoo	5	0
Casearia ulmifolia Vahl	LD-L-Zoo	4	5
Xylosma ciliatifolia (Clos) Eichler	LD-M-Zoo	34	2
SAPINDACEAE			
Allophylus edulis (A. St.-Hil.) Radlk.	ST-M-Zoo	5	1
Cupania emarginata Cambess.	LD-L-Zoo	41	6
Cupania oblongifolia Mart.	LD-L-Zoo	1	0
Cupania vernalis Cambess.	LD-L-Zoo	4	4
Dilodendron elegans (Radlk.) Gentry & Steyerm.	LD-L-Zoo	1	0
Matayba elaeagnoides Radlk.	ST-L-Zoo	16	3
Matayba guianensis Aublet	LD-M-Zoo	19	0
Matayba juglandifolia (Cambess.) Radlk.	ST-L-Zoo	4	1
Toulicia laevigata Radlk.	LD-M-Ane	81	1
SAPOTACEAE			
Micropholis gardneriana (A. DC.) Pierre	LD-L-Zoo	3	4
SIPARUNACEAE			
Siparuna guianensis Aublet	ST-S-Zoo	23	62
SOLANACEAE			
Solanum leucodendron Sendt.	LD-L-Zoo	0	1
URTICACEAE			
Cecropia hololeuca Miq.	PI-L-Zoo	0	19
Pourouma guianensis Aublet	PI-L-Zoo	1	0
VERBENACEAE			
Aloysia virgata (Ruiz & Pavón) A. Juss.	PI-S-Ane	8	2
VOCHYSIACEAE			
Vochysia magnifica Warm.	ST-L-Ane	1	0

either the left or right sides of the DCA biplot (figure 4B), corresponding to the younger and older stands, respectively. *Apuleia leiocarpa*, *Bathysa nicholsonii*, *Brosimum lactescens*, *Cecropia hololeuca*, *Eugenia neoglomerata*, *Siparuna guianensis* and *Trichilia pallida* were significantly more abundant in the older stand in terms of both tree frequency and volume. *Guatteria pogonopus*, *Eugenia florida*, *Ilex cerasifolia*, *Inga striata*, *Melanoxylon brauna* were also significantly more abundant in the older stand but in terms of only tree frequency. All of the above species are also concentrated on the right side of the DCA biplot. *Astronium fraxinifolium*, *Byrsonima sericea*, *Pimenta pseudocaryophyllus*, and *Toulicia laevigata* were

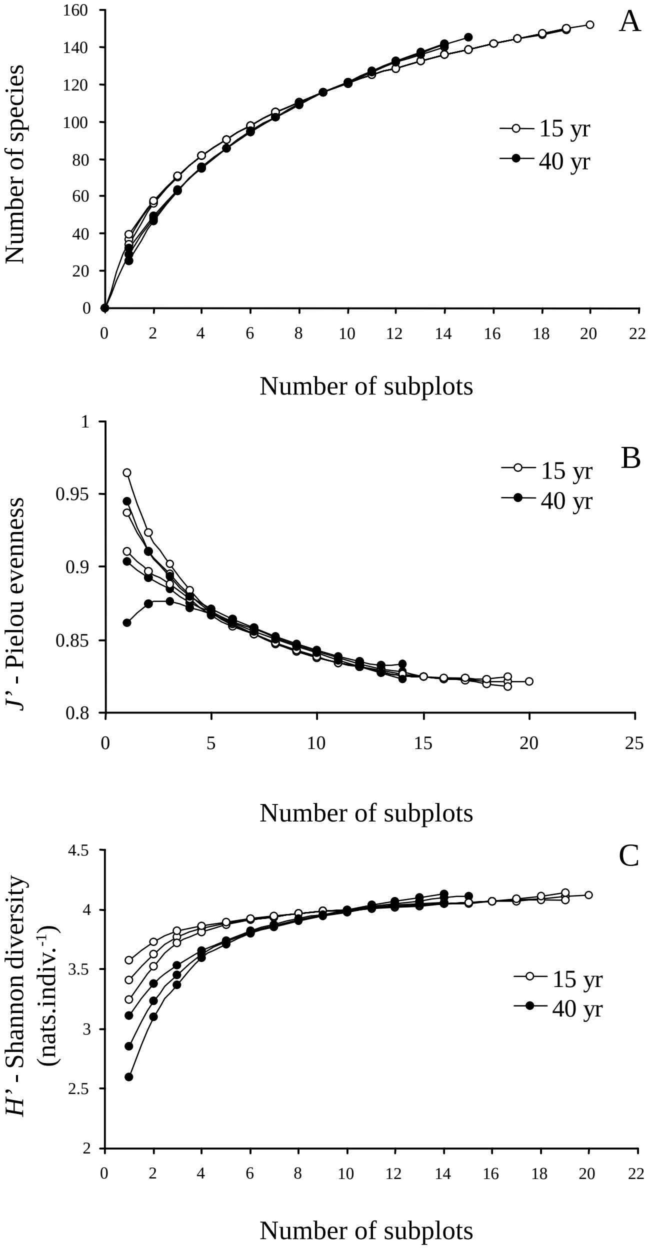

Figure 3. Progression of three measures of species diversity with increasing sample area for the two stand ages, 15- and 40-year-old, of the secondary forest surveyed in Itambé do Mato Dentro, south-eastern Brazil: (A) number of species, (B) Pielou evenness and (C) Shannon diversity. Curves for each stand age are means ± 95% confidence intervals obtained from sub-sampling all possible combinations of subplots.

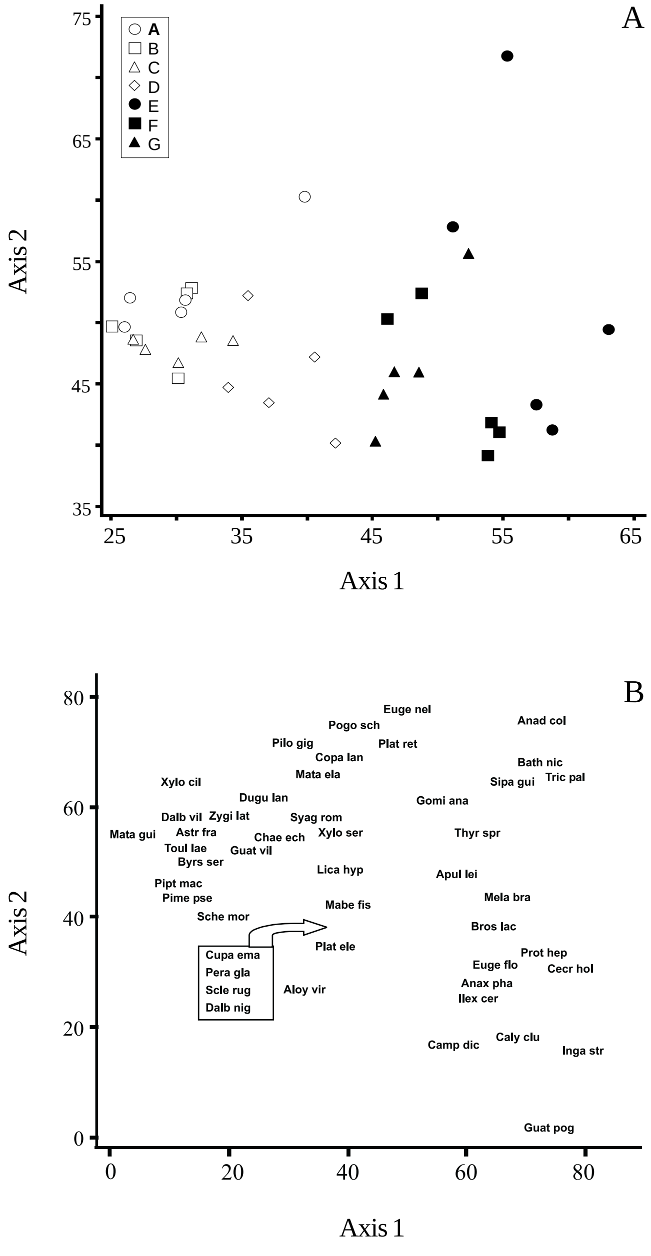

Figure 4. Detrended correspondence analysis. Biplots showing the ordination in the first two axes of (A) 35 subplots of secondary forest surveyed in Itambé do Mato Dentro, south-eastern Brazil and (B) 47 tree species. The seven sample plots (A-G) are indicated by different symbols: open symbols = 15-year-old stand; closed symbols = 40-year-old stand. Species names are abbreviated; full names in table 4.

Table 4. Tree species abundances in the two stands of secondary forest in Itambé do Mato Dentro, south-eastern Brazil. Total number of trees and mean volume per plot in the two stand ages (15- and 40-year-old plots) of the 47 species used in CCA. Full species names are given for the abbreviations used in CCA. The numbers of trees are compared between stand ages with chi-square tests (expected values within brackets are based on the stands' totals) and the distributions of volumes are compared with *t* tests. * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.005$; **** = $P < 0.001$; ns = non significant.

Tree Species		Number of trees		χ^2	Mean volume (m^3)		*t* tests
Abbrev.	Full names	15 yr	40 yr	tests	15 yr	40 yr	
Aloy vir	*Aloysia virgata*	8 (6.6)	2 (3.4)	1.19 ns	0.748	0.175	0.89 ns
Anad col	*Anadenanthera colubrina*	2 (2.6)	2 (1.4)	0.51 ns	0.006	0.751	1.98 ns
Anax pha	*Anaxagorea phaeocarpa*	16 (18.5)	12 (9.5)	0.89 ns	0.124	0.555	1.75 ns
Apul lei	*Apuleia leiocarpa*	90(124.7)	99 (64.3)	28.09 ****	2.133	7.122	3.02 *
Astr fra	*Astronium fraxinifolium*	96 (65.3)	3 (33.7)	42.84 ****	0.596	0.037	2.71 *
Bath nic	*Bathysa nicholsonii*	8 (40.9)	54 (21.1)	77.02 ****	0.075	0.793	4.81 **
Bros lac	*Brosimum lactescens*	7 (11.9)	11 (6.1)	5.56 *	0.050	0.210	2.97 *
Byrs ser	*Byrsonima sericea*	32 (21.8)	1 (11.2)	14.60 ****	1.384	0.098	3.60 *
Caly clu	*Calyptranthes clusiifolia*	7 (6.6)	3 (3.4)	0.24 ns	0.151	0.204	0.19 ns
Camp dic	*Campomanesia dichotoma*	17 (17.2)	9 (8.8)	0.04 ns	0.291	0.624	0.62 ns
Cecr hol	*Cecropia hololeuca*	0 (12.5)	19 (6.5)	35.95 ****	0.000	1.243	2.82 *
Chae ech	*Chaetocarpus echinocarpus*	26 (21.1)	6 (10.9)	3.58 ns	0.458	0.043	1.65 ns
Copa lan	*Copaifera langsdorffii*	18 (15.2)	5 (7.8)	1.77 ns	0.222	0.284	0.20 ns
Cupa ema	*Cupania emarginata*	41 (31)	6 (16)	9.79 ***	0.612	0.341	0.78 ns
Dalb nig	*Dalbergia nigra*	37 (33)	13 (17)	1.57 ns	0.385	0.372	0.05 ns
Dalb vil	*Dalbergia villosa*	20 (14.5)	2 (7.5)	6.50 *	0.355	0.038	1.43 ns
Dugu lan	*Duguetia lanceolata*	9 (7.3)	2 (3.7)	1.56 ns	0.442	0.071	1.80 ns
Euge flo	*Eugenia florida*	13 (19.8)	17 (10.2)	6.56 *	0.070	0.312	1.24 ns
Euge nel	*Eugenia neoglomerata*	0 (2.6)	4 (1.4)	7.09 **	0.307	1.485	5.86 **
Gomi ana	*Gomidesia anacardiifolia*	10 (12.5)	9 (6.5)	1.37 ns	0.138	0.146	0.05 ns
Guat pog	*Guatteria pogonopus*	1 (3.3)	4 (1.7)	4.27 *	0.010	0.716	1.93 ns
Guat vil	*Guatteria villosissima*	34 (25.7)	5 (13.3)	8.15 ***	0.242	0.074	1.42 ns
Ilex cer	*Ilex cerasifolia*	6 (12.5)	13 (6.5)	9.58 ***	0.023	0.215	1.68 ns
Inga str	*Inga striata*	2 (5.3)	6 (2.7)	5.54 *	0.024	0.832	2.07 ns
Lica hyp	*Licania hypoleuca*	71 (66.6)	30 (34.4)	0.92 ns	1.985	1.184	1.11 ns
Mabe fis	*Mabea fistulifera*	69 (71.2)	39 (36.8)	0.19 ns	0.942	1.249	0.54 ns
Mata ela	*Matayba elaeagnoides*	16 (12.5)	3 (6.5)	3.13 ns	0.141	0.347	0.59 ns
Mata gui	*Matayba guianensis*	19 (12.5)	0 (6.5)	10.34 ***	0.314	0.000	1.38 ns
Mela bra	*Melanoxylon brauna*	8 (12.5)	11 (6.5)	4.54 *	0.104	0.824	1.64 ns
Pera gla	*Pera glabrata*	99 (77.2)	18 (39.8)	18.40 ****	4.387	1.500	2.20 ns
Pilo gig	*Pilocarpus giganteus*	23 (19.1)	6 (9.9)	2.53 ns	0.969	0.339	0.85 ns
Pime pse	*Pimenta pseudocaryophyllus*	88 (58.7)	1 (30.3)	43.41 ****	2.145	0.107	3.32 *
Pipt mac	*Piptocarpha macropoda*	9 (5.9)	0 (3.1)	5.25 *	0.358	0.000	1.14 ns
Plat ele	*Platypodium elegans*	17 (14.5)	5 (7.5)	1.46 ns	0.384	0.176	0.72 ns
Plat ret	*Plathymenia reticulata*	8 (7.3)	3 (3.7)	0.42 ns	0.185	0.764	0.87 ns
Pogo sch	*Pogonophora schomburgkiana*	52 (44.9)	16 (23.1)	3.51 ns	0.584	0.596	0.02 ns
Prot hep	*Protium heptaphyllum*	15 (16.5)	10 (8.5)	0.36 ns	0.275	1.138	1.15 ns
Sche mor	*Schefflera morototoni*	9 (7.3)	2 (3.7)	1.56 ns	0.273	0.045	1.85 ns
Scle rug	*Sclerolobium rugosum*	5 (4.6)	2 (2.4)	0.33 ns	1.155	0.896	0.15 ns
Sipa gui	*Siparuna guianensis*	23 (56.1)	62 (28.9)	56.78 ****	0.054	0.265	3.06 *
Syag rom	*Syagrus romanzoffiana*	13 (9.9)	2 (5.1)	3.23 ns	0.325	0.161	0.68 ns
Thyr spr	*Thyrsodium spruceanum*	13 (15.2)	10 (7.8)	0.83 ns	0.408	0.615	0.67 ns
Toul lae	*Toulicia laevigata*	81 (54.1)	1 (27.9)	39.81 ****	0.446	0.023	2.79 *
Tric pal	*Trichilia pallida*	6 (19.8)	24 (10.2)	27.62 ****	0.017	0.189	1.48 *
Xylo cil	*Xylosma ciliatifolia*	34 (23.7)	2 (12.3)	13.44 ****	0.158	0.011	1.39 ns
Xylo ser	*Xylopia sericea*	39 (35)	14 (18)	1.50 ns	0.776	0.548	0.50 ns
Zygi lat	*Zygia latifolia*	15 (11.2)	2 (5.8)	4.14 *	0.228	0.071	0.72 ns

significantly more abundant in the younger stand in terms of both tree frequency and volume. *Cupania emarginata*, *Dalbergia villosa*, *Guatteria villosissima*, *Matayba guianensis*, *Pera glabrata*, *Piptocarpha macropoda*, *Xylosma ciliatifolia* and *Zygia latifolia* were also significantly more abundant in the younger stand but in terms of only tree frequency. All of these species are also concentrated on the left side of the DCA biplot.

The two stand communities differed in the proportions of trees per species guild, for regeneration and stratification but not for dispersion (table 5). With respect to expected values for regeneration guilds, light-demanding trees were more frequent in the younger stand and less frequent in the older stand. Shade-tolerant and pioneer trees followed the opposite pattern, being more frequent in the older stand. With respect to expected values for stratification guilds, only trees of understory species (small size at maturity) were more frequent in the older stand and less frequent in the younger stand.

Discussion

Numerous studies of tropical forests worldwide have demonstrated that tree species distribution is highly influenced by variations of the substratum, particularly ground water regime and soil chemical and textural properties (*e.g.* Newbery *et al.* 1986, ter Steege *et al.* 1993, Duivervoorden 1996, Clark *et al.* 1998, Botrel *et al.* 2002). Therefore, the comparison between the two stand ages could not disregard possible interference from substratum-related variables. On a local scale, topographic variables (*e.g.* elevation, slope grade, plot aspect) have been regarded as the most important substratum-related variable causing spatial variation in the structure of tropical forests because it commonly corresponds to changes in soil properties, particularly drainage, texture and nutritional status (*e.g.* Bourgeron 1983, Newbery & Proctor 1984, Clark *et al.* 1998). As this topographic pattern was present in every plot, we believe it caused no serious impact on the comparisons between the two stand ages. With respect to soil properties, organic matter was the only variable that differed between the two stands, with higher proportions in the younger one; the other variables showed similar variation across both stands. This outcome is rather unexpected because the common pattern in tropical secondary forests as regeneration proceeds is a progressive increase of the soil organic matter pool (*e.g.* Brown *et al.* 1984, Lugo *et al.* 1986), reaching levels similar to mature forests 40-50 years after abandonment (Brown & Lugo 1990). Possible reasons for this may involve both the massive initial litter input left by logging and the higher litterfall rates of the younger stand caused by a more rapid turnover and self-thinning process. However, data on litter input and

Table 5. Number of trees per species guilds in the two stands of secondary forest. Contingency tables and chi-square tests for the frequency of trees of each species guild in the 15- and 40-year old stands (expected values within brackets). * = $P< 0.05$; ** = $P < 0.001$; ns = non-significant.

	Forest stand		
Regeneration guilds	15-year old	40-year old	Chi-square tests
Pioneer	89 (100.9)	64 (52.1)	χ^2 = 4.14 *
Light-demanding	1105 (986.9)	391 (509.1)	χ^2 = 41.55 ns
Shade-tolerant	409 (515.2)	372 (265.8)	χ^2 = 64.33 **
Chi-square tests	χ^2 = 37.44 **	χ^2 = 72.58 **	χ^2 =110.02**
Stratification guilds			
Large	1031 (996.1)	479 (513.9)	χ^2 = 3.59 ns
Medium	526 (524.4)	269 (270.6)	χ^2 = 0.01 ns
Small	46 (82.5)	79 (42.5)	χ^2 = 47.37 **
Chi-square tests	χ^2 = 17.35 **	χ^2 = 33.63 **	χ^2 = 50.97 **
Dispersion guilds			
Anemochorous	456 (466.4)	251 (240.6)	χ^2 = 0.68 ns
Autochorous	194 (192.0)	97 (99.0)	χ^2 = 0.06 ns
Zoochorous	953 (944.6)	479 (487.4)	χ^2 = 0.22 ns
Chi-square tests	χ^2 = 0.33, ns	χ^2 =0.63, ns	χ^2 = 0.96 ns

decomposition rates, as well as on tree community dynamics, would be necessary to confirm this.

The total number of species registered in the two stands (199) is remarkably high compared to similar surveys of fragments of semideciduous forests of the Atlantic Forest Domain, which seldom surpass 140 species (database in Oliveira Filho & Fontes 2000). The reason for these findings may lie in the origin of individual regenerating trees as a result of the local disturbance-recovery history (see Uhl & Clark 1983, Murphy & Lugo 1986). Logging operations were of low impact, using axes and cart-horses. The areas were abandoned shortly after the logs were removed and a considerable proportion of trees re-established, sprouting from stumps and roots. This was indicated by the high proportion of multi-stemmed trees, about 11%, which contrasts with values below 4% found for mature forests in the region (authors' unpublished data). Also, there were always adjacent older stand sectors serving as seed sources. The combination of factors probably minimised the loss of species in the whole fragment.

The typical pattern of species diversity in tropical secondary forests is the accumulation of species, approaching that of a mature forest within a time span of up to 80 years (Brown & Lugo 1990, Tabarelli & Mantovani 1999). In accordance with this, the older stand yielded a higher number of species than did the younger stand. However, this was true only over larger areas (> 12 subplots) because the younger stand had higher species density (*i.e.* number of species per unit area) when smaller areas were compared. Some interactive factors may be involved in this inversion. Firstly, the higher tree density of the younger stand would contribute to increase species density at smaller areas. This relationship would not hold true, however, for larger areas because earlier regeneration phases would contain a smaller species pool than later phases. Secondly, the progression of forest regeneration could also enhance aspects of habitat differentiation related to the substratum and light environment, which are more relevant for species of later regeneration phases.

Despite an age difference of 25 years, the two stands yielded similar values of basal area and volume per hectare. This result is no surprise because tropical secondary forests usually undergo rapid accumulation of biomass during the first 15 years or so and then slow down, often reaching values of basal area and volume comparable to those of a mature forest many decades before maturity (Brown & Lugo 1990). The live stumps and root systems left in the area after logging probably favoured a rapid accumulation of biomass, and the two stands may have reached similar values of basal area and volume before 15 years of age. They could be both continuing to accumulate biomass, though at lower rates. Tabarelli & Mantovani (1999) recorded figures of basal area and volume in secondary Atlantic rain forests aged 40 years considerably below those of nearby mature forests, although the regeneration started from pastures without live tree remnants.

Tree density, particularly for smaller trees, was the most pronounced difference in vegetation structure between the two stand ages. This result agrees with the well-known self-thinning process of aging secondary forests in which a declining tree density, mostly caused by mortality rates concentrated on smaller trees (dbh < 10 cm), is highly compensated by the growth of surviving trees (*e.g.* Crow 1980, Saldarriaga *et al.* 1988, Rao *et al.* 1990, Brown & Lugo 1990, Oliveira Filho *et al.* 1997). Therefore, as forest regeneration proceeds, the average tree size increases while tree density declines.

The structure of the tree species abundance data analysed by DCA contained a large amount of unexplained variance ('noise'). Nevertheless, a species gradient apparently related chiefly to the stands ages did emerge. This main gradient consisted mostly of variations in species abundances than species turnover, characterizing a short gradient, *sensu* ter Braak (1995). In fact, the two stand ages shared 44 out of the 47 species used in the analysis, and 98 out of the 199 species total (49%). Despite this high floristic similarity, the two stands differed significantly on the relative abundance of many species. The interpretation of these patterns as a result of different regeneration ages deserves, however, some restriction because the differences may have resulted, at least in part, to contagious distribution patterns, which predominate among tropical forest tree species (Hubbell & Foster 1986). Therefore, the differences in population abundances between the two stands could result from species clumps and, therefore, spatial autocorrelation. Despite this, there were other findings that fortunately weaken the power of this alternative hypothesis. The differences on the proportion of trees per regeneration and stratification guilds between the two stands provided additional substance to the differences in tree community composition.

Species which were more frequent than expected in the younger stand, such as *Byrsonima sericea*, *Pera glabrata*, *Toulicia laevigata*, *Astronium fraxinifolium* and *Pimenta pseudocaryophyllus*, are shade-intolerants commonly found in disturbed forests or at forest edges in the region. On the other hand, *Bathysa* *nicholsonii*, *Eugenia neoglomerata*, *Siparuna guianensis*, *Astronium graveolens* and *Trichilia pallida*, which were more frequent than expected in the older stand, are shade-tolerant species commonly found regenerating in the understorey of mature forests. As many shade-tolerant species are also typical of the forest understorey (*e.g. Bathysa nicholsonii* and *Siparuna guianensis*), the frequency of small trees was higher in the older stand. The significantly higher abundance of light-demanding and shade-tolerant species in the younger and older stand, respectively, also supports the view of two distinct regeneration phases. Species classification based on regeneration and stratification guilds have been successfully used in the analysis of tropical forest dynamics and regeneration in a number of studies, yielding similar patterns (*e.g.* Manokaran & Kochumenn 1987, Whitmore 1989, Lieberman *et al.* 1990, Oliveira Filho *et al.* 1997, Tabarelli & Mantovani 1999).

The two stands had similar proportions of trees per dispersion guild, failing to show an increasing abundance of zoochorous species with age found in Atlantic secondary forests by some authors (*e.g.* Klein 1980, Mendonça *et al.* 1992, Tabarelli & Mantovani 1999). Two facts may explain this result. First, and quite likely, the predominance of anemochory could have occurred in earlier regeneration phases when wind-dispersed trees and shrubs (*e.g. Toulicia laevigata*, *Astronium fraxinifolium*, *Eremanthus incanus* and *Aloysia virgata*) established. Secondly, many abundant pioneer and light-demanding species are zoochorous (*e.g. Byrsonima sericea*, *Pera glabrata*, *Guatteria villosissima*, *Cecropia hololeuca* and *Vismia guianensis*) and may contribute substantially to the flora of early regeneration phases, as described by other authors (*e.g.* Gómez-Pompa *et al.* 1991, Vieira *et al.* 1996).

In general, tropical secondary forests restore species richness first and then diversity, species guild profile, species composition, and, finally, vegetation structure, particularly tree density and biomass, all within a time span between 50 and 150 years (*e.g.* Uhl *et al.* 1982, Saldarriaga *et al.* 1988, Tabarelli & Mantovani 1999, Saldarriaga & Uhl 1991). In the present case, species richness and diversity, as well as tree volume and basal area, were apparently the first characteristics of the two stands to converge. The relatively rapid restoration of these features was certainly fostered by tree regeneration from stumps and roots and by the existence of adjacent patches of old-growth forests operating as seed sources.

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