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 m² 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

Introduction

The Brazilian Atlantic forests, which once covered an area of about 1.1 million km² 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
lenscape (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 characterized 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,
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 m² 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 Körning & 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 subsampling 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

| Soil variable                  | 15-year-old stand | 40-year-old stand | t tests |
|-------------------------------|-------------------|-------------------|---------|
| pH in H₂O (means ± standard deviations) | 4.44 ±0.02       | 4.37 ± 0.19       | 0.62 n.s|
| P Mehlich (mg.dm⁻³)           | 1.4 ±0.00        | 1.5 ± 0.1         | 2.00 n.s|
| K⁺ (mg.dm⁻³)                  | 46.0 ±5.2        | 41.5 ± 10.8       | 0.62 n.s|
| Ca++ (cmolc.dm⁻³)             | 0.36 ±0.04       | 0.57 ± 0.27       | 1.37 n.s|
| Mg++ (cmolc.dm⁻³)             | 0.12 ±0.03       | 0.28 ± 0.23       | 1.21 n.s|
| Al+++ (cmolc.dm⁻³)            | 1.94 ±0.08       | 1.71 ± 0.38       | 1.00 n.s|
| Total bases (cmolc.dm⁻³)      | 0.60 ±0.07       | 0.96 ± 0.50       | 1.24 n.s|
| Saturation of bases (%)       | 5.68 ±0.88       | 11.00 ± 6.74      | 1.35 n.s|
| 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 n.s|
| Silt (%)                      | 18.3 ±2.7        | 17.8 ± 1.2        | 0.25 n.s|
| Clay (%)                      | 32.2 ±3.1        | 31.3 ± 5.5        | 0.23 n.s|

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 m² 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).
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 m² 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 | 15-year-old stand | 40-year-old stand | \( t \) statistics |
|-----------------------------|--------------|-------------------|-------------------|-------------------|
| \#of trees per plot         | N = 7        | N = 4             | N = 3             |                   |
|                             | 347 ± 78     | 401 ± 42          | 276 ± 49          | 3.07 *            |
| Basal area per plot (m²)    | 4.256 ± 0.182| 4.318 ± 0.088     | 4.174 ± 0.264     | 0.87 ns           |
| Volume per plot (m³)        | 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               |                   |

A 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’ \( H' \) (table 2).

The eigenvalues produced by DCA (axis 1 = 0.305, axis 2 = 0.157) were small, indicating ‘short’ gradients, \textit{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

Figure 2. Distribution of the number of trees per diameter (A) and height (B) classes in the seven 1,125 m² 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.
Table 3. Tree species sampled on seven 1,125 m² 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 (N₁₅ and N₄₀), 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         | N₁₅ | N₄₀ |
|---------------------------|----------------|-----|-----|
| **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   |
| *Thrysodium spriteanum* 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 brasilensis* 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 spriteanum* 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* (Steu.) 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   |
| *Polypodococcos 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 vellosa* 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 (Hoffmrg.) 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**              |             |      |      |
| Stephanodium 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 fraxinfolia Benth.       | ST-L-Zoo    | 0    | 2    |
| Apuleia leiocarpa (Vogel) Macbr. | LD-L-Zoo    | 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
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 janeirensense* 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
*Melanoloxylon brauna* Schott | ST-L-Ane | 8 | 11
*Piptadenia gonoacantha* (Mart.) Macbr. | PI-L-Ane | 0 | 2
*Platymenia 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
*Swaertzia acutifolia* Vogel | ST-L-Zoo | 6 | 0
*Swaertzia apetala* Raddi | ST-L-Zoo | 2 | 0
*Swaertzia flaemingii* Vogel | LD-L-Zoo | 0 | 1
*Swaertzia macrostachya* Benth. | LD-L-Zoo | 16 | 0
*Swaertzia multijuga* Hayne | LD-L-Zoo | 1 | 1
*Swaertzia myrtifolia* (Schott) Cowan | LD-L-Zoo | 0 | 1
*Swaertzia polyphylla* DC. | LD-L-Zoo | 7 | 1
*Sweedia 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*
| Families/Species | Guilds          | N<sub>15</sub> | N<sub>40</sub> |
|-----------------|----------------|--------------|--------------|
| MALVACEAE       |                |              |              |
| Luehea grandiflora Mart. & Zucc. | LD-L-Ane | 0 | 5 |
| MELASTOMATACEAE |                |              |              |
| Miconia calvencens 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-Zoo | 0 | 2 |
| MELIACEAE       |                |              |              |
| Guarea guidonia (L.) Sleumer | ST-M-Zoo | 1 | 1 |
| Guarea kanthiana 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 |
| NYCTAGINACEAE   |                |              |              |
| Guapira hirsuta (Choisy) Lundell | ST-M-Zoo | 3 | 1 |
| Guapira opposita (Vell.) Reitz | ST-M-Zoo | 9 | 3 |
| OLACACEAE       |                |              |              |
| Schoepfia brasiliensis A. DC. | ST-M-Zoo | 2 | 4 |
| PICRAMNIACEAE   |                |              |              |
| Picramnia parvifolia Engler | ST-M-Zoo | 1 | 0 |
| POACEAE         |                |              |              |
| Guadua angustifolia Kunth | LD-L-Ane | 1 | 0 |

*continue*
| Families/Species | Guilds       | N<sub>15</sub> | N<sub>40</sub> |
|------------------|--------------|----------------|---------------|
| 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             |
| *Bathyrsa nicolsonii* K. Schum. | ST-M-Ane     | 8              | 54            |
| *Chomelia catharinæ* (Smith & Downs) Steyerm. | ST-M-Zoo     | 0              | 2             |
| *Genipa infundibuliformis* Zappi & Semir | LD-L-Zoo     | 1              | 1             |
| *Guettarda uruguensis* Cham. & Schltld. | 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. & Schltld.) 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 tongoassuiba* 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* Aulet | LD-M-Zoo     | 19             | 0             |
| *Matayba juglandifolia* (Cambess.) Radlk. | ST-L-Zoo     | 4              | 1             |
| *Toullicia laevigata* Radlk. | LD-M-Ane     | 81             | 1             |
| SAPOTACEAE       |              |                |               |
| *Micropholis gardneriana* (A. DC.) Pierre | LD-L-Zoo     | 3              | 4             |
| SIPARUNACEAE     |              |                |               |
| *Siparuna guianensis* Aulet | 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* Aulet | PI-L-Zoo     | 1              | 0             |
| VERBENACEAE      |              |                |               |
| *Aloysia virgata* (Ruiz & Pavón) A. Juss. | PI-S-Ane     | 8              | 2             |
| VOCYHSIACEAE     |              |                |               |
| *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 *Toullicia 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 Abbrev. | Full names                      | Number of trees | \( \chi^2 \) tests | Mean volume (m³) | t tests |
|---------------------|---------------------------------|-----------------|---------------------|------------------|--------|
| Aloy vir            | Aloysia virgata                 | 8 (6.6)         | 2 (3.4)             | 1.19 ns          | 0.748  |
| Anad col            | Anadenanthera colubrinensis     | 2 (2.6)         | 2 (1.4)             | 0.51 ns          | 0.006  |
| Anax pha            | Anaxagorea phaeocarpa           | 16 (18.5)       | 12 (9.5)            | 0.89 ns          | 0.124  |
| Apul lei            | Apuleia leioarpa                | 90 (124.7)      | 99 (64.3)           | 28.09 ****       | 2.133  |
| Astr fra            | Astronium fraxinifolium         | 96 (65.3)       | 3 (33.7)            | 42.84 ****       | 0.596  |
| Bath nic            | Bathysa nicholsonii            | 8 (40.9)        | 54 (21.1)           | 77.02 ****       | 0.075  |
| Bros lac            | Brosimum lactescens             | 7 (11.9)        | 11 (6.1)            | 5.56 *           | 0.050  |
| Caly clu            | Calyptranthes clusiifolia       | 7 (6.6)         | 3 (3.4)             | 0.24 ns          | 0.151  |
| Camp dic            | Campomanesia dichotoma          | 17 (17.2)       | 9 (8.8)             | 0.04 ns          | 0.291  |
| Cecr hol            | Cecropia hololeuca              | 0 (12.5)        | 19 (6.5)            | 35.95 ****       | 0.000  |
| Chae ech            | Chaetocarpus echinocarpus       | 26 (21.1)       | 6 (10.9)            | 3.58 ns          | 0.458  |
| Copa lan            | Copaifera langsdorffii          | 18 (15.2)       | 5 (7.8)             | 1.77 ns          | 0.222  |
| Cupa ema            | Cupania emarginata              | 41 (31)         | 6 (16)              | 9.79 ****        | 0.612  |
| Dalb nig            | Dalbergia nigra                 | 37 (33)         | 13 (17)             | 1.57 ns          | 0.385  |
| Dalb vil            | Dalbergia villosa               | 20 (14.5)       | 2 (7.5)             | 6.50 *           | 0.355  |
| Dugu lan            | Duguetia lanceolata             | 9 (7.3)         | 2 (3.7)             | 1.56 ns          | 0.442  |
| Euge flo            | Eugenia floridula               | 13 (19.8)       | 17 (10.2)           | 6.56 *           | 0.070  |
| Euge nel            | Eugenia neoglomerata            | 0 (2.6)         | 4 (1.4)             | 7.09 **          | 0.307  |
| Gomia ana           | Gomidesia anacardiifolia        | 10 (12.5)       | 9 (6.5)             | 1.37 ns          | 0.138  |
| Guat pog            | Guatteria pogonopus             | 1 (3.3)         | 4 (1.7)             | 4.27 *           | 0.010  |
| Guat vil            | Guatteria villosissima          | 34 (25.7)       | 5 (13.3)            | 8.15 ****        | 0.242  |
| Ilex cer            | Ilex cerasifolia                | 6 (12.5)        | 13 (6.5)            | 9.58 ****        | 0.023  |
| Ingra str           | Inga striata                    | 2 (5.3)         | 6 (2.7)             | 5.54 *           | 0.024  |
| Lica hyp            | Licania hypoleuca               | 71 (66.6)       | 30 (34.4)           | 0.92 ns          | 1.985  |
| Mabe fis            | Mabea fistulifera               | 69 (71.2)       | 39 (36.8)           | 0.19 ns          | 0.942  |
| Mata ela            | Matayba elaeagnoides            | 16 (12.5)       | 3 (6.5)             | 3.13 ns          | 0.141  |
| Mata gui            | Matayba guianensis             | 19 (12.5)       | 0 (6.5)             | 10.34 ****       | 0.314  |
| Mela bra            | Melanoxylon brauna              | 8 (12.5)        | 11 (6.5)            | 4.54 *           | 0.104  |
| Pera gla            | Pera glabrata                   | 99 (77.2)       | 18 (39.8)           | 18.40 ****       | 4.387  |
| Pilo gig            | Pilocarpus giganteus            | 23 (19.1)       | 6 (9.9)             | 2.53 ns          | 0.969  |
| Pime pse            | Pimenta pseudocaryophyllus      | 88 (58.7)       | 130 (30.3)          | 43.41 ****       | 2.145  |
| Pipt mac            | Piptocarpus macropoda           | 9 (5.9)         | 0 (3.1)             | 5.25 *           | 0.358  |
| Plat ele            | Platypondium elegans            | 17 (14.5)       | 5 (7.5)             | 1.46 ns          | 0.384  |
| Plat ret            | Plathymenia reticulata          | 8 (7.3)         | 3 (3.7)             | 0.42 ns          | 0.185  |
| Pogo sch            | Pogonophora schomburgkiana      | 52 (44.9)       | 16 (23.1)           | 3.51 ns          | 0.584  |
| Prot hep            | Protrium heptaphyllum           | 15 (16.5)       | 10 (8.5)            | 0.36 ns          | 0.275  |
| Sche mor            | Schefflera morototoni           | 9 (7.3)         | 2 (3.7)             | 1.56 ns          | 0.273  |
| Scle rug            | Sclerozollum rugosum            | 5 (4.6)         | 2 (2.4)             | 0.33 ns          | 1.155  |
| Sipa gui            | Siparuna guianensis             | 23 (56.1)       | 62 (28.9)           | 56.78 ****       | 0.054  |
| Syag rom            | Syagrus romanziifania           | 13 (9.9)        | 2 (5.1)             | 3.23 ns          | 0.325  |
| Thyr spr            | Thyrassodrum spruceanum         | 13 (15.2)       | 10 (7.8)            | 0.83 ns          | 0.408  |
| Toul lae            | Toullicia laevigata             | 81 (54.1)       | 1 (27.9)            | 39.81 ****       | 0.446  |
| Tric pal            | Trichilia pallida               | 6 (19.8)        | 24 (10.2)           | 27.62 ****       | 0.017  |
| Xylo cuc            | Xylomisia ciliatifolia          | 34 (23.7)       | 2 (12.3)            | 13.44 ****       | 0.158  |
| Xylo ser            | Xylopia sericea                 | 39 (35)         | 14 (18)             | 1.50 ns          | 0.776  |
| Zygi lat            | Zygia latifolia                 | 15 (11.2)       | 2 (5.8)             | 4.14 *           | 0.228  |
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

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

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.
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, Toulcicia 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 n.icholsonii 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 & Kochmenn 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. Toulencia laevigata, Astronium fraxinifolium, Eremanthus incanuu 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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