

Horizontal and vertical tree community structure in a lowland Atlantic Rain Forest, Southeastern Brazil

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ABSTRACT – (Horizontal and vertical tree community structure in a lowland Atlantic Rain Forest, Southeastern Brazil). The horizontal and vertical tree community structure in a lowland Atlantic Rain Forest was investigated through a phytosociological survey in two 0.99 ha plots in the Intervales State Park, São Paulo State. All trees ≥ 5 cm diameter at breast height were recorded. 3,078 individuals belonging to 172 species were identified and recorded. The Shannon diversity index was $H' = 3.85 \text{ nat.ind.}^{-1}$. The Myrtaceae family showed the greatest floristic richness (38 species) and the highest density (745 individuals) in the stand. *Euterpe edulis* Mart. had the highest importance value (33.98%) accounting for 21.8% of all individuals recorded. The quantitative similarity index was higher than the qualitative index, showing little structural variation between plots. However, the large number of uncommon species resulted in pronounced floristic differences. A detrended correspondence analysis (DCA) generated three arbitrary vertical strata. Stratum A (≥ 26 m), where *Sloanea guianensis* (Aubl.) Benth. and *Virola bicusyba* (Schott. ex A.DC.) Warb. were predominant showed the lowest density. Stratum B ($8 \text{ m} < h < 26 \text{ m}$) had the greatest richness and diversity, and stratum C (≤ 8 m) showed the highest density. *Euterpe edulis*, *Guapira opposita* (Vell.) Reitz, *Garcinia gardneriana* (Planch. & Triana) Zappi, and *Eugenia mosenii* (Kausel) Sobral were abundant in strata B and C. The occurrence of strata in tropical forests is discussed and we recommend the use of DCA for others studies of the vertical distribution of tropical forest tree communities.

Key words - diversity, multivariate analysis, phytosociology, tree stratification, tropical forest

RESUMO – (Estruturas horizontal e vertical do componente arbóreo em floresta atlântica baixo-montana no sudeste do Brasil). A estrutura horizontal e vertical do componente arbóreo foi investigada em um trecho de Floresta Atlântica baixo-montana através de um levantamento fitossociológico em dois blocos amostrais de 0,99 ha cada no Parque Estadual Intervales. Todos os indivíduos com DAP ≥ 5 cm foram registrados. Foram amostrados 3.078 indivíduos distribuídos em 172 espécies. O índice de diversidade de Shannon foi de $H' = 3,85 \text{ nat.ind.}^{-1}$. A família Myrtaceae se destacou tanto em número de espécies (38) quanto em número de indivíduos (745) no levantamento. *Euterpe edulis* Mart. teve o maior valor de importância (33,98%), abrangendo 21,8% do total de indivíduos registrados. O índice de similaridade quantitativo foi maior do que o qualitativo, mostrando pouca variação estrutural entre os blocos amostrais, mas a grande quantidade de espécies pouco abundantes, resultou em pronunciadas diferenças florísticas entre eles. Uma análise de correspondência retificada (DCA) gerou três estratos verticais arbitrários. O estrato A (≥ 26 m) teve a menor densidade e foi bem representado pelas espécies *Sloanea guianensis* (Aubl.) Benth. e *Virola bicusyba* (Schott. ex A.DC.) Warb. O estrato B ($8 \text{ m} < h < 26 \text{ m}$) mostrou a maior riqueza e diversidade florística, e o estrato C (≤ 8 m) a maior densidade. *Euterpe edulis*, *Guapira opposita* (Vell.) Reitz, *Garcinia gardneriana* (Planch. & Triana) Zappi e *Eugenia mosenii* (Kausel) Sobral foram bem representadas nos estratos B e C da floresta. A existência de estratos verticais em florestas tropicais é discutida, recomendando-se o uso da DCA para estudos da estratificação vertical em outras florestas tropicais.

Palavras-chave - análise multivariada, diversidade, estratificação, fitossociologia, floresta tropical

Introduction

The Atlantic Rain Forest *sensu stricto* (Oliveira Filho & Fontes 2000) originally covered an area of 1.2 million km² along the Eastern coastline of Brazil, but today it is reduced to approximately 7.5% of its original extent (Myers *et al.* 2000). This biome presents one of

the greatest species richness as well as high levels of plant and animal endemisms (Mori *et al.* 1981, Leitão Filho 1994). These characteristics put the Atlantic Rain Forest among the eight most important 'hotspots' for biodiversity conservation (Myers *et al.* 2000).

The largest and most preserved remnants of Atlantic Rain Forest are located nearby the most developed coastal urban centers, particularly in the States of São Paulo and Paraná, Southeastern Brazil, due to the irregular landscapes of Serra do Mar and Serra de Paranapiacaba (Leitão Filho 1994). For instance, the Intervales State Park, located in the Vale do Ribeira

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region in the south of the São Paulo State, the Park was granted the status of Preservation Unit due to its extreme ecological importance. The Intervales, along with other Preservation Units, makes up for the largest continuous area of Atlantic Rain Forest hosting a biodiversity which has not yet been thoroughly studied (Dietz 2001).

Although several studies have been carried out with regard to the structure of the vegetation of the Atlantic Rain Forest, specially in the São Paulo State (Silva & Leitão Filho 1982, Mantovani *et al.* 1990, Leitão Filho 1993, Melo & Mantovani 1994, Melo *et al.* 1998, Oliveira *et al.* 2001, Sztutman & Rodrigues 2002, among others), the data available remain insufficient for the understanding of abundance, distribution, richness, and diversity of species. Besides the lack of data, the floristic and structure of such vegetations are rather complex, varying according to edaphic-climatic and geomorphological characteristics of each region (Leitão Filho 1987, Mantovani 1998, Ivanauskas *et al.* 2000, Oliveira Filho & Fontes 2000). Another aspect of the Atlantic Rain Forest which has not been thoroughly investigated so far is the characterization of the vertical structure of tree community. According to Richards (1996), tropical forests have vertical stratification. These strata are composed by several plant species with different capabilities of occupation resulting from an adaptative response to the different conditions of light. This interaction may also justify the great diversity present in more structurally complex ecosystems. Considering that existing methods to quantify the vertical structure of forests are defined arbitrarily (Latham *et al.* 1998) making them a controversial issue, and that the strata in tropical forests are much less defined than those in temperate forests (Terborgh 1992), studies of stratification or of the vertical structure of the canopy can offer insights to a better understanding of the natural history of the tropics. Therefore, these studies may incentive further discussions about the evolution of the types of dispersion (Roth 1987) and the distribution of the epiphytic component along a vertical gradient (Kersten & Silva 2001, 2002), among others.

This study aimed (a) to describe the horizontal structure of the tree community of a lowland Atlantic Rain Forest and to compare it with other studies carried out in this vegetation; (b) to investigate the vertical structure of such community, assessing how the stratification or the vertical structure of canopy can be defined along a section of the forest and in which ways the composition and importance of species in each stratum can vary, based on the most extensive survey (~2 ha) carried out up today.

Material and methods

Study site – This study was conducted in the Intervales State Park (Parque Estadual Intervales - PEI), Base Saibadela (24°14' S and 48°04' W), located in the Serra de Paranapiacaba, municipality of Sete Barras, southern São Paulo State, southeast Brazil. The PEI stretches along an area of approximately 48,000 ha and it is surrounded by three other Preservation Units (Parque Estadual Carlos Botelho, Estação Ecológica do Xitué and Parque Estadual Turístico do Alto Ribeira), accounting for 200,000 ha of preserved forest. It is one of the most important areas for the preservation of the Atlantic Forest Biosphere Reserve (Dietz 2001).

The PEI has a very irregular landscape and the local altitude ranges from 60 to 1,100 m. At the Base Saibadela, the altitude ranges from around 70 to 250 m. Base Saibadela is situated on the coastal mountain chain of Serra de Paranapiacaba that presents ample erosive landscapes of mountainous aspects, formed by steep scarps and deep valleys, which represent the rim of the Atlantic Crystalline Plateau, composed mainly of granitic and gneissic rocks of high structural complexity (Almeida 1974). The climatic data registered at the study area show a wet tropical climate, with frequent rains without a period of hydric deficit and annual precipitation around 4,000 mm, with a less rainy season from May to August and a wet season from September to April (Morellato *et al.* 2000). The average temperature in the coldest month (July) is 18.1 °C and in the warmest month (January) is 25.7 °C. According to Setzer (1966) the region presents a Cfb type climate in the Köppen system - temperate without a dry season.

The study area is covered mainly by primary Atlantic Rain Forest with little anthropogenic intervention and is situated within domain of lowland Atlantic Rain Forest (*sensu* Oliveira Filho & Fontes 2000). The most representative families found in the tree community are Myrtaceae, Lauraceae and Rubiaceae, and the palmito-juçara, *Euterpe edulis* Mart. (Arecaceae), is among the most abundant species in the area (R.J. Almeida-Scabbia, unpublished data). The epiphytes are very abundant and represented especially by several species of ferns, Orchidaceae, Bromeliaceae, and Araceae. The number of liana species is also high, with 43 species registered until the present moment (V.B. Zipparro *et al.*, unpublished data). On the foothills and in the less drained plains, due to the proximity to the water courses, clumps of *Aphelandra liboniana* Linden ex Hook. (Acanthaceae) and *Calathea* spp. (Marantaceae) cover extensive areas of the forest understorey.

Vegetation structure – The sampling was conducted from October 2000 to November 2001. Two sample plots were established for the analysis of the tree component structure. One was established in low and another in midland topographic conditions. Each was composed of 44 continuous 15 × 15 m quadrats, totaling a 0.99 ha (60 × 165 m) area per topographic condition. The plots were located 1,500 m

away from each other in the lowland Atlantic Rain Forest.

Plot 1 is situated perpendicular and ca. 25 m away from the Saibadela river margin, and was located at a mean altitude of 120 m (amplitude of 110-130 m), with predominance of dystrophic cambisoils. The first four quadrats are situated over the old river course, since there is a great number of pebbles in a dystrophic neosoils. As one moves away from the river, the capacity of soil drainage generally increases, except in one point in the center of Plot 1 where the water table rises permanently above the soil surface over the dystrophic gleisoils. Plot 2 is situated in an area of low altitude, ranging from 86 to 97 m, far from the river, in a well drained dystrophic cambisoil. In Plot 1, there has been human interference since 1998, such as clandestine exploration of the palm tree palmito-juçara, which stems still stood in the soil after being partly cut.

All tree individuals with DBH \geq 5 cm, including the palms and the ferns, were sampled, labeled and measured at breast height. The height of all individuals was estimated with the use of a 2 m rod. Considering the great number of palms that had been cut down in Plot 1 (n=63), they were included in the same group with living *Euterpe edulis* for the assessment of horizontal structure. The vouchers of all sampled individuals are deposited at the Herbario Rioclarense (HRCB). All species in this study were grouped according to the Angiosperm Phylogeny Group (APG 2003), except the Cyatheaceae family. Data analysis – The phytosociological parameters calculated for each sample plot were: species density, frequency and relative dominance, and value of importance (VI) (Mueller-Dombois & Ellenberg 1974); the Shannon diversity index (H') and the Pielou equability index (J') (Brower & Zar 1984). Calculations were made with the use of the software FITOPAC (Shepherd 1994).

Detrended correspondence analysis (DCA), which allows an indirect analysis of gradients (Hill & Gauch 1980), was used to verify the abundance of species in each quadrat between the plots. An abundance matrix of species was generated and expressed by the number of individuals from each taxon by plot. Taxa with less than 13 individuals were excluded, leaving a total 48 species in the analysis. The less abundant species contribute very little to the analysis and only increase the number of calculations to be made (Causton 1988). The Jaccard (qualitative) and the Morisita (quantitative) similarity indexes were used to analyze the floristic and structural similarities between the two sample plots (Krebs 1999). To characterize the vertical structure of the forest, DCA analysis was also used based on a matrix of the number of individuals in each taxon by height classes. The height records were grouped in class intervals of one meter. The analysis points simultaneously to the number of individuals per height class, relating the highest occurrence of species in each class. The resulting diagram displays a distribution of height classes split into arbitrary groups and generates the vertical distribution of the stand. The palms that had been cut were excluded from this analysis. The

phytosociological parameters were separately calculated for the components of each stratum identified in the analysis of vertical distribution. The distribution of abundance of the main species was assessed in each stratum in terms of the total number of individuals in the stand with the use of chi-square test (χ^2) with Yates correction (Zar 1996), in order to verify whether any tree species was significantly associated to a given stratum. In this study the terms stratification and stratum are used in accordance with Richards' proposal (1996).

Results

Horizontal structure – We recorded 3,078 individuals of 172 species distributed in 102 genera and 51 botanic families. The estimated total density was 1,554.6 ind.ha⁻¹ and the estimated basal area was 34.64 m².ha⁻¹. The Shannon diversity index was 3.85 nat.ind.⁻¹ and the equability index was 0.75.

The *Euterpe edulis* palm was the most abundant species adding 21.8% of the total recorded individuals. It had the highest density, frequency and value of importance (VI) (table 1). *Sloanea guianensis*, *Bathysa australis*, *Virola bicuhyba* and *Alchornea triplinervia* high VI values were due to their elevated basal areas. *Guapira opposita*, *Eugenia mosenii*, *Garcinia gardneriana*, *Marlierea obscura* and *Psychotria suterella* high VI values were due to their high abundance and frequency. These 10 species accounted for 39.6% of the total VI (table 1). The most abundant families represented 82.9% of the total number of individuals sampled (figure 1) wherein Myrtaceae alone contributed with 24.2% (745 individuals). Myrtaceae was the family with the highest number of species (38), followed by Fabaceae (19), Rubiaceae (13), Lauraceae (10), Sapotaceae (7) and Euphorbiaceae (6). Comparison of the floristic structure and similarities between the sample plots – Plot 1 presented lower density of trees and higher basal area (1,495 ind.ha⁻¹ and 35.6 m².ha⁻¹) than Plot 2 (1,614 ind.ha⁻¹ and 33.7 m².ha⁻¹). Nine out of the twelve species with highest VI in the stand were the most representative in both plots, only showing variation in the VI ranking (table 2). *Bathysa australis* and *Marlierea tomentosa* presented higher density in Plot 1, whereas *Euterpe edulis*, *Garcinia gardneriana* and *Psychotria suterella* had higher density in Plot 2. Despite present a similar density in both plots, individuals of *Virola bicuhyba* reached larger sizes in Plot 1, resulting in a greater basal area.

When analyzing the DCA diagram in regard to species abundance (figure 2), short gradients were found for the first two axes (8.29 and 9.09), with eigenvalues

Table 1. Phytosociological descriptors of tree species with DBH \geq 5 cm sampled in 1.98 ha of lowland Atlantic Rain Forest, Intervalles State Park, Southeastern Brazil. NI = number of individuals; BA = basal area (m²); Q = number of quadrats where it occurs; RD = relative density (%); RDo = relative dominance (%); RF = relative frequency (%); VI = value of importance (%). * 63 out of 671 individuals of *E. edulis* had been cut by clandestine collectors. †: species exclusively found in Plot 1; ‡: species exclusively found in Plot 20.

Family	Species	NI	BA	Q	RD	RDo	RF	VI
Arecaceae	<i>Euterpe edulis</i> Mart.	*671	4.936	88	21.8	7.2	5.0	33.98
Elaeocarpaceae	<i>Sloanea guianensis</i> (Aubl.) Benth.	93	7.173	54	3.0	10.5	3.1	16.54
Nyctaginaceae	<i>Guapira opposita</i> (Vell.) Reitz	172	2.044	71	5.6	3.0	4.0	12.59
Rubiaceae	<i>Bathysa australis</i> (A.St.-Hil.) Benth. & Hook. f.	100	2.777	51	3.3	4.1	2.9	10.19
Myrtaceae	<i>Eugenia mosenii</i> (Kausel) Sobral	114	0.938	64	3.7	1.4	3.6	8.70
Clusiaceae	<i>Garcinia gardneriana</i> (Planch. & Triana) Zappi	117	0.998	53	3.8	1.5	3.0	8.26
Myrtaceae	<i>Marlierea obscura</i> O.Berg	94	1.115	60	3.1	1.6	3.4	8.08
Myristicaceae	<i>Virola bicuhyba</i> (Schott. ex A.DC.) Warb.	24	3.604	20	0.8	5.3	1.1	7.17
Euphorbiaceae	<i>Alchornea triplinervia</i> (Spreng.) Müll.Arg.	25	3.329	23	0.8	4.9	1.3	6.97
Rubiaceae	<i>Psychotria suterella</i> Müll.Arg.	95	0.411	48	3.1	0.6	2.7	6.40
Myrtaceae	<i>Marlierea tomentosa</i> Cambess.	78	0.516	44	2.5	0.8	2.5	5.78
Monimiaceae	<i>Mollinedia schottiana</i> (Spreng.) Perkins	66	0.322	46	2.1	0.5	2.6	5.22
Olacaceae	<i>Tetrastylidium grandifolium</i> (Baill.) Sleumer	46	1.081	32	1.5	1.6	1.8	4.88
Myrtaceae	<i>Calycorectes australis</i> D.Legrand	41	1.105	31	1.3	1.6	1.8	4.70
Phyllanthaceae	<i>Hyeronima alchorneoides</i> Allemão	17	2.136	15	0.6	3.1	0.9	4.52
Myrtaceae	<i>Eugenia riedeliana</i> O.Berg	34	1.134	27	1.1	1.7	1.5	4.29
Lauraceae	<i>Ocotea elegans</i> Mez	18	1.743	16	0.6	2.5	1.0	4.09
Cyatheaceae	<i>Cyathea phalerata</i> Mart.	54	0.286	31	1.8	0.4	1.8	3.93
Myrtaceae	<i>Eugenia cuprea</i> (O.Berg) Nied.	51	0.221	34	1.7	0.3	1.9	3.91
Myrtaceae	<i>Eugenia neoglomerata</i> Sobral	45	0.284	35	1.5	0.4	2.0	3.86
Myrtaceae	<i>Eugenia oblongata</i> O.Berg	43	0.438	31	1.4	0.6	1.8	3.79
Rubiaceae	<i>Ixora burchelliana</i> Müll.Arg.	47	0.160	34	1.5	0.2	1.9	3.69
Fabaceae	<i>Swartzia flaemingii</i> Raddi	23	1.187	21	0.8	1.7	1.2	3.67
Cyatheaceae	<i>Alsophila sternbergii</i> (Pohl ex Sternb.) D.S.Conant †	64	0.604	10	2.1	0.9	0.6	3.53
Fabaceae	<i>Pterocarpus rohrii</i> Vahl	21	1.131	18	0.7	1.7	1.0	3.35
Lauraceae	<i>Ocotea teleiandra</i> (Meisn.) Mez	39	0.210	30	1.3	0.3	1.7	3.27
Myrtaceae	<i>Calycorectes acutatus</i> (Miq.) Toledo	29	0.750	20	0.9	1.1	1.1	3.17
Vochysiaceae	<i>Callisthene</i> cf. <i>dryadum</i> A.P.Duarte	6	1.638	6	0.2	2.4	0.3	2.92
Urticaceae	<i>Pourouma guianensis</i> Aubl.	22	0.714	19	0.7	1.0	1.1	2.83
Lecythidaceae	<i>Cariniana estrellensis</i> (Raddi) Kuntze	11	1.256	11	0.4	1.8	0.6	2.81
Myrtaceae	<i>Eugenia multicostata</i> D.Legrand	14	0.955	14	0.5	1.4	0.8	2.64
Olacaceae	<i>Heisteria silvianii</i> Schwacke	22	0.433	22	0.7	0.6	1.3	2.59
Lauraceae	<i>Cryptocaria moschata</i> Nees & Mart. ex Nees	13	0.892	13	0.4	1.3	0.7	2.46
Monimiaceae	<i>Mollinedia uleana</i> Perkins	21	0.448	18	0.7	0.7	1.0	2.35
Fabaceae	<i>Pseudopiptadenia warmingii</i> (Harms) Bukart	9	1.057	9	0.3	1.5	0.5	2.34
Bignoniaceae	<i>Tabebuia serratifolia</i> (Vahl) G.Nicholson	21	0.414	18	0.7	0.6	1.0	2.31
Rubiaceae	<i>Psychotria mapoureoides</i> DC.	18	0.614	14	0.6	0.9	0.8	2.27
Fabaceae	<i>Copaifera trapezifolia</i> Hayne	5	1.154	5	0.2	1.7	0.3	2.13
Apocynaceae	<i>Aspidosperma compactinervium</i> Kuhlm.	5	1.147	5	0.2	1.7	0.3	2.12
Myrtaceae	<i>Eugenia bocainensis</i> Mattos	30	0.104	17	1.0	0.2	1.0	2.09
Moraceae	<i>Ficus gomelleira</i> Kunth & Bouché †	1	1.325	1	0.0	1.9	0.1	2.02
Euphorbiaceae	<i>Aparisthium cordatum</i> (A.Juss.) Baill.	27	0.200	15	0.9	0.3	0.9	2.02
Lauraceae	<i>Endlicheria paniculata</i> (Spreng.) J.F.Macbr.	20	0.112	20	0.7	0.2	1.1	1.95
Myrtaceae	<i>Gomidesia spectabilis</i> (DC.) O.Berg	20	0.128	18	0.7	0.2	1.0	1.86
Sapindaceae	<i>Cupania oblongifolia</i> Mart.	13	0.500	12	0.4	0.7	0.7	1.83
Sapindaceae	<i>Matayba guianensis</i> Aubl.	8	0.739	8	0.3	1.1	0.5	1.79

continue

continuation

Family	Species	NI	BA	Q	RD	RDo	RF	VI
Polygonaceae	<i>Ruprechtia laxiflora</i> Meisn.	18	0.241	15	0.6	0.4	0.9	1.79
Meliaceae	<i>Cabralea canjerana</i> (Vell.) Mart.	6	0.845	6	0.2	1.2	0.3	1.77
Myrtaceae	<i>Calyptanthus lanceolata</i> O.Berg	20	0.058	17	0.7	0.1	1.0	1.70
Quiinaceae	<i>Quiina glaziovii</i> Engl.	9	0.670	7	0.3	1.0	0.4	1.67
Symplocaceae	<i>Symplocos</i> cf. <i>celastrinea</i> Mart. ex Miq.	14	0.373	11	0.5	0.5	0.6	1.62
Myrtaceae	<i>Eugenia cambucarana</i> Kiaersk. †	13	0.498	8	0.4	0.7	0.5	1.60
Fabaceae	<i>Schizolobium parahyba</i> (Vell.) S.F. Blake	3	0.890	3	0.1	1.3	0.2	1.56
Euphorbiaceae	<i>Alchornea glandulosa</i> Poepp.	6	0.684	6	0.2	1.0	0.3	1.53
Fabaceae	<i>Inga edulis</i> Mart.	15	0.184	13	0.5	0.3	0.7	1.49
Myrtaceae	<i>Myrciaria floribunda</i> (West ex Willd.) O.Berg	11	0.309	11	0.4	0.5	0.6	1.43
Urticaceae	<i>Coussapoa microcarpa</i> (Schott) Rizzini	8	0.448	8	0.3	0.7	0.5	1.37
Rutaceae	<i>Pilocarpus pauciflorus</i> A.St.-Hil.	17	0.096	12	0.6	0.1	0.7	1.37
Sapotaceae	<i>Pouteria venosa</i> (Mart.) Baehni	10	0.330	9	0.3	0.5	0.5	1.32
Apocynaceae	<i>Malouetia cestroides</i> Müll.Arg.	10	0.308	9	0.3	0.5	0.5	1.28
Proteaceae	<i>Roupala brasiliensis</i> Klotzsch	10	0.254	9	0.3	0.4	0.5	1.20
Lauraceae	<i>Ocotea dispersa</i> (Nees) Mez	12	0.119	11	0.4	0.2	0.6	1.19
Rubiaceae	<i>Rudgea jasminoides</i> subsp. <i>jasminoides</i> (Cham.) Müll.Arg.	14	0.064	11	0.5	0.1	0.6	1.17
Celastraceae	<i>Maytenus robusta</i> Reissek ‡	10	0.327	6	0.3	0.5	0.3	1.14
Sapotaceae	<i>Diploon cuspidatum</i> (Hoehne) Cronquist	13	0.087	10	0.4	0.1	0.6	1.12
Myrtaceae	<i>Plinia complanata</i> M.L.Kawas. & B.Holst	13	0.048	11	0.4	0.1	0.6	1.12
Rubiaceae	<i>Alseis floribunda</i> Schott	7	0.336	6	0.2	0.5	0.3	1.06
Myrtaceae	<i>Eugenia subavenia</i> O.Berg ‡	11	0.085	10	0.4	0.1	0.6	1.05
Fabaceae	<i>Myrocarpus frondosus</i> Allemão	6	0.317	6	0.2	0.5	0.3	1.00
Icacinaceae	<i>Citronella megaphylla</i> (Miers) Howard	9	0.128	9	0.3	0.2	0.5	0.99
Arecaceae	<i>Astrocarium aculeatissimum</i> (Schott) Burret	10	0.109	9	0.3	0.2	0.5	0.99
Myrtaceae	<i>Eugenia cerasiflora</i> Miq. ‡	5	0.349	5	0.2	0.5	0.3	0.95
Myrtaceae	<i>Eugenia pruinosa</i> D.Legrand	6	0.282	6	0.2	0.4	0.3	0.95
Sapotaceae	<i>Pouteria caimito</i> (Ruiz & Pav.) Radlk.	8	0.165	7	0.3	0.2	0.4	0.90
Rubiaceae	<i>Alibertia myrcifolia</i> K.Schum.	9	0.043	9	0.3	0.1	0.5	0.86
Fabaceae	<i>Dahlstedtia pentaphylla</i> (Taub.) Burkart	9	0.042	9	0.3	0.1	0.5	0.86
Annonaceae	<i>Guatteria australis</i> A.St.-Hill.	9	0.031	9	0.3	0.0	0.5	0.85
Chrysobalanaceae	<i>Hirtella hebeclada</i> Moric. ex DC.	7	0.123	7	0.2	0.2	0.4	0.80
Chrysobalanaceae	<i>Parinari excelsa</i> Sabine	4	0.295	4	0.1	0.4	0.2	0.79
Myrtaceae	<i>Myrcia macrocarpa</i> Barb.Rodr.	7	0.084	7	0.2	0.1	0.4	0.75
Myrtaceae	<i>Eugenia neoverrucosa</i> Sobral	8	0.063	7	0.3	0.1	0.4	0.75
Myrtaceae	<i>Eugenia beaurepairiana</i> (Kiaersk.) D.Legrand	6	0.131	6	0.2	0.2	0.3	0.73
Myrtaceae	<i>Eugenia</i> sp. 1	7	0.073	7	0.2	0.1	0.4	0.73
Lamiaceae	<i>Aegiphyla sellowiana</i> Cham.	6	0.105	6	0.2	0.2	0.3	0.69
Bignoniaceae	<i>Jacaranda</i> cf. <i>montana</i> Morawetz	4	0.202	4	0.1	0.3	0.2	0.65
Celastraceae	<i>Maytenus</i> cf. <i>alaternoides</i> Reissek	6	0.074	6	0.2	0.1	0.3	0.64
Meliaceae	<i>Guarea macrophylla</i> Vahl	6	0.071	6	0.2	0.1	0.3	0.64
Sapotaceae	<i>Ecclinusa ramiflora</i> Mart. †	7	0.079	5	0.2	0.1	0.3	0.63
Myrtaceae	<i>Myrcia tenuivenosa</i> Kiaersk.	4	0.182	4	0.1	0.3	0.2	0.62
Myrtaceae	<i>Gomidesia anacardiifolia</i> (Gardner) O.Berg	6	0.044	6	0.2	0.1	0.3	0.60
Fabaceae	<i>Machaerium</i> sp. †	1	0.334	1	0.0	0.5	0.1	0.58
Fabaceae	<i>Sclerolobium denudatum</i> Vogel ‡	1	0.334	1	0.0	0.5	0.1	0.58
Euphorbiaceae	<i>Actinostemon concolor</i> (Spreng.) Müll.Arg.	6	0.073	5	0.2	0.1	0.3	0.58
Euphorbiaceae	<i>Tetrorchidium rubrivenium</i> Poepp.	4	0.143	4	0.1	0.2	0.2	0.57
Myrtaceae	<i>Eugenia melanogyna</i> (D.Legrand) Sobral	6	0.055	5	0.2	0.1	0.3	0.56
Fabaceae	<i>Ormosia</i> cf. <i>arborea</i> (Vell.) Harms	5	0.060	5	0.2	0.1	0.3	0.53
Sapotaceae	<i>Chrysophyllum inornatum</i> Mart. †	3	0.175	3	0.1	0.3	0.2	0.52

continue

continuation

Family	Species	NI	BA	Q	RD	RDo	RF	VI
Myrtaceae	<i>Myrceugenia myrcioides</i> (Cambess.) O.Berg	6	0.023	5	0.2	0.0	0.3	0.51
Myrtaceae	<i>Myrceugenia</i> sp.	4	0.098	4	0.1	0.1	0.2	0.50
Rubiaceae	<i>Rudgea recurva</i> Müll.Arg.	5	0.023	5	0.2	0.0	0.3	0.48
Boraginaceae	<i>Cordia silvestris</i> Fresen. †	3	0.141	2	0.1	0.2	0.2	0.47
Fabaceae	<i>Inga sessilis</i> (Vell.) Mart.	4	0.069	4	0.1	0.1	0.2	0.46
Rubiaceae	<i>Posoqueria latifolia</i> (Rudge) Roem. & Schult.	4	0.053	4	0.1	0.1	0.2	0.43
Myrtaceae	<i>Eugenia</i> cf. <i>platysema</i> O.Berg	4	0.041	4	0.1	0.1	0.2	0.42
Fabaceae	<i>Platymiscium floribundum</i> Vogel ‡	3	0.097	3	0.1	0.1	0.2	0.41
Moraceae	<i>Sorocea bonplandii</i> (Baill.) W.C.Burger. <i>et al.</i> †	3	0.095	3	0.1	0.1	0.2	0.41
Urticaceae	<i>Cecropia pachystachya</i> Trécul †	4	0.075	3	0.1	0.1	0.2	0.41
Cyatheaceae	<i>Alsophila setosa</i> Kaulf. ‡	6	0.034	3	0.2	0.1	0.2	0.41
Euphorbiaceae	<i>Pera glabrata</i> (Schott) Poepp. ex Baill. ‡	3	0.089	3	0.1	0.1	0.2	0.40
Cannellaceae	<i>Cinnamodendron dinisii</i> Schwacke	2	0.108	2	0.1	0.2	0.1	0.34
Rubiaceae	<i>Amaioua guianensis</i> Aubl.	3	0.051	3	0.1	0.1	0.2	0.34
Myrtaceae	<i>Neomitranthes glomerata</i> (D.Legrand) D.Legrand †	3	0.049	3	0.1	0.1	0.2	0.34
Myrsinaceae	<i>Rapanea umbellata</i> Mart.	3	0.034	3	0.1	0.1	0.2	0.32
Myrtaceae	<i>Eugenia</i> sp. 3 ‡	2	0.091	2	0.1	0.1	0.1	0.31
Moraceae	<i>Brosimum</i> cf. <i>glaziovii</i> Taub. †	2	0.090	2	0.1	0.1	0.1	0.31
Sapotaceae	<i>Pouteria grandiflora</i> (Wall.) Baehni †	3	0.070	2	0.1	0.1	0.1	0.31
Bombacaceae	<i>Spirotheca passifloroides</i> Cuatrec.	3	0.023	3	0.1	0.0	0.2	0.30
Salicaceae	<i>Casearia decandra</i> Jacq.	3	0.019	3	0.1	0.0	0.2	0.30
Magnoliaceae	<i>Talauma ovata</i> A.St.-Hil.	2	0.077	2	0.1	0.1	0.1	0.29
Fabaceae	<i>Dalbergia frutescens</i> (Vell.) Britton ‡	1	0.128	1	0.0	0.2	0.1	0.28
Picramniaceae	<i>Picramnia gardneri</i> subsp. <i>gardneri</i> Planch. ‡	3	0.007	3	0.1	0.0	0.2	0.28
Sapindaceae	<i>Matayba juglandifolia</i> (Cambess.) Radlk. ‡	2	0.060	2	0.1	0.1	0.1	0.27
Rubiaceae	<i>Coussarea contracta</i> (Walp.) Müll.Arg. ‡	4	0.017	2	0.1	0.0	0.1	0.27
Myrtaceae	<i>Eugenia</i> sp. 2 ‡	2	0.056	2	0.1	0.1	0.1	0.26
Rubiaceae	<i>Simira</i> cf. <i>sampaioana</i> (Standley) Steyererm. †	2	0.048	2	0.1	0.1	0.1	0.25
Elaeocarpaceae	<i>Sloanea monosperma</i> Vell.	2	0.033	2	0.1	0.1	0.1	0.23
Araliaceae	<i>Oreopanax capitatus</i> (Jacq.) Decne. & Planch. ‡	1	0.091	1	0.0	0.1	0.1	0.22
Lauraceae	<i>Ocotea aciphylla</i> (Nees) Mez ‡	1	0.089	1	0.0	0.1	0.1	0.22
Myrtaceae	<i>Gomidesia tijucensis</i> (Kiaersk.) D.Legrand ‡	2	0.031	2	0.1	0.0	0.1	0.22
Sabiaceae	<i>Meliosma sinuata</i> Urb. †	2	0.021	2	0.1	0.0	0.1	0.21
Boraginaceae	<i>Cordia ecalyculata</i> Vell. ‡	2	0.012	2	0.1	0.0	0.1	0.20
Myrtaceae	<i>Marlierea eugeniopsoides</i> (D.Legrand & Kaus.) D.Legran. †	2	0.012	2	0.1	0.0	0.1	0.20
Celastraceae	<i>Maytenus communis</i> Reissek ‡	1	0.072	1	0.0	0.1	0.1	0.19
Moraceae	<i>Ficus enormis</i> (Mart. ex Miq.) Mart. ‡	1	0.070	1	0.0	0.1	0.1	0.19
Lauraceae	<i>Ocotea tabacifolia</i> (Meisn.) Rohwer †	1	0.066	1	0.0	0.1	0.1	0.19
Fabaceae	<i>Andira</i> cf. <i>ormosioides</i> Benth.	2	0.011	2	0.1	0.0	0.1	0.19
Melastomataceae	<i>Henriettella glabra</i> Cogn. †	2	0.006	2	0.1	0.0	0.1	0.19
Lauraceae	<i>Licaria armeniaca</i> (Nees) Kosterm. †	1	0.064	1	0.0	0.1	0.1	0.18
Lauraceae	<i>Nectandra megapotamica</i> (Spreng.) Mez †	1	0.048	1	0.0	0.1	0.1	0.16
Caricaceae	<i>Jacaratia spinosa</i> (Aubl.) A.DC. †	1	0.047	1	0.0	0.1	0.1	0.16
Fabaceae	<i>Zollernia ilicifolia</i> (Brongn.) Vogel ‡	1	0.034	1	0.0	0.1	0.1	0.14
Monimiaceae	<i>Mollinedia triflora</i> (Spreng.) Tul. ‡	2	0.015	1	0.1	0.0	0.1	0.14
Sapotaceae	<i>Chrysophyllum viride</i> Mart. & Eichler †	2	0.011	1	0.1	0.0	0.1	0.14
Moraceae	<i>Brosimum</i> cf. <i>guianense</i> (Aubl.) Huber ‡	1	0.026	1	0.0	0.0	0.1	0.13
Fabaceae	<i>Inga marginata</i> Willd. †	2	0.009	1	0.1	0.0	0.1	0.13
Myrtaceae	<i>Eugenia capitulifera</i> O.Berg †	1	0.022	1	0.0	0.0	0.1	0.12
Aquifoliaceae	<i>Ilex amara</i> (Vell). Loes. ‡	1	0.021	1	0.0	0.0	0.1	0.12

continue

continuation

Family	Species	NI	BA	Q	RD	RDo	RF	VI
Symplocaceae	<i>Symplocos</i> cf. <i>tetrandra</i> Mart. ‡	1	0.015	1	0.0	0.0	0.1	0.11
Cyatheaceae	<i>Cyathea corcovadensis</i> (Raddi) Domin ‡	1	0.010	1	0.0	0.0	0.1	0.10
Fabaceae	<i>Lonchocarpus cultratus</i> (Vell.) A.M.G.Azevedo & H.C.Lima †	1	0.010	1	0.0	0.0	0.1	0.10
Myrtaceae	<i>Plinia pauciflora</i> M.L. Kawas. & B.Holst †	1	0.010	1	0.0	0.0	0.1	0.10
Fabaceae	<i>Andira</i> cf. <i>fraxinifolia</i> Benth. †	1	0.009	1	0.0	0.0	0.1	0.10
Aquifoliaceae	<i>Ilex theezans</i> Mart. ‡	1	0.009	1	0.0	0.0	0.1	0.10
Rutaceae	<i>Zanthoxylum rhoifolium</i> Lam. ‡	1	0.009	1	0.0	0.0	0.1	0.10
Myristicaceae	<i>Virola gardnerii</i> (A.DC.) Warb. ‡	1	0.008	1	0.0	0.0	0.1	0.10
Lamiaceae	<i>Vitex</i> cf. <i>polygama</i> Cham. ‡	1	0.008	1	0.0	0.0	0.1	0.10
Anacardiaceae	<i>Tapirira guianensis</i> Aubl. †	1	0.007	1	0.0	0.0	0.1	0.10
Lauraceae	<i>Nectandra membranacea</i> (Sw.) Griseb. †	1	0.005	1	0.0	0.0	0.1	0.10
Malpighiaceae	<i>Bunchosia fluminensis</i> Griseb. †	1	0.005	1	0.0	0.0	0.1	0.10
Rubiaceae	<i>Randia nitida</i> (Kunth) DC. †	1	0.005	1	0.0	0.0	0.1	0.10
Myrtaceae	<i>Myrceugenia reitzii</i> D.Legrand & Kausel †	1	0.005	1	0.0	0.0	0.1	0.10
Melastomataceae	<i>Miconia holosericea</i> (L.) DC. ‡	1	0.005	1	0.0	0.0	0.1	0.10
Erythroxylaceae	<i>Erythroxylum ambiguum</i> Peyr. †	1	0.004	1	0.0	0.0	0.1	0.10
Piperaceae	<i>Piper aduncum</i> L. †	1	0.004	1	0.0	0.0	0.1	0.10
Melastomataceae	<i>Miconia tristis</i> subsp. <i>australis</i> Wurdack †	1	0.004	1	0.0	0.0	0.1	0.10
Myrtaceae	<i>Myrceugenia kleinii</i> D.Legrand & Kausel †	1	0.004	1	0.0	0.0	0.1	0.09
Melastomataceae	<i>Miconia rigidiuscula</i> Cogn. ‡	1	0.003	1	0.0	0.0	0.1	0.09
Celastraceae	<i>Maytenus schumanniana</i> Loes. ‡	1	0.003	1	0.0	0.0	0.1	0.09
Annonaceae	<i>Rollinia</i> cf. <i>dolabripetala</i> (Raddi) R.E.Fr. †	1	0.002	1	0.0	0.0	0.1	0.09
Solanaceae	<i>Solanum</i> sp. 2 †	1	0.002	1	0.0	0.0	0.1	0.09
Solanaceae	<i>Solanum</i> sp. 1 ‡	1	0.002	1	0.0	0.0	0.1	0.09
Salicaceae	<i>Xylosma glaberrimum</i> Sleumer †	1	0.002	1	0.0	0.0	0.1	0.09

of 0.444 for axis 1 and 0.145 for axis 2. Although some species were predominant in one of the plots, there was no great structural differentiation among them. *Eugenia bocainensis*, *E. cuprea*, *Calyptanthus lanceolata*,

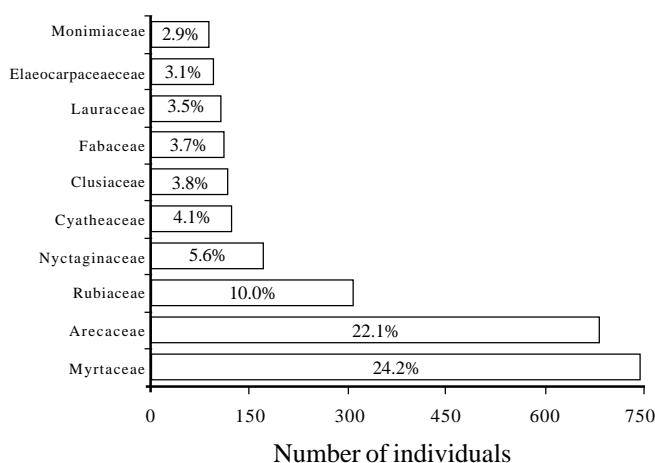


Figure 1. Distribution of the percentage of individuals by botanic family in the lowland Atlantic Rain Forest, Intervales State Park, Southeastern Brazil.

Ruprechtia laxiflora, *Cyathea phalerata* and *Alsophila sternbergii* were more abundant in Plot 1, and the latter was found exclusively in Plot 1. The individuals of *A. sternbergii* were predominant in all four quadrats close to the Saibadela River (46 out of 64 individuals sampled), as shown in figure 2. *Eugenia cambucarana* also had 13 individuals exclusively sampled in the quadrats close to the river in Plot 1. On the other hand, *Psychotria mapoureoides*, *Mollinedia uleana*, *Calycorectes acutatus*, *Eugenia oblongata* and *Pilocarpus pauciflorus* were more abundant in Plot 2. It is important to point out that *Maytenus robusta* and *Eugenia subavenia*, with 10 and 11 individuals respectively, were exclusively present in Plot 2.

Out of the 172 species found, 59 (34.3%) presented a maximum of two individuals in the stand, wherein 41 of them were represented by only one individual (table 1). Moreover, only four out of the 18 species surveyed with two individuals had one individual per plot. The qualitative similarity between plots ($S_j = 0.58$) was outstandingly lower than the quantitative similarity

Table 2. Comparisons of the number of individuals (NI) and basal area (BA) for 12 species with high value of importance (VI) sampled in two areas of lowland Atlantic Rain Forest, Intervaes State Park, Southeastern Brazil. c: value of importance position of species in each plot.

Species	Plot 1			Plot 2		
	c	NI	BA	c	NI	BA
<i>Euterpe edulis</i>	1	287	2.335	1	384	2.601
<i>Sloanea guianensis</i>	4	45	2.226	2	48	4.946
<i>Guapira opposita</i>	3	87	0.973	3	85	1.071
<i>Bathysa australis</i>	2	69	2.105	9	31	0.673
<i>Eugenia mosenii</i>	6	56	0.455	6	58	0.483
<i>Garcinia gardneriana</i>	14	28	0.276	4	89	0.721
<i>Marlierea obscura</i>	7	44	0.621	7	50	0.494
<i>Virola bicuhyba</i>	5	14	2.744	22	10	0.860
<i>Alchornea triplinervia</i>	9	11	1.924	8	14	1.405
<i>Psychotria suterella</i>	25	21	0.096	5	74	0.315
<i>Marlierea tomentosa</i>	8	53	0.372	24	25	0.144
<i>Mollinedia schottiana</i>	11	35	0.188	16	31	0.134
Total		750	14.316		899	13.847

($S_M = 0.94$), due to the taxa found with greater abundance in the stand.

Vertical structure – The DCA analysis of species distribution throughout the height classes for all the species surveyed presented a gradient length of 20.99 and 10.15 and eigenvalues of 0.499 and 0.226, for axes 1 and 2, respectively. The high eigenvalue of axis 1 showed a strong distribution of height classes in relation to the composition of species, forming three arbitrary groups (figure 3): stratum A (≥ 26 m), stratum B ($8 \text{ m} < h < 26$ m) and stratum C (≤ 8 m). The stratum A was mainly distributed along the axis 2 due to the small number of individuals per species. These low densities in stratum A resulted in a lower floristic richness and diversity (table 3). Stratum B had higher basal area, richness and diversity of species. Stratum C had higher density, however it concentrated many individuals in few species, in which 12 represented 67.9% of the total number of individuals, generating the lowest values of equability (table 3).

Table 4 displays the 12 species with the highest VI in each stratum. *Euterpe edulis* was the most abundant species in strata B and C, although it was more significantly associated with stratum C. *Garcinia gardneriana* and *Eugenia mosenii* were also well-represented in these two forest strata, although they did not present significantly higher density in any of the strata. *Guapira opposita* was more abundant in stratum C than in stratum B, where it showed a lower than

expected number of individuals according to chi-square test (χ^2). The tree species significantly associated with stratum C were *Psychotria suterella*, *Ixora burchelliana*, *Mollinedia schottiana*, *Marlierea*

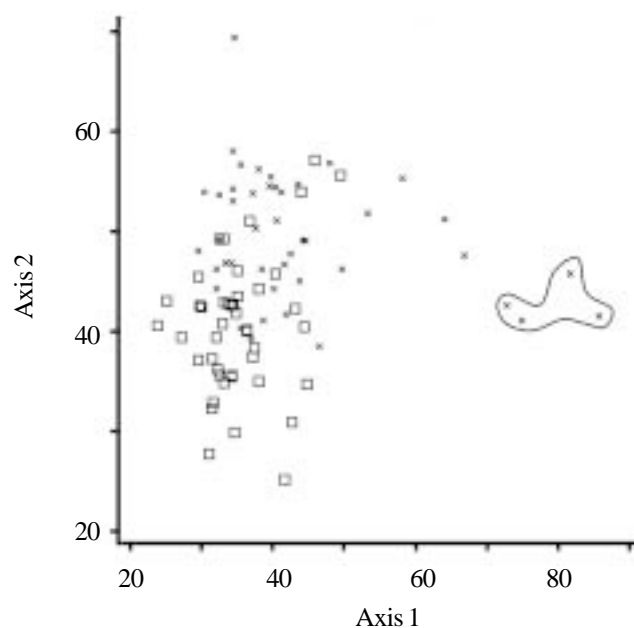


Figure 2. Ordination diagram produced by DCA, based on the distribution of the 48 most abundant species in 88 quadrats surveyed in the lowland Atlantic Rain Forest, Intervaes State Park, Southeastern Brazil. The quadrats are classified for each sample plot. Quadrats in evidence are those closest to the Saibadela river in Plot 1. Eigenvalues (axis 1: 0.444; axis 2: 0.145). Plot 1 = ×, Plot 2 = □.

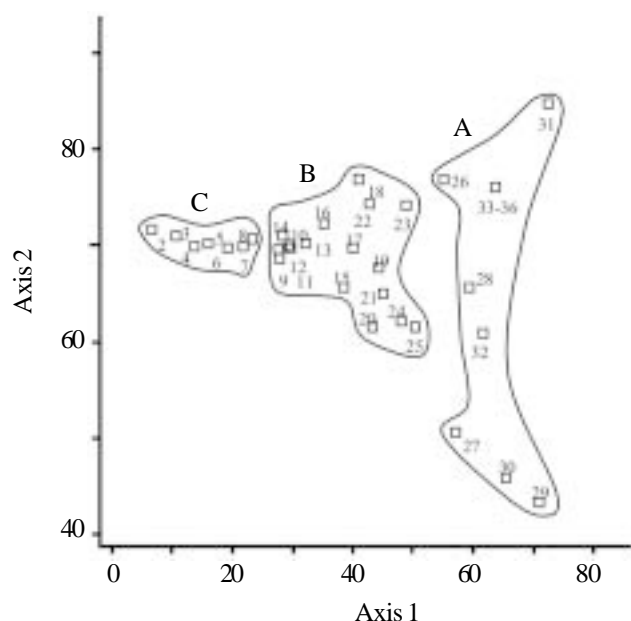


Figure 3. Ordination diagram of the height classes produced by DCA, based on estimated height of individuals of all species sampled in the stand of lowland Atlantic Rain Forest, Intervales State Park, Southeastern Brazil. The intervals of class are numbered in a sequence from 2 (individuals measuring up to 2 m height) to 33-36 m (individuals measuring from 33 to 36 m height). Eigenvalues (axis 1: 0.499; axis 2: 0.226).

tomentosa, *Eugenia cuprea*, *Alsophila sternbergii* and *Cyathea phalerata*. The species significantly associated with stratum B were *Bathysa australis*, *Marlierea obscura*, *Eugenia riedeliana*, *Tetrastylidium grandifolium* and *Swartzia flaemingii*. Despite the fact that *Alchornea triplinervia* and especially *Sloanea guianensis* were included among the most important species in stratum B, both were significantly associated with stratum A, joined with

Table 3. Phytosociological data for the three vertical strata (A, B, and C) of lowland Atlantic Rain Forest, Intervales State Park, Southeastern Brazil.

Phytosociological data	Strata		
	A	B	C
Number of individuals	103	1,356	1,556
Basal area (m ² .ha ⁻¹)	12.298	18.066	3.910
Height average (m)	28.7	13.9	5.8
Diameter average (cm)	50.8	15.9	7.6
Number of families	19	45	41
Number of species	36	145	119
Diversity index (H')	3.172	3.895	3.440
Equability index (J')	0.885	0.782	0.720

Table 4. Phytosociological descriptors for 12 tree species with high value of importance (VI) in each vertical stratum of lowland Atlantic Rain Forest, Intervales State Park, Southeastern Brazil. Qui-square (χ^2) tests the null hypothesis of the distribution of species abundance in each stratum (A, B, and C) in relation to the total number of individuals in the stand. Values of χ^2 followed by 'plus' (+) or 'minus' (-) indicate abundance above or below expected, respectively. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns: not significant. § insufficient number of individuals for a qui-square test (χ^2).

Species	NI	BA	RD	RDo	RF	VI	χ^2	P
Stratum A								
<i>Sloanea guianensis</i>	16	4.610	15.5	18.9	14.1	48.6	+47.80	***
<i>Virola bicuhyba</i>	10	3.184	9.7	13.1	10.1	32.9	+91.89	***
<i>Hyeronima alchorneoides</i>	8	1.566	7.8	6.4	7.1	21.3	+82.44	***
<i>Alchornea triplinervia</i>	7	1.349	6.8	5.5	6.1	18.4	+37.32	***
<i>Pseudopiptadenia warmingii</i>	6	1.029	5.8	4.2	6.1	16.1	+87.69	***
<i>Callisthene cf. dryadum</i>	4	1.505	3.9	6.1	4.0	14.1	§	-
<i>Pterocarpus rohrii</i>	6	0.433	5.8	1.8	6.1	13.7	+31.88	***
<i>Copaifera trapezifolia</i>	4	1.152	3.9	4.7	4.0	12.7	§	-
<i>Cariniana estrellensis</i>	3	1.143	2.9	4.7	3.0	10.6	§	-
<i>Aspidosperma cf. compactinervium</i>	2	1.063	1.9	4.7	2.0	8.3	§	-
<i>Schizolobium parahyba</i>	2	0.864	1.9	3.6	2.0	7.5	§	-
<i>Ficus gomelleira</i>	1	1.325	1.0	5.4	1.0	7.4	§	-
Stratum B								
<i>Euterpe edulis</i>	249	2.550	7.1	7.8	18.4	33.3	2.10	ns
<i>Bathysa australis</i>	78	2.603	7.3	4.7	5.8	17.7	+23.52	***

continue

continuation

Species	NI	BA	RD	RDo	RF	VI	χ^2	<i>P</i>
Stratum B (cont.)								
<i>Sloanea guianensis</i>	60	2.407	6.7	4.5	4.4	15.6	+ 7.47	**
<i>Marlierea obscura</i>	70	1.014	2.8	4.8	5.2	12.8	+ 17.53	***
<i>Guapira opposita</i>	55	1.460	4.1	4.0	4.1	12.1	- 6.18	*
<i>Garcinia gardneriana</i>	57	0.720	2.0	3.8	4.2	10.0	0.29	ns
<i>Eugenia mosenii</i>	46	0.547	1.5	3.7	3.4	8.6	0.44	ns
<i>Alchornea triplinervia</i>	16	1.850	5.2	1.6	1.2	8.0	1.61	ns
<i>Tetrastilidium grandifolium</i>	36	0.733	2.1	2.4	2.7	7.1	+ 10.60	**
<i>Eugenia riedeliana</i>	25	1.103	3.1	2.1	1.8	7.1	+ 5.55	*
<i>Swartzia flaemingii</i>	18	0.967	2.7	1.8	1.3	5.9	+ 4.95	*
<i>Calycorectes australis</i>	22	0.808	2.3	1.9	1.6	5.8	0.51	ns
Stratum C								
<i>Euterpe edulis</i>	359	1.645	23.1	21.2	8.98	53.3	+ 6.73	**
<i>Guapira opposita</i>	117	0.584	7.5	7.5	6.82	21.9	+ 8.66	**
<i>Psychotria suterella</i>	95	0.411	6.1	5.3	5.19	16.6	+ 42.17	***
<i>Eugenia mosenii</i>	68	0.392	4.4	5.1	4.87	14.3	1.28	ns
<i>Mollinedia schottiana</i>	63	0.295	4.1	3.8	4.65	12.5	+ 23.74	***
<i>Marlierea tomentosa</i>	62	0.356	4.0	4.6	3.8	12.4	+ 11.21	***
<i>Alsophila sternbergii</i>	59	0.534	3.8	6.9	1.1	11.8	+ 19.64	***
<i>Garcinia gardneriana</i>	60	0.278	3.9	3.6	3.9	11.3	0.00	ns
<i>Cyathea phalerata</i>	54	0.286	3.5	3.7	3.4	10.5	+ 23.57	***
<i>Ixora burchelliana</i>	47	0.160	3.0	2.1	3.7	8.8	+ 20.40	***
<i>Eugenia cuprea</i>	45	0.190	2.9	2.5	3.4	8.7	+ 12.56	***
<i>Ocotea teleiandra</i>	27	0.098	1.7	1.3	2.4	5.4	2.02	ns

Virola bicuhyba, *Hyeronima alchorneoides*, *Pseudopiptadenia warmingii* and *Pterocarpus rohrii*.

Discussion

Horizontal structure – The six families with the largest number of species found in this study presented the greatest floristic richness in previous studies of the Atlantic Rain Forest at Serra do Mar, Ubatuba (Silva & Leitão Filho 1982, Sanches *et al.* 1999), and the hill slopes of Ilha do Cardoso, Cananéia (Melo & Mantovani 1994). This confirms their importance in the general characterization of the Atlantic Rain Forest. Myrtaceae was the family with the largest number of species in this study, with the genus *Eugenia* alone represented by 19 species. This great richness of Myrtaceae, especially the genus *Eugenia*, corroborates the pattern found for the Atlantic Rain Forest in São Paulo State (Scudeller *et al.* 2001) and in Brazil (Oliveira Filho & Fontes 2000). According to Mori *et al.* (1983) and Peixoto & Gentry (1990), the Myrtaceae family has great ecological importance on the entire Brazilian coast due to its great abundance and species richness.

Arecaceae followed Myrtaceae in number of individuals, as previously recorded by Melo *et al.* (1998) in Juréia and by Sanches *et al.* (1999) in Ubatuba. The Arecaceae family, although represented by only two species in the present study, had great influence on the structure of the studied tree community, due mostly to the high abundance of *Euterpe edulis*. Sztutman & Rodrigues (2002) found the same pattern for another forest on the south of São Paulo State. At Base Saibadela, *E. edulis* occurred abundantly in several distinct environmental conditions. This pattern may be linked to the great investment and success in the reproduction of the species, as reported by Reis & Kageyama (2000). The importance of *E. edulis* in the Atlantic Rain Forest is due also to the great availability of fruits produced annually, which can reach up to 377.000 ha⁻¹ year⁻¹ (Reis & Kageyama 2000). They serve as a main source of food to many mammals and large birds (Galetti & Chivers 1995, Galetti *et al.* 1997).

Despite the high abundance of *Euterpe edulis* (see also Scudeller *et al.* 2001), its genetic diversity has been seriously threatened by clandestine exploration of palm-hearts (Reis & Reis 2000). In our study, harvested palms

had an average (\pm SD) diameter at breast height (DBH) of 12.15 cm \pm 1.53, larger than DBH of the living individuals (9.04 cm \pm 2.96), showing that the largest individuals were the favorite to be harvested by the clandestine collectors.

Diversity, floristic, and structural comparisons – Phytosociological surveys conducted in the Atlantic Rain Forest in the São Paulo State often showed tree diversity indexes ranging from 4.07 to 4.31 nat.ind.⁻¹ (Silva & Leitão Filho 1982, Mantovani *et al.* 1990, Leitão Filho 1993, Melo *et al.* 1998). The lowest diversity index ($H' = 3.85$ nat.ind.⁻¹) found here may have been the result of the method employed, which restricted the number of ecotones within the stand, and consequently reduced the environmental heterogeneity of the forest mosaic which composes the Atlantic Rain Forest.

Some species presented different abundance between the two sample plots, especially in quadrats associated with the Saibadela rivercourse and the permanent rise of the water table in Plot 1, where the soil is poorly drained. These factors generate greater floristic and structural differentiation of these sites compared to the rest of the stand. Therefore, the short gradients shown by DCA, may possibly derive from variations occurred in the ordination of the main species, which was small in both plots, resulting in great quantitative similarity between them. On the other hand, in terms of qualitative similarity, the floristic differences between the plots were high. Such floristic distinction results from the large amount of little abundant taxa found at the Base Saibadela, confirming what had already been observed in previous studies, that the great richness results in great diversity of the tree species in the Atlantic Rain Forest (Silva & Leitão Filho 1982, Mantovani *et al.* 1990, Melo *et al.* 1998, Sanches *et al.* 1999).

Vertical Structure – Souza *et al.* (2003) argued that the cluster and discriminant multivariate analyses, are viable to assess the vertical tree structure in a Semideciduous Seasonal Forest where three levels of distribution are found. In the present study, although the DCA is an indirect method, it generated both a gradient of height intervals and a trend of occurrence of three arbitrary strata in the sampled area. Thus, we argue then that A is the canopy stratum, composed by emerging individuals; B is the subcanopy stratum, composed by large to medium-size trees and representatives of stratum A; and C is the understorey stratum, composed by small individuals and immature representatives from strata A and B.

Stratum B showed the highest floristic richness and diversity of the three strata considered in this study. As

argued by Terborgh (1992), tree diversity must be higher in the intermediate levels in tropical forests, where trees are more susceptible to a great variety of light conditions due to shadowing provided by the various shapes of crowns of emerging trees and the canopy, and by gaps created in the forest.

Euterpe edulis and *Garcinia gardneriana*, besides several species of Myrtaceae, were expressively represented in strata B and C in the sample plots. *Guapira opposita* (Nyctaginaceae), which is abundant and highly spread throughout the Atlantic Rain Forest (Mantovani *et al.* 1990, Leitão Filho 1993, Scudeller *et al.* 2001), was also among the most important species in strata B and C, and the most abundant species in the understorey of the stand. Despite being seldom discussed in literature, other taxa are very characteristics of understorey. As observed in the present study, stratum C was well represented by the Cyatheaceae, with species such as *Alsophila sternbergii* and *Cyathea phalerata*, and by the Rubiaceae, with *Psychotria suterella*, *Ixora burchelliana* and *Rudgea jasminoides*, besides other immature individuals, e.g. *Bathysa australis*.

Terborgh (1992) argued that in mature tropical forests, the canopy and emerging tree component present a smaller number of individuals and a smaller floristic richness, as seen in this study. Nevertheless, the Fabaceae family was well represented in stratum A of the stand, showing the greatest richness (8 species) and density (22 individuals). Besides the Fabaceae, other important species in this stratum were *Virola bicuhyba*, *Hyeronima alchorneoides*, *Sloanea guianensis* and *Alchornea triplinervia*. As reported by Sztutman & Rodrigues (2002), *S. guianensis* and *A. triplinervia* have large size representatives occurring respectively in well-drained soils of the Atlantic Rain Forest and in the Coastal Plain or Restinga Forest located in Pariquera-Açu, SP. It is possible to assert that these species are peculiar of the canopy in the Atlantic Rain Forest which can occasionally appear as emergent trees.

The method herein applied disregard the mosaic character in which tropical forests are in general organized, where there are spots of different ages, compositions and structures (Whitmore 1975), in which the vertical distribution varies. Moreover, such distribution in tropical forests is not always evident and although the limits may be imperceptible along the stratification, Richards (1996) argues that for descriptive purposes it is convenient to consider the existence of three strata (A, B and C). Therefore we recommended that the method used in the present study be applied to other

types of forests whose stratification is poorly defined, aiming to test the effectiveness of the DCA analysis in these situations. More refined discussions with regard to the definition of strata, and the ecology of the occupation by plants and animals along stratification, can result from such investigations. Thus, the study of vertical structure, so little investigated up to now, must be very important, maybe more than those related with the horizontal structure, considering that the difference of occupation of niches in different strata is one of the most crucial factors to explain the high diversity in tropical forests (Terborgh 1992).

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