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COMPARISON OF THE WOODY FLORA AND SOILS OF SIX AREAS OF MONTANE SEMIDECIDUOUS FOREST IN SOUTHERN MINAS GERAIS, BRAZIL

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Qualitative and quantitative descriptions of the woody flora and soil analyses are provided for six areas of montane semideciduous forest in the upper Rio Grande region, southern Minas Gerais, Brazil. Comparisons are made of the floristic composition of these six areas and 24 other forest areas of southeastern Brazil using ordination by detrended correspondence analysis (DCA) and hierarchical classifications, both agglomerative (UPGMA) and divisive (TWINSPAN). The variation in community structure of five of the six forest areas was analysed using a two-way table yielded by TWINSPAN. The floristic analyses indicated the strongest link between the forests of the upper Rio Grande region and other montane forest formations of southeastern Brazil as well as secondary links with the gallery forests that extend into the cerrado domain and the submontane semideciduous forests of the Rio Paraná basin. Variations in community structure among the five forest areas were apparently associated mainly with riverside effects and soil fertility.

Descrições qualitativas e quantitativas da flora lenhosa e análises de solos são apresentadas para seis áreas de floresta semidecídua montana na região do alto rio Grande, sul de Minas Gerais, Brasil. São feitas comparações florísticas das seis florestas e de outras 24 áreas de floresta do sudeste brasileiro usando ordenação por análise de correspondência (DCA) e classificações hierárquicas, tanto aglomerativa (UPGMA) como divisiva (TWINSPAN). As variações em estrutura comunitária de cinco das seis florestas foram analisadas usando uma tabela bidirecional produzida por TWINSPAN. As análises florísticas indicaram uma ligação mais forte entre as florestas do alto rio Grande e outras formações florestais montanas do sudeste do Brasil, bem como laços florísticos secundários com as florestas de galeria que penetram o domínio dos cerrados e com as florestas semidecíduas submontanas do vale do rio Paraná. As variações em estrutura comunitária entre as cinco florestas mostraram-se aparentemente associadas principalmente com o efeito da margem dos rios e com a fertilidade dos solos.

INTRODUCTION

The Serra da Mantiqueira, in southeastern Brazil, is a system of mountain ridges situated mainly in the state of Minas Gerais, and with its southern and eastern fringes roughly delimiting the borders with the states of São Paulo, Rio de Janeiro and Espírito Santo. These fringes are considered as the maximum inland extension of the Atlantic coastal rainforest, since the slopes of the Serra da Mantiqueira, in the latter three states, suffer a stronger influence from the ocean and the figures for rainfall are much higher there than in the hills of the hinterland of southern Minas Gerais (Fernandes & Bezerra, 1990). In this region, the natural vegetation is a complicated mosaic of *campos limpos de altitude* (alpine grasslands), *campos rupestres* (rocky alpine fields), cerrado (savanna), *mata seca* (semideciduous forest) and *mata de Araucaria* (mixed upper montane forest)

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(IBGE, 1993). According to Eiten (1982), the campo limpo and the campo rupestre in southern Minas Gerais are associated with the shallow soils of mountain tops, while the cerrados and semideciduous forests share the deeper soils, the latter being found in the more fertile sites. The patches of mata de *Araucaria* occur in deep fertile soils at higher altitude.

As has occurred in other parts of Brazil where European occupation goes back to colonial times, the natural vegetation of southern Minas Gerais has been reduced to sparse remnants, most of which have been disturbed by fire, extensive cattle raising and/or selective cutting of trees. The semideciduous forests in particular have been severely reduced, since their distribution is generally associated with more fertile soils. Very little is known about the floristic composition of the forest relics of southern Minas Gerais (although some checklists were provided by Ferreira & Magalhães, 1977; Ferreira et al., 1977/78; Brandão et al., 1989, 1991; Brandão & Gavilanes, 1990; Brandão, 1992; Carvalho et al., 1992; Gavilanes et al., 1992a, 1992b, and Oliveira-Filho & Machado, 1993) while phytosociological data are virtually absent from the literature (Martins, 1989). In comparison to the attention and efforts devoted to the conservation of the Atlantic coastal and the Amazonian rainforests, the semideciduous forest of southeastern Brazil has been greatly neglected, despite the fact that its remnants are under a more severe threat, especially in Minas Gerais.

In 1985 our research team at the Forestry and Biology Departments of the Escola Superior de Agricultura de Lavras (ESAL) started a series of floristic and phytosociological surveys of forest remnants in the upper Rio Grande region, southern Minas Gerais. Since 1989 these studies have been supported by the Electricity Company of Minas Gerais (CEMIG), which is interested in environmental rehabilitation of areas affected by its hydroelectric reservoirs. Since the company intends to use native species in its reforestation projects, it required floristic and ecological information on the forests of the region.

In the present communication we summarize the results of the floristic and soil surveys of six areas of montane semideciduous forest in the region, as well as the phytosociological survey carried out in five of these areas. We compare these forests with 24 checklists published for other forest areas of southeastern Brazil by means of multivariate analyses, with the aim of assessing their floristic links with other forest types of the region. Five of the six forest areas are also analysed for their differences in community structure to investigate the possible relationship between environmental factors and the relative abundance of the most important species.

Description of the Study Areas

The study region, shown in Fig. 1, comprises the section of the Serra da Mantiqueira that shelters the upper course of the Rio Grande. This river, after merging with the Rio Paranaíba in western Minas Gerais, becomes the Rio Paraná which is the main watercourse of the second largest river system in the whole of South America. The topography of the upper Rio Grande region is predominantly hilly, with altitudes ranging in most of the region between 700 and 1000m. However, altitudes of between 1100 and 1400m occur on the higher mountain ridges of the Serra de São José in Tiradentes, and Serra da Bocaina in Ingaí, Carrancas and Luminárias.

The predominant soil types of the region are the Latosols, Cambisols, Podzolic Soils, Alluvial Soils and Lithosols, while the most important parent materials are quartzites, granitic gneisses,

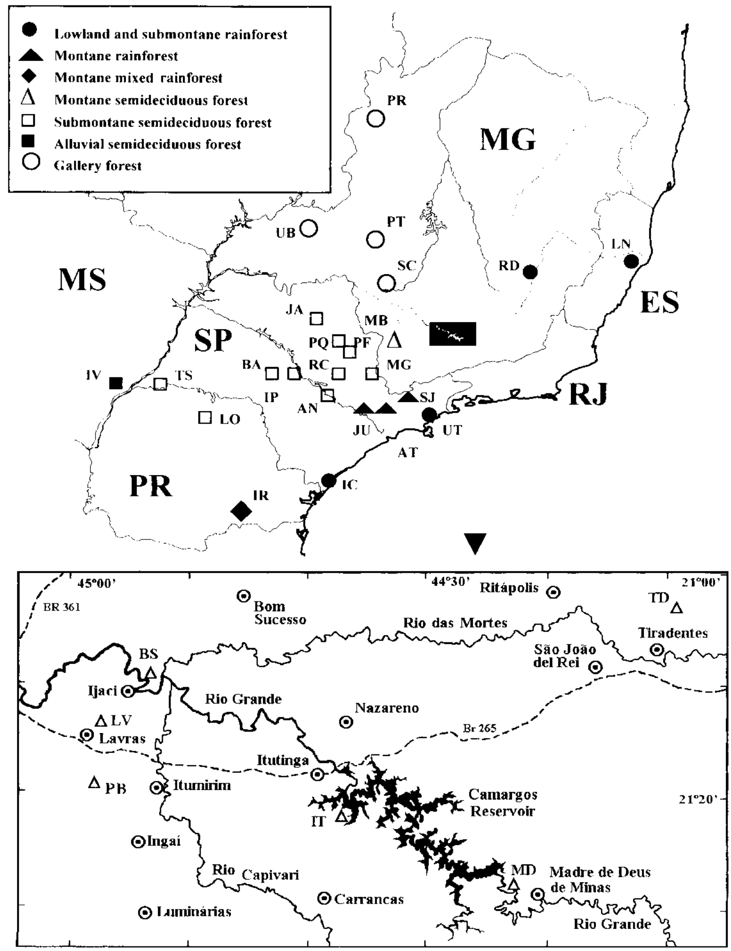

FIG. 1. Map of southeastern Brazil, with the upper Rio Grande region enlarged, showing the location of the 30 forest areas used in the floristic analyses. The forest areas are classified according to the modified IBGE system (see text) and are identified by their two-letter codes in Table 1. Brazilian states: MG, Minas Gerais; ES, Espírito Santo; RJ, Rio de Janeiro; SP, São Paulo; MS, Mato Grosso do Sul; PR, Paraná. Towns are indicated by circles. BR 361 and BR 265 are federal roads.

mica-slates and calcareous gneisses (Curi et al., 1990). In this study we adopted the nomenclature of the Brazilian soil taxonomy system (Camargo & Bennema, 1966; Adámoli et al., 1985) together with the classification of the soils in the dystrophic (< 10% of base saturation) and mesotrophic fertility categories (Askew et al., 1970).

The climate of the region is classified as the Cwb type of Köppen, i.e. temperate with a mild summer and a dry winter (Eidt, 1968). Data collected by the Meteorological Station of Lavras (21°13'40''S, 44°57'50''W, 918m altitude) provided the following average figures for the period of 1960–1992: annual air temperature 19.61°C, with monthly temperatures ranging from 16.03°C (July) to 21.82°C (February); annual rainfall 1517mm, concentrated during October–

April (93% of the total rainfall), the monthly means ranging from 19.2mm (July) to 293.3mm (January).

We chose six areas of montane semideciduous forest for detailed study after inspection of aerial photographs and field visits to several forest relic areas. They were chosen from among the less disturbed forest patches of more than 3ha in order to represent different habitats. Their precise location is indicated in Fig. 1; a brief description of each area is given below:

Area 1 (LV) : Lavras, Forest Reserve of the ESAL (21°13'40''S, 44°57'50''W, c.925m alt.). This is a small forest relic of 5.8ha protected as a Forest Reserve in the campus of the Escola Superior de Agricultura de Lavras (ESAL). The reserve lies at the top of a broad interfluve in an area with very even topography. The site is well drained and all watercourses lie far from the reserve so that only the upland type of montane semideciduous forest occurs. Pastures and plantations of *Eucalyptus* spp. and *Pinus* spp. surround the forest. The soils are very fine-textured dystrophic (epialic) Reddish-Purple Latosols.

Area 2 (PB) : Lavras, Biological Reserve of Poço Bonito (21°19'50''S, 44°59'20''W, c.1150m alt.). This municipal reserve of c.70ha is situated in the Serra do Carrapato, a hilly mountain ridge that borders the municipalities of Lavras and Ingaí. The vegetation is a complex mosaic of campo rupestre (rocky alpine fields), cerrado and montane semideciduous forest, this last covering about 15ha. The forest occurs partially along the Villas Boas stream, so it includes tracts of both the riverine and upland semideciduous forest types. The soils are all coarse-textured, alic and dystrophic, being classified as Cambisols in the slopes, and as Alluvial Soils next to the stream. A detailed study of this area is given by Gavilanes et al. (1992b).

Area 3 (BS) : Bom Sucesso, District of Macaia (21°09'35''S, 44°54'10''W, c.825m alt.). This area is the largest continuous tract of forest that can still be found in the region, with an area of about 84ha, all within a single ranch, the Fazenda Botelhos. The forest covers the outer side of a curve of the Rio Grande so that the river banks are presently suffering fluvial erosion. The forest fringes the steep bank of the river and extends inland through several erosion gullies that acted as natural hindrances to the expansion of the farmlands. The soils have an intermediate texture, are mainly mesotrophic (with some dystrophic patches), and are classified as podzolic Dark-Red Latosols in the upper sites (crests and slopes of gullies), and Alluvial Soils in the lower sites (at the bottom of gullies). A detailed study of this area is given by Oliveira-Filho et al. (1994a).

Area 4 (IT): Itutinga, Camargos Reservoir (21°21'50''S, 44°37'00''W, c.917m alt.). This area, of about only 3.5ha, is the relic of a semideciduous forest that probably extended in the past along the whole course of a stream from its source to its discharge into the Rio Grande. After the dam was built in 1961 only the headwaters section remained, while the rest of the forest was submerged. Two small creeks ending in the Camargos Reservoir still flow within the forest so that the area includes upland and riverine forest types. The forest is entirely surrounded by campos limpos de altitude (alpine grasslands). The soils have an intermediate texture, are alic and mesotrophic (with some dystrophic patches), and are classified as Red-Yellow Podzolic Soils in the lower sites, and as Cambisols in the upper sites. A detailed study of this area is given by Vilela et al. (1994).

Area 5 (MD) : Madre de Deus de Minas, Fazenda Patrimônio (21°29'22''S, 44°22'35''W, c.925m alt.). This area occurs in the inner part of a meander of the Rio Grande so that a great extent of the forest, of the riverine inundatable type, covers a point bar (the inside curve of river bends where rapid accretion of sediments occurs during the river floods). The remaining upland forest sector covers a gentle slope, the whole forest occupying an area of about 20ha. The soils have an intermediate texture, vary from dystrophic to mesotrophic, and are classified as Alluvial Soils in the point bar, and (cambic) Yellow-Red Latosols in the upland slope. A detailed study of this area is given by Oliveira-Filho et al. (1994b).

Area 6 (TD) : Tiradentes, Serra de São José (21°01'00''S, 44°14'30''W, c.900m alt.). The Serra de São José is a small mountain ridge formed mainly by quartzitic sandstones that extends east–west by c.12km. On its south face the ridge rises suddenly from altitudes of c.900m at the base to c.1400m at the top. Below the escarpments there are steep foothills which are covered by a strip of montane semideciduous forest with an area of about 25ha. These foothills also shelter the springs of several streams that flow southwards to the Rio das Mortes, so that the forest includes both the riverine and the upland types. The soils are mainly coarse-textured dystrophic alic Cambisols. A detailed study of the area is given by Oliveira-Filho & Machado (1993).

METHODS

We carried out a floristic survey in the forest areas described above (hereafter designated by initials) by general observation and collecting on regular visits from August 1985 to June 1992, with more systematic collecting in sample plots during the phytosociological surveys. We gave special attention to non-climbing species with a stem diameter >2cm at the base, so that the survey included trees, shrubs, palms, arborescent ferns, bamboos and ground aroids. Voucher specimens are lodged in the herbarium of Escola Superior de Agricultura de Lavras (ESAL) with duplicates at the Royal Botanic Garden Edinburgh (E) and Universidade Estadual de Campinas (UEC).

In the phytosociological surveys carried out in each forest area, we used the following sampling procedure: LV = 126, 20 x 20m contiguous plots covering the whole reserve; PB = 16, 10 x 30m contiguous plots in a 20 x 80m transect traversing the watercourse; BS = 24, 15 x 15m plots arranged in three blocks of 2 x 4 contiguous plots situated along the margin of the Rio Grande; IT = 42, 15 x 15m plots in two transects, the first (2 x 10 plots) along a creek and the second (2 x 11 plots) traversing the interfluve; MD = 71, 15 x 15m contiguous plots in a triangle with two points at the margin of the Rio Grande and the third inland and upslope; TD = 85, 10 x 10m plots arranged in two transects (45 and 40 plots) running upslope in the foothills of the Serra. In all surveys, we recorded the species and circumference at the base of the stem (cbs) for all individuals with cbs > 15.7cm (= 5cm in diameter). We estimated the individual heights in all areas except for LV. The relative density and the relative dominance (based on the basal area per hectare) were calculated and used to obtain the cover value index (CVI = relative density + relative dominance) for each species in each area except for TD, for which field data records are no longer available. We calculated the Shannon–Wiener diversity index and the Pielou evenness index (Brower & Zar, 1984) for each sample area (except TD).

In each of the six forest areas we collected a number of 0.5 litre samples of soil from a depth of 0–20cm. Chemical and granulometric analyses were made at the Soil Laboratory of the Escola Superior de Agricultura de Lavras. Laboratory procedures followed those recommended by EMBRAPA (1979). Soil pH was measured with a potentiometer in a 1:2.5 soil to water suspension. Phosphorus and potassium were extracted with Melish solution and measured in a photometer. Exchangeable calcium, magnesium and aluminium were extracted with a 1N KCl solution; aluminium was titrated with 1N NaOH solution while calcium plus magnesium, and the calcium separately, were titrated with 0.025N EDTA. Organic carbon was determined by the Tiurim method and the percentage of organic matter obtained with the Bremelen constant (1.724). Texture was obtained by the densimetric method of Bouyoucos.

In order to perform a comprehensive floristic analysis of the six forest areas we obtained from the literature 24 additional checklists of the woody flora of forest areas in southeastern Brazil. The 24 localities are shown on the map (Fig. 1) and listed in Table 1 along with the six forest areas of the present study. The 30 forest physiognomies were classified according to the IBGE's classification system for Brazilian vegetation (IBGE, 1993; Veloso et al., 1991). However, we made two modifications for convenience: (a) gallery forests, which are part of the cerrado physiognomy in the IBGE system, are here considered as a distinct forest formation; (b) the altitudinal limit between the submontane and montane formations was changed from 500 to 750m, for this latter figure proved to be very effective in distinguishing floristically the montane forests of the state of São Paulo (Torres et al., 1994). The resulting classification, given both in Table 1 and on the map (Fig. 1), was assessed for its floristic consistency in the multivariate analyses described below.

The floristic information from the 30 checklists was organized in a presence/absence matrix. All taxa in this matrix were checked in the literature for synonymity and growth forms using the monograph index of the Royal Botanic Garden Edinburgh. After agglutinating 117 synonyms and eliminating 19 species of shrubs and climbers, the final matrix contained 1052 species of small to tall trees in the 30 forest areas. We carried out three different techniques of multivariate analyses with the floristic matrix in order to seek main patterns of data structure that could be eventually accentuated by all three methods. These were: (a) an ordination by detrended correspondence analysis (DCA) (Hill & Gauch, 1980) using the package DECORANA (Hill, 1979a), (b) an agglomerative hierarchical classification by UPGMA (unweighted pair-groups method using arithmetic averages) using the Sørensen Coefficient of Community (CC) as a measure of similarity (Kent & Coker, 1992), and (c) a divisive hierarchical classification by two-way indicator species analysis (TWINSPAN) (Hill, 1979b). For the case of DCA and TWINSPAN, we eliminated from the matrix the 411 species that occurred in only one forest area, reducing the number of species to 641. Unicates do not contribute any inter-site comparative information to those analyses and are essentially redundant (Ratter & Dargie, 1992).

We analysed five of the forest areas for their variation in community structure (TD was not included, since phytosociological data are no longer available) with the purpose of seeking patterns of species abundance that could possibly be associated with underlying environmental factors. To this end, we prepared an abundance data matrix containing the CVIs of the 87 species that presented a CVI > 2 in at least one of the five areas. The five forests were compared using the Squared Average Euclidean Distance (I), which is a measure of dissimilarity determined mostly by larger abundance values (Sneath & Sokal, 1973). The 87 species and five forest areas were also ordered and classified on a two-way table yielded by TWINSPAN. It is worth noting that all analyses in this paper were performed as an explorative approach to vegetation variation and must be seen merely as hypothesis-generating processes.

TABLE 1. Location, vegetation formation, geographical coordinates, altitude, climate type and reference for each of the 30 forest areas used in the floristic analyses. The double capitals after the localities are the official abbreviations of Brazilian states (see Fig. 1). Vegetation formation according to the modified IBGE's classification system (see text). Latitudes are South. Altitudes are medians where a range was given in the reference. Climate type according to Köppen's classification system.

Code and locality		Vegetation formation	Latitude	Longitude	Altitude (m)	Climate	Reference
LV	ESAL, Lavras - MG	Montane semideciduous forest	21°13'	45°00'	925	Cw	This work
PB	RB Poço Bonito, Lavras - MG	Montane semideciduous forest	21°20'	45°00'	1150	Cw	This work
BS	Bom Sucesso - MG	Montane semideciduous forest	21°09'	44°54'	825	Cw	This work
IT	Camargos, Itutinga - MG	Montane semideciduous forest	21°22'	44°37'	917	Cw	This work
MD	Madre de Deus de Minas - MG	Montane semideciduous forest	21°29'	44°22'	925	Cw	This work
TD	Serra S. José, Tiradentes - MG	Montane semideciduous forest	21°01'	44°14'	900	Cw	This work
MB	Monte Belo - MG	Montane semideciduous forest	21°24'	46°16'	878	Cw	Vieira 1990
SC	PN Serra da Canastra - MG	Gallery forest	20°30'	46°30'	950	Aw/Cw	Mota 1984
UB	EE Panga, Uberlândia - MG	Gallery forest	19°10'	48°24'	800	Aw	Schiavini 1992
PR	Paracatu - MG	Gallery forest	17°10'	46°57'	900	Aw	Felfili 1990, 1993
PT	Patrocínio - MG	Gallery forest	19°20'	46°47'	950	Aw	Felfili 1990, 1993
RD	RF Rio Doce - MG	Submontane dense rainforest	19°40'	42°35'	450	Af/Aw	CETEC 1982, Silva Jr et al. 1994
LN	RF CVRD, Linhares - ES	Lowland dense rainforest	19°18'	40°04'	50	Af	Peixoto & Gentry 1990
UT	EE Ubatuba - SP	Lowland dense rainforest	23°27'	45°04'	105	Af	Silva & Leitão Filho 1982
IC	PE Ilha do Cardoso - SP	Lowland dense rainforest	25°10'	48°00'	100	Af	Barros et al. 1991
AT	PM Grota Funda, Atibaia - SP	Montane dense rainforest	23°10'	46°25'	1200	Cf	Meira Neto et al. 1989, Grombone et al. 1990
JU	Serra do Japi, Jundiaí - SP	Montane dense rainforest	23°11'	46°52'	1020	Cf	Rodrigues 1986, Rodrigues et al. 1989
SJ	FR S. José dos Campos - SP	Montane dense rainforest	23°05'	45°55'	840	Cf	Silva 1989
AN	Anhembi - SP	Submontane semideciduous forest	22°40'	48°10'	500	Cw	Cesar & Leitão-Filho 1990a, 1990b
IP	APA Corumbataí, Ipeúna - SP	Submontane semideciduous forest	22°25'	48°45'	600	Cw	Mantovani et al. 1986, Rodrigues 1991
RC	Rio Claro - SP	Submontane semideciduous forest	22°22'	47°28'	630	Cw	Pagano & Leitão Filho 1987
MG	RB Mogi Guaçu - SP	Submontane semideciduous forest	22°16'	47°10'	595	Cw	Gibbs & Leitão Filho 1978, Mantovani et al. 1989
JA	UNESP, Jaboticabal - SP	Submontane semideciduous forest	21°15'	48°20'	560	Cw	Pinto 1989, Marchiori et al. 1992
PF	RE Porto Ferreira - SP	Submontane semideciduous forest	21°49'	47°25'	580	Cw	Bertoni & Martins 1987
PQ	PE S. Rita Passa Quatro - SP	Submontane semideciduous forest	21°40'	47°38'	630	Cw	Bertoni et al. 1988, Martins 1991
BA	RE Bauru - SP	Submontane semideciduous forest	22°19'	49°04'	570	Cw	Cavassan et al. 1984
TS	PE Teodoro Sampaio - SP	Submontane semideciduous forest	22°30'	52°20'	300	Cw	Campos & Heinsdijk 1970, Baitello et al. 1988
IV	Rio Ivinheima - MS	Alluvial semideciduous forest	22°47'	53°32'	250	Cw	Assis 1991
LO	PE Mata Godoy, Londrina - PR	Submontane semideciduous forest	23°27'	51°15'	700	Cw	Soares-Silva & Barroso 1992
IR	FN Irati, Teixeira Soares - PR	Montane mixed rainforest	25°26'	50°24'	870	Cf	Galvão et al. 1989

RESULTS AND DISCUSSION

Space does not allow the reproduction here of the full species list for the 30 forest areas, but we can provide copies to those who are interested. A list of the 456 species and 86 families recorded in the six semideciduous forests of the upper Rio Grande region, together with their growth forms and estimates of abundance, is given in the Appendix. The results of the soil analyses are represented by their standard deviation and total range in the diagrams of Fig. 2. Table 2 summarizes some average and total figures for each sampled community, while the formal comparisons of the surveyed forest areas for their floristic composition and community structure are given by the dissimilarity matrix in Table 3. The two-way table arranged by TWINSPAN for the 87 most important species (CVI > 2) in the five areas for which quantitative data are available is given in Table 4. The results of the multivariate analyses are given by the ordination diagram and the classification dendrograms of Figs 3 and 4, respectively. Table 5 lists the indicator species given by TWINSPAN for the groups of montane forest areas.

The soils of the Forest Reserve of the ESAL (LV) are particularly clayey, have a low pH, high levels of exchangeable aluminium (alic) and are very poor in mineral nutrients in general, although they are richer in organic matter than the other soils examined (Fig. 2). As the topography is very even (slopes less than 10°), no soil catena is observed and the soil properties are relatively homogeneous throughout the Reserve. The most important (hereafter expressed by CVI) species of this forest are *Copaifera langsdorffii*, *Ocotea odorifera*, *Sclerolobium rugosum*, *Amaioua guianensis* and *Tapirira obtusa* (Table 4, pp. 366/7). The forest is relatively open, as demonstrated by the low values of total density and basal area (Table 2), with a few scattered tall emergents (up to 20m in height) and a lower layer of smaller trees (heights between 10 and 15m). This forest presented the lowest diversity index values, despite the survey having by far the highest number of registered individuals (Table 2). The low diversity is probably correlated with the homogeneity of the site, which affects diversity mostly by its 'within habitat' (or alpha) component (Kershaw & Looney, 1985). However, soil nutrient shortage in tropical forests can cause strong ecological dominance by fewer species which in turn reduces species diversity (Tilman, 1982, 1986).

The soils surveyed in the forest of the Biological Reserve of Poço Bonito (PB) are also among the poorest in mineral nutrients, together with LV and TD, and are very sandy, as in TD (Fig. 2). However, they are even more acidic and alic than LV and TD, besides containing the highest amounts of exchangeable P among all the soils studied. The topography is steep, with slopes

TABLE 2. Total and average figures for the vegetation of the five areas of montane semideciduous forest studied. A, total sampled area (ha); N, number of individuals; TAD, total absolute density (individuals/ha); TADo, total absolute dominance (m/ha); H, average height (m); D, average diameter (cm); S, number of species; H', Shannon–Wiener diversity index; J', Pielou evenness index.

Study area		A	N	TAD	TADo	H	D	S	H'	J'
LV	Lavras/ESAL	5.04	10259	2035.5	20.03	–	11.2	136	3.605	0.734
PB	Lavras/Poço Bonito	0.48	1045	2177.1	39.04	8.8	12.1	119	4.204	0.880
BS	Bom Sucesso	0.54	1615	2990.7	47.61	8.6	11.3	157	4.331	0.857
IT	Itutinga	0.94	3169	3353.4	40.09	8.3	10.4	176	3.896	0.753
MD	Madre de Deus	0.60	1952	1221.9	30.81	10.1	14.3	118	3.764	0.789

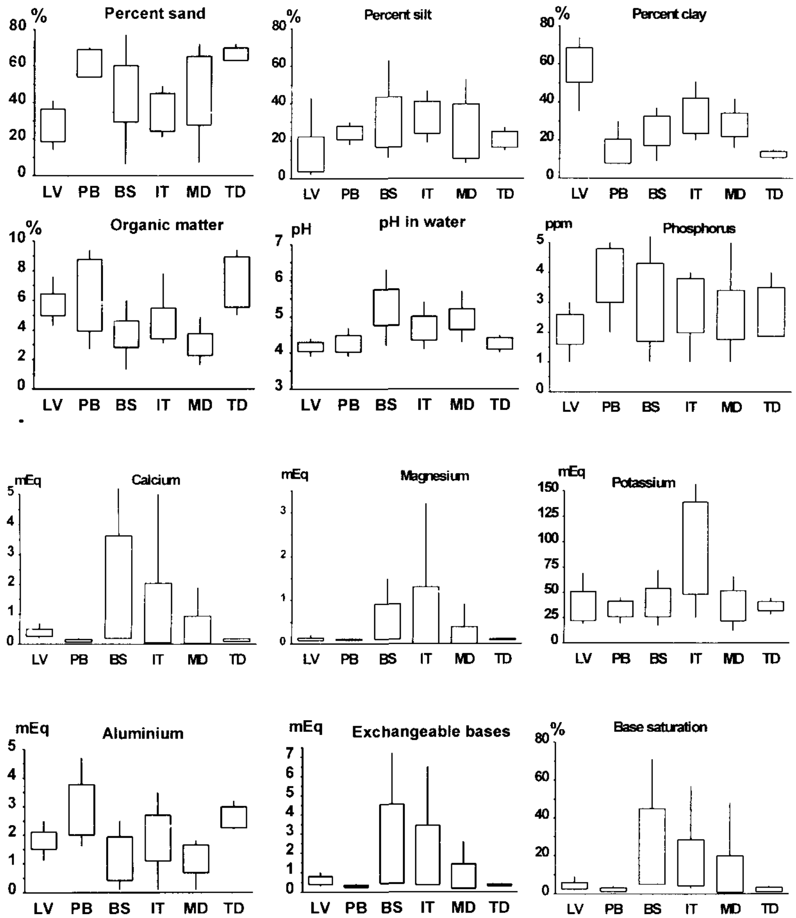

FIG. 2. Textural and chemical properties of the upper soil layer (0–20cm) of the six areas of montane semideciduous forests of the upper Rio Grande region. Forest areas are identified by their two-letter codes in Table 1. The boxes represent the standard deviation while the vertical lines represent the observed range.

up to 40°, and the sample area also includes an erosion gully and the channel of a stream with its narrow neighbouring strip of riverine forest and alluvial soils. These features strongly influence the amount of organic matter, which is lower in the gully and beside the stream. The most important species are *Sclerolobium rugosum*, *Siphoneugena densiflora*, *Tapirira obtusa*, *Alchornea triplinervea* and *Miconia chartacea* (Table 4, pp. 366/7). The physiognomy is of a very tall forest (up to 25m), although the values of total density and basal area are intermediate (Table 2). The high and broad crowns which form the forest canopy are mostly of *Sclerolobium rugosum*. The species diversity indices for the PB forest are among the highest (together with those for BS). This fact can probably be explained by two factors. On the one hand there are the steep slopes, the gully and the stream which produce a great amount of environmental heterogeneity in a relatively small area. This probably results in a strong 'between habitat' (or beta) component for diversity (Kershaw & Looney, 1985), which is typical of headwaters riverine forests (Oliveira-Filho et al., 1990). On the other hand, the proportion of light-demanding species (e.g. *Tapirira obtusa*, *Alchornea triplinervea*, *Croton celtidifolius* and *Croton floribundus*) is very high among the most important species, indicating a considerable degree of natural disturbance which could increase species diversity (Connell, 1971; Grubb, 1977; Ashton, 1990; Oldeman, 1990).

The soils of the Bom Sucesso forest (BS) presented the highest average levels of overall mineral nutrients (especially Ca and Mg), besides being less alic and acidic, having an intermediate texture and containing lower amounts of organic matter (Fig. 2). Nevertheless, most parameters show a wide variation within the sampled area, probably caused either by the uneven topography, which is characterized by several erosion gullies (slopes up to 35°) with their two types of soil (at ridges and bottoms), or by the sampling method which used three separate blocks of plots. The most important species of this forest are *Copaifera langsdorffii*, *Cupania vernalis*, *Actinostemon communis*, *Tapirira obtusa* and *Calycorectes acutatus* (Table 4, pp. 366/7). The physiognomy is very homogeneous and the forest is very dense as expressed by its total density and basal area values (Table 2). The top canopy layer normally lies between 18 and 22m in height. The species diversity indices are among the highest (together with those for PB) and this can be explained partially, as mentioned above for PB, by the great environmental heterogeneity, here caused mainly by the uneven topography and varying soil properties. However, species diversity in tropical forest can also be influenced by soils, those with intermediate fertility (as in BS) corresponding to highest diversity (Tilman, 1982, 1986; Ashton, 1990).

The soils surveyed in the forest of Itutinga (IT) are also among the richest in overall mineral nutrients, and are quite similar in several properties to the soils of BS (Fig. 2). Compared with the soils of BS, those of IT are somewhat more acidic and alic but poorer in Ca and present lower variances for most parameters. However, the most remarkable difference is in the high values of exchangeable K they contain when compared with the other areas. The topography is dominated by smooth convex slopes (10° to 30°), and most soil and plant community variations are caused by the soil catena from the stream to the upper interfluve. The most important species of this forest are *Copaifera langsdorffii*, *Tapirira guianensis*, *Protium almecega*, *Dendropanax cuneatum*, *Myrcia venulosa* and *Protium widgrenii* (Table 4, pp. 366/7). The physiognomy is characterized by smaller trees (top canopy layer between 15 and 20m in height) at higher density, as expressed by the lowest values of average height and diameter and by the highest value of total density of all forests surveyed (Table 2). The diversity indices are lower than BS and PB and higher than LV and this can probably be explained by the range of variation in topographic features and soil fertility, which is also intermediate between these latter areas.

The soils of the Madre de Deus de Minas forest (MD) are quite heterogeneous in various properties, since the seasonal floods and the sedimentation in the point bar sector cause the local soils to be finer textured, richer in P, Ca and Mg, and poorer in K than the upland forest soils. Nevertheless, in general, the soils of MD are less fertile than BS and IT and more fertile than LV, PB and TD (Fig. 2). The topography is quite even and the slopes gentle in the upland forest (less than 12°), while the point bar presents the typical outer levée and internal depression forms. Almost all trees occurring in the point bar forest are of two species, *Inga affinis* and *Salix humboldtiana*, that grow in separate clumps surrounded by the flood-tolerant grass *Paspalum plenum* Chase. The most important species in the upland forest are *Xylopia brasiliensis*, *Myrcia multiflora*, *Cryptocarya aschersoniana*, *Trichilia emarginata*, *Calyptranthes clusiaefolia* and *Copaifera langsdorffii*. There is also a massive belt of the understorey bamboo *Merostachys neesii* in this sector. The physiognomy of the forest is characterized by the dominance of very tall trees (of up to 35m in height) as expressed by the highest values of average height and diameter and by the lowest value of total density among all forests (Table 2). The latter is partially explained by the occupation of the understorey by grasses in the point bar forest, and by bamboos in the upland forest. This also explains, to a great extent, the relatively low figures for species diversity.

The soils surveyed at Tiradentes (TD) showed a great similarity in most properties with those of PB, except for their lower levels of P and lower variance in general (Fig. 2). These soils were certainly the most infertile of all the surveyed areas, and in many places they are very shallow, as shown by the common rocky outcrops. The topography is very steep, with slopes normally 25°, and the streams that flow down the foothills are turbulent and cascading. Although precise quantitative data are lacking for this area, field notes indicate *Copaifera langsdorffii*, *Myrcia venulosa*, *Myrsine umbellata*, *Ocotea corymbosa*, *Machaerium villosum* and *Miconia pepericarpa* as the most abundant species. We registered 227 species for this area, the highest total number recorded in the study, showing that this forest shelters a high level of biodiversity of trees and shrubs.

The floristic paired comparisons of the six forest areas with the Sørensen Coefficient of Community (CC) (Table 3) show little variation for the values, which ranged mostly between 38.4 and 45.9. Only a lower value of 32.8 was found between IT and TD, and a higher one of 48.2 between PB and IT. However, PB is not as dissimilar to TD as would be expected from these figures. In fact, most areas share a considerable number of species: from the total of 456, 54 (11.8%) were present in all six areas, 101 (22.1%) were found in five or more areas, and 160 (35.1%) were found in four or more areas. The numbers of exclusive species in the lists of each area were also comparatively low: LV = 4 (2.2%), PB = 24 (10.9%), BS = 14 (5.8%), IT = 22 (8.6%), MD = 12 (6.2%), and TD = 25 (9.0%). All the above results certainly indicate that the six forest areas have very close levels of similarity in floristic composition. Two facts

TABLE 3. Dissimilarity indices for the areas of semideciduous forest surveyed. In the case of Tiradentes (TD), only coefficients of community were calculated.

Sørensen Coefficient of Community (CC)		Squared Average Euclidean Distance (*I*) LV	PB	BS	IT	MD
LV	Lavras/ESAL	–	18.44	15.23	24.01	28.72
PB	Lavras/Poço Bonito	43.92	–	17.70	34.20	28.62
BS	Bom Sucesso	40.71	44.35	–	14.29	23.58
IT	Itutinga	45.91	48.21	38.43	–	41.17
MD	Madre de Deus	43.09	42.09	39.49	45.09	–
TD	Tiradentes	40.13	40.73	39.00	32.08	44.99

TABLE 4. Two-way table with the five forest areas and 87 tree species ordered and classified by TWINSPAN. Values are the cover value indices (CVI) for the 87 species which presented CVI > 2.0 in at least one of the areas. Forest areas are identified by their two-letter codes in Table 1. Small letters represent the hierarchical divisions of forest areas and species by TWINSPAN (cut levels for pseudospecies: 0, 0.1, 0.2, 0.3, 0.4; weights: 1, 4, 8, 12, 16, respectively).

	Forest areas and groups					
	IT	BS	LV	PB	MD	Species
Species	aa	aa	ab	ab	b	groups
Sclerolobium rugosum	–	0.33	10.23	21.72	–	aaa
Miconia hispida	–	–	2.88	3.18	–	aaa
Miconia chartacea	–	0.07	2.41	8.04	–	aaa
Siphoneugena densiflora	–	–	0.35	12.32	–	aaa
Eremanthus incanus	–	–	–	2.51	–	aaa
Croton celtidifolius	–	–	–	4.72	–	aaa
Ocotea aciphylla	–	–	–	6.68	–	aaa
Cyathea delgadii	2.35	0.21	–	4.68	–	aaa
Psychotria sessilis	0.04	0.21	–	2.80	–	aaa
Byrsonima laxiflora	–	0.44	0.50	2.94	–	aaa
Ocotea laxa	–	3.25	0.70	–	–	aaa
Metrodorea stipularis	–	2.79	0.19	–	–	aaa
Luehea divaricata	–	2.40	–	–	–	aaa
Bauhinia longifolia	–	2.22	–	–	–	aaa
Gomidesia affinis	0.04	2.59	–	0.36	–	aaa
Acacia glomerosa	–	2.15	–	–	–	aaa
Trichilia pallens	–	3.87	–	–	–	aaa
Machaerium stipitatum	–	4.65	–	–	–	aaa
Rollinia laurifolia	1.57	1.54	4.10	–	–	aab
Maprounea guianensis	–	–	5.04	–	–	aab
Miconia pepericarpa	–	–	6.38	–	–	aab
Bowdichia virgilioides	0.16	–	2.25	–	–	aab
Myrcia rostrata	0.04	–	9.53	0.25	–	aab
Persea pyrifolia	0.55	0.81	8.01	0.62	–	aab
Siphoneugena widgreniana	0.36	0.37	3.08	–	–	aab
Lamanonia ternata	0.04	1.48	3.04	–	–	aab
Nectandra grandiflora	0.09	–	–	2.12	–	aab
Gomidesia eriocalyx	0.13	–	–	2.28	–	aab
Trichilia pallida	0.31	2.25	0.02	–	–	aab
Matayba juglandifolia	0.78	2.53	–	–	–	aab
Guazuma ulmifolia	0.41	2.38	0.06	0.66	–	aab
Copaifera langsdorffii	39.02	19.52	25.41	5.47	5.92	aab
Protium widgrenii	6.47	1.95	3.13	–	–	aab
Lithraea molleoides	2.58	0.44	–	–	–	aab
Myrcia venulosa	8.27	0.09	0.26	–	–	aab
Nectandra nitidula	2.44	0.13	–	–	–	aab
Blechnum brasiliense	3.83	–	–	–	–	aab
Diospyros hispida	2.74	–	–	–	–	aab
Luehea rufescens	3.05	–	–	–	–	aab
Ocotea corymbosa	0.19	1.66	6.93	2.37	4.86	aba
Amaioua guianensis	0.24	0.72	10.07	2.05	2.97	aba
Ocotea odorifera	0.06	0.35	13.43	3.70	3.82	aba
Myrsine umbellata	0.86	1.72	0.02	3.00	0.11	aba

TABLE 4. (Contd)

Species	IT aa	BS aa	LV ab	PB ab	MD b	Species groups
Tapirira obtusa	6.23	6.58	9.78	11.30	0.38	aba
Nectandra oppositifolia	0.05	2.41	0.21	0.73	0.22	aba
Machaerium nictitans	1.96	5.98	1.68	0.91	2.73	aba
Ocotea pulchella	3.37	0.29	0.64	0.80	0.42	aba
Tapirira guianensis	19.19	1.50	0.17	–	1.14	aba
Protium almecega	17.11	5.74	–	3.82	2.42	aba
Casearia sylvestris	3.24	0.34	0.06	0.11	0.45	aba
Ixora warmingii	0.62	3.00	3.14	0.83	3.63	aba
Calyptranthes clusiaefolia	0.24	0.12	2.01	5.18	6.39	aba
Geonoma schottiana	4.44	2.14	0.09	0.35	4.87	aba
Salacia elliptica	–	0.54	0.02	2.11	0.60	abb
Siparuna guianensis	1.10	0.60	4.30	–	2.95	abb
Cordia sellowiana	0.25	–	2.50	1.56	1.51	abb
Styrax pohlii	–	1.55	2.07	0.12	0.17	abb
Hymenaea courbaril	0.14	1.87	2.70	–	1.63	abb
Pera obovata	1.08	–	1.09	3.68	3.45	abb
Actinostemon communis	2.25	6.78	–	1.86	6.51	abb
Calophyllum brasiliense	1.53	4.82	–	0.83	1.72	abb
Machaerium villosum	1.78	5.86	0.50	–	3.18	abb
Cabralea canjerana	0.15	3.40	–	1.70	0.20	abb
Dendropanax cuneatum	8.52	5.62	0.02	–	0.07	abb
Machaerium aculeatum	2.91	1.10	0.06	–	0.34	abb
Trichilia emarginata	–	1.40	1.94	2.75	8.67	abb
Platycyamus regnellii	0.12	0.63	0.15	–	2.51	abb
Pithecellobium incuriale	–	–	0.07	–	2.14	baa
Miconia pusilliflora	–	–	0.07	–	3.04	baa
Connarus regnellii	–	3.85	0.11	–	0.63	bab
Cupania vernalis	2.61	6.22	–	–	0.11	bab
Calycorectes acutatus	–	5.75	0.02	–	1.16	bab
Andira anthelmia	2.35	1.25	–	–	0.27	bab
Myrcia multiflora	0.41	0.21	–	–	11.38	bab
Prunus sellowii	0.08	1.02	–	–	2.04	bab
Salix humboldtiana	–	–	–	–	9.16	bab
Inga affinis	0.59	0.37	0.92	0.14	28.71	bab
Miconia argyrophylla	–	–	8.40	3.41	0.11	bba
Casearia arborea	–	–	9.40	0.68	1.36	bba
Alchornea triplinervea	–	–	0.11	7.83	4.40	bba
Protium heptaphyllum	0.31	–	–	2.62	0.14	bba
Mollinedia argyrogyna	0.12	–	–	2.07	0.58	bba
Cryptocarya aschersoniana	0.04	0.97	6.73	1.43	10.13	bba
Xylopia brasiliensis	0.20	0.30	6.43	1.72	16.36	bba
Miconia cinnamomifolia	–	–	–	4.98	0.29	bbb
Matayba elaeagnoides	–	–	–	2.03	0.41	bbb
Eugenia myrtifolia	–	–	–	0.20	2.29	bbb

can probably explain this:

(1) The six forests occur in the same catchment basin (upper Rio Grande), within the same mountain system (Serra da Mantiqueira) and in an altitudinal range of 800 to 1200m, so that they are classified in the same physiognomic type: the montane semideciduous tropical forest (Veloso et al., 1991).

(2) A great level of environmental heterogeneity was sampled in all areas except LV, related mainly to varying topographic features and corresponding variations in ground-water regimes and soil types or catenas. The internal heterogeneity of each particular area is probably increasing the species diversity of each area via its beta component so that this, paradoxically, overshadows to a certain extent the floristic differences among the forest areas caused by the gamma (or inter-regional) component of diversity.

Differences among five of the forest areas are clearer in terms of community structure, i.e., considering the relative importance of the species in sample plots. The comparisons by Squared Average Euclidean Distance (*I*) show a wider range of values if compared with the CC values (Table 3). The greatest distance was found between MD and IT (41.2) and the least between IT and BS (14.3). The hierarchical classification of the five areas by TWINSPAN (Table 4) indicated that MD was the most dissimilar in terms of community structure, as it splits off at the highest division level while IT/BS and PB/LV only split up at the following level.

The tract of seasonally flooded forest in MD is unique among all five areas and this probably explains why this area was differentiated at the first level. Gallery forests of Central Brazil are known to be strongly influenced by differences in ground-water regime, and their floristic composition and community structure markedly change from well-drained to moist and swampy sites (Ratter, 1980; Oliveira-Filho et al., 1990). This same variation certainly exists in the studied areas since three of them included streams (PB, IT and TD) and two other occurred at the margins of the Rio Grande (BS and MD). Therefore, differences between riparian and upland forests occurred within those areas and could not be detected in a comparison between areas. Nevertheless, the influence of water on the structure of forest tree communities seems to be even greater in the case of seasonal floods as long as forests under these conditions are frequently composed of a particular set of species. As shown in Table 4, the abundance of *Salix humboldtiana* and *Inga affinis*, the two species that prevail in the seasonally flooded levée, played an important role in discriminating MD.

The second division level actually distinguished the two forests of the more fertile soils, BS and IT, from those of more infertile soils (LV and PB). The influence of soil fertility on floristic composition of seasonal forests has already been identified for fringing Amazonian forests by Ratter et al. (1973). Further studies in Central Brazil indicated that a group of species were reliable indicators of mesotrophic soils, both for forest (deciduous or semideciduous) and cerradão (tree savanna) vegetation (Ratter et al., 1977, 1978; Furley & Ratter, 1988; Furley et al., 1988). Although some of these indicator species, such as *Chorisia speciosa*, *Guazuma ulmifolia*, *Maclura tinctoria*, *Cedrella fissilis*, *Tabebuia impetiginosa* and *Pseudobombax tomentosum*, did occur in some of the studied areas, they were only found in low density, even in BS and IT, which were the areas with the more fertile soils.

The scarcity of mesotrophic soil indicator species among the most abundant species in those two forests could be partially explained by the heterogeneity of their soils, which included patches of dystrophic soils along with the predominant mesotrophic soils. Additionally, even these latter lie within the lower section of the mesotrophic soils range. The base saturation was 10–45% in BS and 10–30% in IT, while typical figures for mesotrophic soils in Central Brazil lie between 50 and 85% (e.g. Furley et al., 1988). Nevertheless, mesotrophic soils in the upper Rio Grande region are certainly also identified by indicator species. A forest area that we visited in the municipality of Itumirim (and which we ignored because of evidence of disturbance) had an average soil base saturation of 55%, while the dominant species were *Chorisia speciosa, Maclura tinctoria*, *Cariniana estrellensis*, *Colubrina glandulosa* and *Lithraea molleoides*, all of which, except for *C. estrellensis* (which is a species of a more southern distribution), have been reported as indicators of mesotrophic soils of Central Brazil (Ratter et al., 1973, 1977, 1978 and pers. comm.; Furley & Ratter, 1988; Furley et al., 1988).

The multivariate analyses performed with the floristic information from the 30 forest areas showed a great deal of coincidence in the arising patterns since the classification categories (modified IBGE) applied to the forest types appear as cohesive groups in most cases (Figs 3 and 4). The ordination by DCA shows different patterns in each of the first two axes (Fig. 3). The first axis is apparently related to a coast-interior component because it separates to the right the four lowland and submontane atlantic rainforests from the remaining areas. Although they appear in the same diagram field those four areas are comparatively distant from one another,

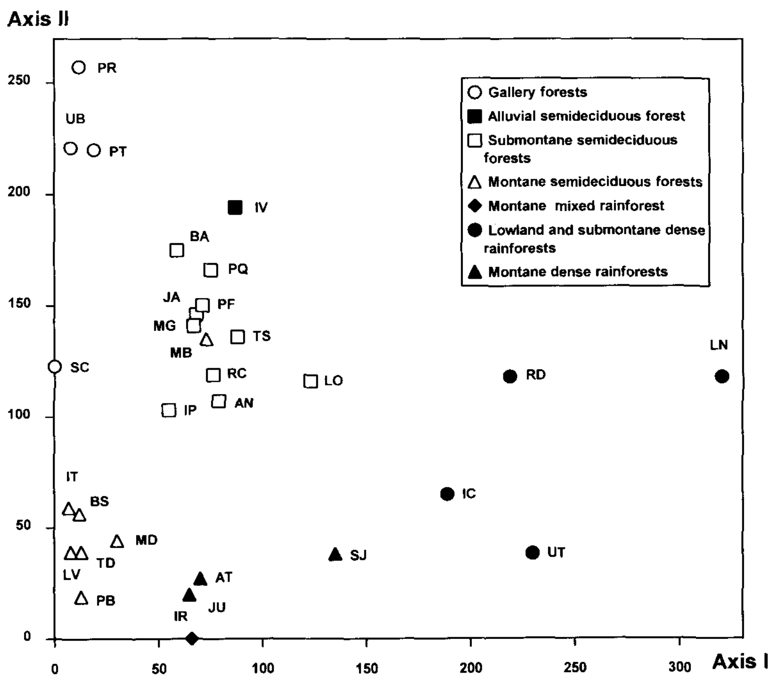

FIG. 3. Ordination of the 30 forest areas in the first two DCA axes. Forest areas are identified by their two-letter codes in Table 1 and classified according to the modified IBGE system (see text). First four eigenvalues: 0.39; 0.25; 0.14; 0.11.

probably reflecting the high level of floristic heterogeneity of the atlantic rainforests. The second ordination axis seems to identify a gradient related to altitude and interiority since the montane forests (of the three types) all appear on the bottom while the gallery forests appear on the top and the submontane forests in between. Montane rainforests and the montane mixed rainforest appear on the bottom at an intermediate position, as a kind of link to the atlantic coastal rainforests. Only two areas show some disparity: SC, the southernmost gallery forest, and MB, the most interior of the montane forests.

The distinctness and heterogeneity of the atlantic rainforests are also reflected in the UPGMA clustering dendrogram (Fig. 4A) and TWINSPAN cladogram (Fig. 4B). Both separated at a high level the two northern areas, LN and RD, from the two southern ones, UT and IC. Montane, submontane and gallery forests are also clearly discriminated by both methods. UPGMA, in particular, was able to detect the distinctness of the montane mixed rainforest and the alluvial semideciduous forest. The dubious position of SC is reproduced here since the two methods grouped it in a different manner. In spite of its high altitude and the presence of *Araucaria*

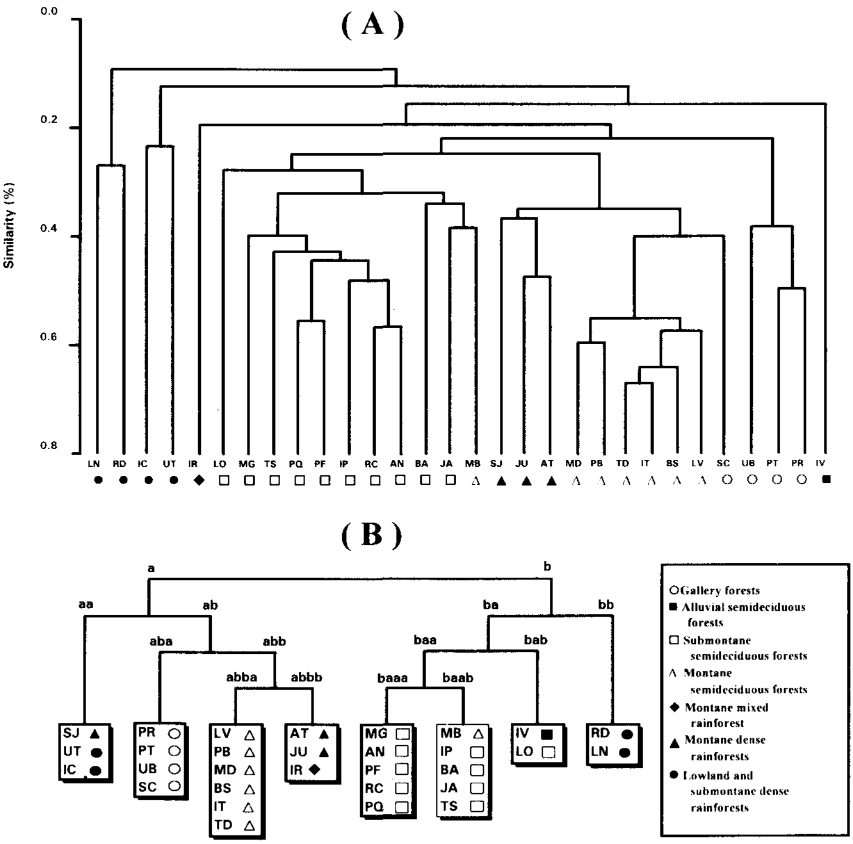

FIG. 4. Hierarchical classification of the 30 forest areas. (A) Similarity dendrogram yielded by UPGMA using Sørensen Coefficients of Community. (B) Cladogram yielded by TWINSPAN showing the groups after four levels of division. Forest areas are identified by their two-letter codes in Table 1 and classified according to the modified IBGE system (see text).

TABLE 5. Preferential species indicated by TWINSPAN for the montane forests of southeastern Brazil. Montane forests in general (rainforests, mixed rainforests and semideciduous forests) and montane semideciduous forests (upper Rio Grande region) correspond to the groups 'abb' and 'abba', respectively, in TWINSPAN's cladogram (Fig. 4). Species are ordered by descending frequency in the groups.

Montane forests in general ($n = 9$)	freq.	Semideciduous montane forests ($n = 6$)	freq.
Lamanonia ternata	9	*Xylopia brasiliensis*	6
Casearia decandra	9	*Bowdichia virgilioides*	6
Lithraea molleoides	9	*Sorocea bonplandii*	6
Cedrella fissilis	9	*Qualea multiflora*	6
Ocotea corymbosa	9	*Inga affinis*	6
Vernonia discolor	8	*Ocotea odorifera*	6
Geonoma schottiana	8	*Myrcia velutina*	6
Actinostemon communis	8	*Ixora warmingii*	6
Gomidesia affinis	8	*Faramea cyanea*	6
Croton floribundus	8	*Guazuma ulmifolia*	6
Ocotea pulchella	8	*Siparuna guianensis*	6
Alchornea triplinervea	8	*Tapirira guianensis*	6
Cryptocarya aschersoniana	8	*Terminalia glabrescens*	6
Myrsine coriacea	8	*Machaerium villosum*	6
Tapirira obtusa	8	*Annona cacans*	6
Machaerium nictitans	8	*Calyptranthes clusiaefolia*	6
Nectandra oppositifolia	8	*Machaerium aculeatum*	6
Guatteria nigrescens	8	*Guarea guidonia*	6
Sloanea monosperma	7	*Platypodium elegans*	6
Casearia lasiophylla	7	*Calycorectes acutatus*	5
Piper aduncum	7	*Protium almecega*	5
Rollinia sylvatica	7	*Calophyllum brasiliense*	5
Styrax pohlii	7	*Gomidesia eriocalyx*	5
Machaerium stipitatum	7	*Croton urucurana*	5
Miconia cinnamomifolia	7	*Miconia chartacea*	5
Clethra scabra	7	*Miconia pepericarpa*	5
Dendropanax cuneatum	7	*Myrcia tomentosa*	5
Luehea grandiflora	7	*Alibertia macrophylla*	5
Schinus terebinthifolius	7	*Rheedia gardneriana*	5
Cordia sellowiana	7	*Alchornea glandulosa*	5
Persea pyrifolia	7	*Platycyamus regnellii*	5
Vitex polygama	7	*Galipea multiflora*	5
Cyatea delgadii	7	*Rollinia sericea*	5
Arecastrum romanzoffianum	6	*Maytenus glazioviana*	5
Protium widgrenii	6	*Hieronyma ferruginea*	5
Vismia brasiliensis	6	*Andira anthelmia*	5
Salacia elliptica	6	*Hedyosmum brasilense*	4
Connarus regnellii	6	*Casearia arborea*	4
Ocotea diospyrifolia	6	*Miconia argyrophylla*	4
Piptocarpha axillaris	6	*Tibouchina stenocarpa*	4
Jacaranda macrantha	6	*Myrcia multiflora*	4
Casearia obliqua	6	*Siphoneugena widgreniana*	4
Pithecellobium incuriale	6	*Sclerolobium rugosum*	4
Eugenia involucrata	6	*Byrsonima laxiflora*	4
Hirtella hebeclada	6	*Trichilia emarginata*	4
Eugenia myrtifolia	6	*Ficus mexiae*	4
Pimenta pseudocaryophyllus	6	*Schefflera calva*	4
Daphnopsis fasciculata	6	*Trichilia pallida*	4
Myrcia venulosa	6	*Euplassa incana*	4
Lacistema hasslerianum	6	*Blepharocalyx salicifolius*	4

angustifolia, MB once again appeared along with the submontane semideciduous forests. One of the montane rainforests, SJ, was grouped with the lowland atlantic rainforests by TWINSPAN.

Despite the few disparities, all methods showed that altitude plays an important role in the floristic differentiation of the forests of southeastern Brazil. For the state of São Paulo, Torres et al. (1994) have already demonstrated that the altitudinal range is the most important factor determining floristic patterns for semideciduous forests. The forests of the upper Rio Grande region have certainly their strongest floristic links with the montane rainforests. In fact, all those forests are sheltered in the same mountain system that extends in parallel to the ocean in southeastern Brazil. The montane rainforests are essentially on the oceanic and rainy face of the mountain system while the montane semideciduous forests occur under the more seasonal climate of the continental face. In both cases, low temperatures can eventually bring frosts during the winter and this factor is certainly important in differentiating the montane forests' flora. Meira Neto et al. (1989) produced a list of 41 species of shrubs and trees that can be considered as indicator species of forests of high altitude (> 1000m) in southeastern Brazil, all of which are also present in the forests of the upper Rio Grande region. Table 5 lists the species given by TWINSPAN as the indicator species of groups 'abb' and 'abba' in Fig. 4 that bring together, respectively, the montane forests in general and the semideciduous montane forests (upper Rio Grande region) in particular.

Besides their montane component, the forests of the upper Rio Grande region also have secondary but nevertheless important floristic links with the gallery forests, that extend to the northwest into the cerrado domain, and with the submontane forests, that extend to the southwest, on the Rio Paraná basin. The environmental factor common to these forests is the seasonal climate, marked by a more or less dry winter, especially in the cerrado region. In the latter case, the watercourses are actual channels through which the forest physiognomies permeate the cerrado domain.

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APPENDIX

Species recorded in the study areas: LV, Lavras/ESAL; PB, Lavras/Poço Bonito; BS, Bom Sucesso; IT, Itutinga; MD, Madre de Deus de Minas; TD, Tiradentes.

Abundance estimates for the species in each area[1]: a, abundant; c, common; f, frequent; o, occasional; r, rare; +, present.

Growth forms: tt, tall tree (> 10m); st, small tree (3–10m); sh, shrub (< 3m); pl, palm; ar, ground aroid; bb, bamboo; af, arborescent fern.

	Growth form	Study areas LV	PB	BS	IT	MD	TD
ANACARDIACEAE							
Astronium graveolens Jacquin	tt	r	–	–	–	–	–
Lithraea molleoides (Vell.) Engler	st	+	+	r	f	+	o
Schinus terebinthifolius Raddi	st	r	–	+	r	–	r
Tapirira guianensis Aublet	tt	r	+	o	a	o	f
T. obtusa (Benth.) Mitchell	tt	c	a	c	c	r	c
ANNONACEAE							
Annona cacans Warm.	tt	r	r	+	+	o	o
Duguetia lanceolata A.St.-Hil.	st	r	o	r	–	–	–
Guatteria nigrescens Mart.	st	r	+	r	f	r	o
G. villosissima A.St.-Hil.	st	–	–	–	–	–	+
Rollinia dolabripetala (Raddi) R.E.Fries	st	–	–	+	–	–	–
R. emarginata Schltdl.	tt	–	–	–	r	–	–
R. laurifolia Schltdl.	tt	f	–	o	o	–	o
R. mucosa (Jacquin) Baillon	st	–	–	–	r	–	–
R. sericea R. E. Fr.	tt	+	–	+	–	r	f
R. sylvatica Mart.	tt	r	–	o	r	r	+
Xylopia brasiliensis Sprengel	tt	c	o	r	r	a	r
X. emarginata Mart.	tt	–	+	–	–	–	–
X. sericea A.St.-Hil.	tt	+	–	–	+	+	r
APOCYNACEAE							
Aspidosperma cylindrocarpon Müll.Arg.	tt	–	–	r	r	–	+
A. parvifolium A.DC.	tt	–	–	r	–	o	+
A. polyneuron Müll.Arg.	tt	–	–	–	–	r	o
A. ramiflorum Müll.Arg.	tt	–	–	r	–	–	r
A. spruceanum Benth.	tt	+	–	+	–	r	–
Rauvolfia sellowii Müll.Arg.	st	–	+	+	+	+	+
AQUIFOLIACEAE							
Ilex cerasifolia Reisseck	st	r	–	–	–	+	o
I. conocarpa Reisseck	tt	–	r	–	r	–	r
I. dumosa Reisseck	st	–	–	–	–	–	r
ARACEAE							
Philodendron brasiliense Engler	ar	–	–	–	r	–	–
ARALIACEAE							
Dendropanax cuneatum (DC.) Decne & Planchon	tt	r	+	c	c	r	f
Schefflera angustissima (Marchand) D.Frodin	tt	r	–	–	–	–	r
S. calva (Cham.) D.Frodin	tt	–	o	r	r	r	–
S. macrocarpa (Cham. & Schltdl.) D.Frodin	st	–	–	–	+	–	–
ARAUCARIACEAE							
Araucaria angustifolia (Bert.) O.Kuntze	tt	–	+	–	–	–	–

	Growth form	LV	PB	BS	IT	MD	TD
ARECACEAE							
Acrocomia aculeata (Jacquin) Lodd.	pl	–	–	+	–	–	–
Arecastrum romanzoffianum (Cham.) Becc.	pl	–	–	r	r	r	o
Geonoma brevispatha Barb. Rodr.	pl	–	–	–	+	r	–
G. schottiana Mart.	pl	r	r	f	f	f	f
Syagrus flexuosa (Mart.) Becc.	pl	–	–	–	r	–	–
S. oleracea (Mart.) Becc.	pl	–	–	+	–	–	r
ASTERACEAE							
Baccharis dentata (Vell.) G.M.Barroso	sh	–	–	–	r	–	r
Dasyphyllum brasiliense (Spr.) Cabrera	st	–	+	+	+	–	+
Eremanthus incanus Less.	st	–	f	–	+	–	o
Gochnatia polymorpha (Less.) Cabrera	st	–	–	–	+	–	+
Piptocarpha axillaris (Less.) Baker	tt	–	+	–	+	–	+
P. macropoda Baker	tt	o	–	–	+	–	r
P. rotundifolia (Less.) Baker	sh	+	–	–	–	–	+
Vanillosmopsis erythropappa Schultz	st	–	r	–	+	–	o
Vernonia diffusa Less.	st	+	–	–	r	–	o
V. discolor Less.	st	r	+	+	r	+	r
BIGNONIACEAE							
Cybistax antisyphillitica Mart.	st	r	–	r	–	–	–
Jacaranda macrantha Cham.	tt	r	r	r	–	r	+
Sparattosperma leucanthum (Vell) K.Schum.	st	–	–	–	+	–	r
Tabebuia alba (Cham.) Sandw.	tt	–	–	–	–	–	r
T. chrysotricha (Mart.) Standl.	tt	–	+	–	r	–	–
T. impetiginosa (Mart.) Standl.	tt	–	–	+	+	–	–
T. ochracea (Cham.) Rizz.	st	+	+	–	r	–	o
T. roseo-alba (Ridl.) Sandw.	tt	–	–	–	–	–	+
T. serratifolia (Vahl) Nichols	tt	r	–	r	r	+	+
T. umbellata (Sond.) Sandw.	tt	–	–	–	r	–	–
T. vellosoi Toledo	tt	–	+	+	–	r	–
Zeyheria tuberculosa (Vell.) Bureau	tt	r	–	–	–	–	–
BLECHNACEAE							
Blechnum brasiliense Desv.	af	–	+	+	c	–	r
BOMBACACEAE							
Ceiba speciosa (A.St.-Hil.) Gibbs & Semir	tt	–	–	–	+	–	r
Eriotheca candolleana (K.Schum.) A.Robyns	tt	–	–	–	r	–	–
Pseudobombax grandiflorum (Cav.) A.Robyns	tt	–	–	–	–	r	–
P. longiflorum (Mart. & Zucc.) A.Robyns	st	–	–	–	+	–	+
P. tomentosum (A.St.-Hil.) A. Robyns	st	–	–	–	r	+	–
BORAGINACEAE							
Cordia ecalyculata Vell.	tt	–	r	–	–	r	–
C. rufescens A.DC.	st	–	r	–	r	–	+
C. sellowiana Cham.	tt	f	o	–	r	o	o
C. superba Cham.	st	+	–	–	r	–	+
C. trichotoma (Vell.) Arrab.	tt	r	–	–	+	–	–
BURSERACEAE							
Protium almecega Marchand	tt	–	f	c	a	f	f
P. brasiliense (Sprengel) Engler	st	–	–	–	–	–	r
P. heptaphyllum (Aublet) Marchand	tt	+	f	+	r	r	f
P. widgrenii Engler	tt	f	+	o	c	+	c

	Growth form	LV	PB	BS	IT	MD	TD
		Study areas					
CAESALPINIACEAE							
Bauhinia longifolia (Bongard) Stendel	st	+	–	f	–	–	–
Cassia ferruginea (Schrad.) Schrad.	tt	–	r	r	–	–	+
Copaifera langsdorffii Desf.	tt	a	c	a	a	c	a
Hymenaea courbaril L.	tt	f	–	o	r	o	o
Peltophorum dubium (Sprengel) Taub.	tt	–	–	+	r	–	–
Sclerolobium aureum (Tul.) Benth.	st	–	–	–	+	–	–
S. rugosum Mart. form. *plurijugum* Mell. Barr.	tt	a	a	r	–	–	f
Senna macranthera (Vell.) Irwin & Barneby	st	r	+	–	–	–	o
S. multijuga (L.C.Rich.) Irwin & Barneby	tt	+	–	+	+	–	–
CARICACEAE							
Jacaratia spinosa (Aublet) A.DC.	st	–	–	+	+	–	–
CECROPIACEAE							
Cecropia glaziovi Snethl.	tt	–	+	r	–	–	+
C. hololeuca Miq.	tt	–	+	–	–	+	+
C. pachystachya Trécul	tt	r	+	+	r	r	r
Coussapoa microcarpa (Schott) Rizz.	tt	–	–	–	–	r	–
CELASTRACEAE							
Austroplenckia populnea (Reisseck) Lundell	st	–	+	–	+	–	+
Maytenus aquifolium Mart.	st	–	–	–	r	–	r
M. glazioviana Loesen	tt	r	r	r	+	r	–
M. gonoclados Mart.	tt	–	–	–	r	–	+
M. salicifolia Reisseck	tt	–	r	–	+	r	–
CHLORANTHACEAE							
Hedyosmum brasiliense Mart.	tt	–	–	+	r	+	o
CHRYSOBALANACEAE							
Hirtella glandulosa Sprengel	tt	–	–	–	–	–	r
H. hebeclada Moric.	tt	r	–	+	r	r	–
Licania hoehnei Pilger	tt	–	–	–	–	–	r
CLETHRACEAE							
Clethra scabra Pers.	tt	r	+	–	r	+	o
CLUSIACEAE							
Calophyllum brasiliense Cambess.	tt	–	r	c	o	o	o
Clusia criuva Cambess.	st	–	–	–	r	–	+
Kielmeyera lathrophyton Saddi	tt	–	–	–	r	+	+
Rheedia gardneriana Planchon & Triana	tt	r	r	–	r	r	r
Tovomitopsis saldanhae Engler	tt	–	–	–	–	r	r
Vismia brasiliensis Choisy	st	r	f	r	r	r	o
COMBRETACEAE							
Terminalia glabrescens Mart.	tt	r	r	+	r	r	o
T. januariensis DC.	tt	–	r	–	–	–	–
CONNARACEAE							
Connarus regnellii Schelemberg	tt	r	–	f	–	r	o
CUNONIACEAE							
Lamanonia ternata Vell.	tt	f	+	r	r	+	o
CYATHEACEAE							
Cyathea delgadii Stemb.	af	–	f	r	f	+	f
Nephelea sternbergii (Sternb.) Tryon	af	–	r	–	+	–	r
Trichipteris corcovadensis (Raddi) Copel	af	–	+	–	–	–	–
T. phalerata (Mart.) Barr.	af	–	–	–	–	+	–

	Growth form	Study areas LV	PB	BS	IT	MD	TD
DICKSONIACEAE							
Dicksonia sellowiana (Presl.) Hook.	af	–	–	+	r	–	–
EBENACEAE							
Diospyros hispida A. DC.	tt	–	–	+	f	–	–
ELAEOCARPACEAE							
Sloanea monosperma Vell.	tt	r	r	o	–	r	o
ERYTHROXYLACEAE							
Erythroxylum campestre A.St.-Hil.	sh	r	+	r	r	+	+
E. citrifolium A.St.-Hil.	sh	r	–	–	+	–	r
E. cuneifolium (Mart.) Schulz.	sh	+	+	r	r	+	–
E. deciduum A.St.-Hil.	sh	–	–	+	–	–	–
EUPHORBIACEAE							
Acalypha brasiliensis Müll.Arg.	sh	–	+	+	+	–	–
Actinostemon communis (Müll.Arg.) Pax	st	+	o	c	f	c	o
A. concolor (Sprengel) Müll.Arg.	tt	–	–	r	–	–	–
Alchornea glandulosa Poepp. & Endl.	tt	–	+	r	+	r	o
A. triplinervea (Sprengel) Müll.Arg.	tt	r	c	+	–	f	f
Aparisthmium cordatum (Juss.) Baill.	tt	–	–	–	r	–	r
Croton celtidifolius Baillon	tt	–	f	–	–	+	–
C. echinocarpus Müll.Arg.	tt	–	–	–	r	–	r
C. floribundus Sprengel	tt	r	o	r	r	r	f
C. lobatus L.	h	–	–	–	+	–	–
C. urucurana Baillon	tt	–	+	+	r	r	r
Drypetes sessiliflora Fr.Allem.	tt	–	r	–	–	–	r
Hieronyma ferruginea Tul.	tt	–	r	r	r	+	o
Mabea fistulifera Mart.	st	–	–	+	–	–	+
Maprounea guianensis Aublet	st	c	–	–	–	+	–
Pera obovata Baillon	tt	o	f	+	r	o	f
Phyllanthus claussenii Müll.Arg.	sh	–	–	–	r	–	–
Sapium longifolium (Müll.Arg.) Huber	st	+	–	+	r	+	–
Sebastiania brasiliensis Sprengel	tt	–	–	+	r	–	–
S. edwalliana Pax & Hoffmg.	tt	–	–	–	r	–	–
S. schottiana (Müll.Arg.) Müll.Arg.	sh	–	–	+	–	r	–
S. serrata Müll.Arg.	tt	–	–	–	r	–	r
FABACEAE							
Acosmium dasycarpum (Vogel) Yakovlev	sh	–	+	–	+	+	+
A. subelegans (Vogel) Yakovlev	sh	–	–	+	+	–	r
Andira anthelmia (Vell.) Macbr.	st	–	+	o	f	r	o
Bowdichia virgilioides Kunth	tt	f	+	+	r	+	r
Dalbergia brasiliensis Vogel	tt	–	–	–	–	–	r
D. frutescens (Vell.) Britton	tt	–	r	–	–	–	–
D. miscolobium Benth.	st	–	–	–	+	–	+
D. nigra (Vell.) Fr.Allem.	tt	r	–	–	–	r	–
D. villosa (Benth.) Benth.	tt	–	r	r	–	r	o
Erythrina falcata Benth.	tt	–	–	r	–	+	–
Lonchocarpus guilleminianus (Tul.) Malme	tt	–	–	r	–	–	–
Machaerium aculeatum Raddi	tt	r	+	r	f	r	o
M. acutifolium Vogel	tt	–	–	–	–	r	–
M. brasiliensis Vogel	tt	r	o	–	–	–	–
M. condensatum Kuhlman & Hoehne	st	–	r	r	–	+	–
M. nictitans Benth.	tt	o	r	c	o	f	f

	Growth form	LV	PB	BS	IT	MD	TD
				Study areas			
FABACEAE (contd)							
M. scleroxylum Tul.	tt	–	–	–	–	–	r
M. stipitatum (DC.) Vogel	tt	+	–	f	+	–	r
M. villosum Vogel	tt	r	+	c	o	f	c
Myroxylon peruiferum L.f.	tt	r	r	r	–	–	–
Ormosia arborea (Vell.) Harms.	tt	–	r	+	–	–	–
O. fastigiata Tul.	tt	–	–	–	r	+	–
Platycyamus regnellii Benth.	tt	r	–	r	r	f	r
Platypodium elegans Vogel	tt	r	+	r	o	+	+
Sesbania sesban (L.) Merr.	sh	–	–	+	–	+	–
Zollernia ilicifolia (Brongn.) Vogel	tt	–	+	–	–	–	–
FLACOURTIACEAE							
Casearia arborea (L.C.Rich.) Urban	tt	c	r	+	–	r	–
C. decandra Jacquin	st	+	r	r	o	+	o
C. gossypiosperma Briquet	tt	–	–	r	–	–	+
C. lasiophylla Eichler	st	r	r	r	r	+	o
C. obliqua Sprengel	tt	r	r	–	–	r	–
C. sylvestris Swartz	st	r	r	r	c	r	f
Xylosma ciliatifolium (Clos.) Eichler	tt	r	r	r	–	–	–
X. pseudosalzmanii Sleumer	tt	–	–	r	–	+	–
HIPPOCRATEACEAE							
Cheiloclinum cognatum (Miers.) A.C. Smith	st	–	–	r	r	–	–
Salacia elliptica (Mart.) E. Don.	st	r	f	r	–	r	+
HUMIRIACEAE							
Humiriastrum glaziovii (Urban) Cuatrec.	tt	–	o	–	–	o	–
ICACINACEAE							
Citronella paniculata (Mart.) Howard	st	–	–	r	–	–	–
LACISTEMACEAE							
Lacistema hasslerianum Chodat	st	r	+	+	r	+	c
LAMIACEAE							
Hyptis arborea Benth.	st	–	–	–	r	–	+
LAURACEAE							
Aiouea acaradomatifera Kosterm.	tt	–	–	+	–	–	–
Aniba firmula (Nees & Mart.) Mez	tt	–	+	o	–	–	–
Beilschmiedia emarginata (Meisner) Kosterm.	tt	–	r	–	–	–	+
Cinnamomum glaziovii (Mez) Vattimo	tt	–	r	r	–	r	–
Cryptocarya aschersoniana Mez	tt	c	o	r	r	a	f
C. moschata Nees & Mart.	tt	–	r	–	–	–	–
Endlicheria paniculata (Sprengel) Macbr.	tt	–	+	r	o	–	o
Licaria armeniaca (Nees) Kosterm.	tt	–	–	–	–	+	–
Nectandra cissiflora Nees	tt	–	–	+	+	r	+
N. grandiflora Nees	tt	–	f	–	r	–	–
N. lanceolata Nees	tt	+	–	r	–	–	–
N. megapotamica (Sprengel) Mez	tt	–	–	+	–	r	–
N. nitidula Nees & Mart.	tt	–	–	r	f	+	f
N. oppositifolia Nees	tt	r	r	f	r	r	f
N. puberula (Schott.) Nees	tt	+	–	+	r	–	+
N. reticulata Mez	tt	+	–	–	+	–	–
N. warmingii Meisner	tt	–	–	–	–	–	+
Ocotea aciphylla Nees	tt	–	c	–	–	+	–

	Growth form	LV	PB	Study areas BS	IT	MD	TD
LAURACEAE (contd)							
O. acutifolia (Nees) Mez	tt	–	–	–	–	–	r
O. catharinensis Mez	tt	+	–	+	r	+	–
O. corymbosa (Meisner) Mez	tt	c	f	o	r	f	c
O. diospyrifolia (Meisner) Mez	tt	–	–	+	–	r	–
O. laxa (Nees) Mez	st	r	–	f	–	–	–
O. odorifera (Vell.) Rohwer	tt	a	f	r	r	f	r
O. pulchella (Nees) Mez	tt	r	r	r	f	r	f
O. velloziana Meisner	tt	–	r	–	–	–	–
Persea pyrifolia Nees & Mart.	tt	c	r	r	r	–	o
LECYTHIDACEAE							
Cariniana estrellensis (Raddi) Kuntze	tt	–	–	r	r	–	–
C. legalis (Mart.) Kuntze	tt	–	–	+	–	–	+
Lecythis lanceolata Poiret	tt	–	–	+	–	–	–
LOGANIACEAE							
Strychnos brasiliensis Mart.	sh	–	–	r	–	–	+
S. gardneri A.DC.	st	–	+	–	+	–	–
LYTHRACEAE							
Lafoensia densiflora Pohl	tt	–	–	r	–	–	–
L. pacari A.St.-Hil.	st	–	–	–	r	+	+
MAGNOLIACEAE							
Talauma ovata A.St.-Hil.	tt	–	r	–	r	–	r
MALPIGHIACEAE							
Byrsonima intermedia A. Juss.	sh	+	+	–	–	–	r
B. laxiflora Griseb.	tt	r	f	r	–	–	o
Heteropteris acutifolia Juss.	sh	–	–	–	r	–	–
H. byrsonimifolia Juss.	st	r	r	–	–	–	–
MALVACEAE							
Abutilon belfordianum (Hook.) A.St.-Hil. & Naudin	sh	–	–	–	r	–	–
MELASTOMATACEAE							
Leandra pectinata Cogn.	sh	–	+	–	–	–	–
L. scabra DC.	sh	r	r	+	r	+	f
Miconia albicans Triana	sh	r	–	–	+	–	f
M. argyrophylla DC.	tt	c	f	–	–	r	o
M. brunnea Mart.	st	–	+	–	–	–	+
M. chamissois Naudin	st	–	+	–	–	–	–
M. chartacea Triana	st	f	c	r	–	+	o
M. cinnamomifolia (DC.) Naudin	tt	+	f	+	–	r	r
M. corallina Spring	st	+	+	–	+	–	o
M. cubatanensis Hoehne	st	–	–	–	+	–	+
M. hispida Cogn.	st	f	f	+	–	–	r
M. ligustroides (DC.) Naudin	st	r	–	+	+	–	–
M. minutiflora (Bonpl.) Triana	st	+	–	+	+	–	f
M. pepericarpa DC.	st	c	+	+	+	–	c
M. pusilliflora Triana	tt	r	–	–	–	f	–
M. rigidiuscula Cogn.	tt	o	r	–	–	–	r
M. sellowiana Naudin	tt	–	+	r	–	–	–
M. tristis Sprengel	tt	+	–	r	–	–	r
Mouriri glazioviana Cogn.	st	–	–	–	–	–	r
Tibouchina candolleana (DC.) Cogn.	st	–	–	–	r	+	o

	Growth form	LV	PB	BS	IT	MD	TD
		Study areas					
MELASTOMATACEAE (contd)							
T. stenocarpa (DC.) Cogn.	st	r	+	–	+	–	o
Trembleya parviflora (Don) Cogn.	sh	–	+	–	+	–	r
MELIACEAE							
Cabralea canjerana (Vell) Mart.	tt	–	o	f	r	r	o
Cedrela fissilis Vell.	tt	r	+	o	r	+	o
Guarea guidonia (L.) Sleumer	st	r	+	f	f	+	f
G. kunthiana A.Juss.	tt	–	–	r	r	–	–
G. macrophylla Vahl.	st	–	–	–	–	–	r
Trichilia emarginata (Turcz.) C.DC.	st	o	f	o	–	c	–
T. pallens DC.	st	–	–	f	–	–	–
T. pallida Swartz	st	r	–	f	r	+	–
MIMOSACEAE							
Acacia glomerosa Benth.	tt	–	–	f	–	–	–
A. recurva Benth.	st	–	–	–	–	r	–
Albizia polycephala (Benth.) Killip	tt	r	–	r	+	–	–
Anadenanthera colubrina (Vell.) Brenan	tt	–	+	–	r	–	+
A. peregrina (Benth.) Speg.	tt	r	+	–	+	–	o
Enterolobium contortisiliquum (Vell.) Morong	tt	–	+	–	–	–	–
Inga affinis DC.	tt	r	r	r	r	a	r
I. fagifolia (L.) Willd.	st	–	+	+	–	–	–
I. guilleminiana Benth.	tt	–	+	–	–	–	–
I. luschnatiana Benth.	tt	–	r	r	+	–	+
I. marginata Willd.	st	–	–	–	r	–	–
I. sessilis (Vell.) Mart.	tt	–	+	–	–	+	–
I. striata Benth.	tt	–	–	+	–	–	r
Piptadenia gonoacantha (Mart.) Macbr.	tt	r	+	–	–	–	f
Pithecellobium incuriale (Vell.) Benth.	tt	r	+	–	–	f	o
Pseudopiptadenia leptostachya (Benth.) Rausch.	st	r	–	–	–	–	+
Stryphnodendron polyphyllum Mart.	st	–	–	–	+	–	+
MONIMIACEAE							
Mollinedia argyrogyna Perk.	st	–	f	–	r	r	o
M. triflora (Sprengel) Tul.	sh	–	+	–	+	+	+
M. uleana Perk.	st	–	–	–	+	–	r
M. widgrenii A.DC.	st	r	–	f	r	–	–
Siparuna apiosyce (Mart.) DC.	sh	–	+	r	r	–	+
S. guianensis Aublet	st	f	+	r	o	o	o
MORACEAE							
Ficus gomelleira Kunth & Bouché	tt	–	–	+	+	–	–
F. insipida Willd.	tt	r	–	+	r	–	–
F. luschnatiana (Miq.) Miq.	tt	–	–	–	+	–	+
F. mexiae Standl.	tt	–	o	r	–	r	+
F. pertusa L.f.	tt	r	–	–	–	–	r
Maclura tinctoria (L.) Don.	tt	+	–	o	r	–	–
Naucleopsis mello-barretoi (Standl.) C.C.Berg	tt	–	o	–	r	–	–
Sorocea bonplandii (Baillon) W.Burger	st	r	+	+	r	r	r
MYRISTICACEAE							
Virola oleifera (Schott.) A.C.Sm.	tt	–	–	–	–	r	–
MYRSINACEAE							
Cybianthus brasiliensis (Mez) Agostini	st	–	r	–	–	–	–

	Growth form	LV	PB	BS	IT	MD	TD
				Study areas			
MYRSINACEAE (contd)							
C. cuneifolius Mart.	sh	–	+	–	–	r	–
Myrsine coriacea (Swartz) R.Br.	tt	r	+	–	r	+	r
M. guianensis (Aublet) Kuntze	st	+	+	–	–	–	+
M. lancifolia Mart.	tt	o	r	+	r	–	o
M. oblonga (Pohl.) Pipoly	st	–	–	–	–	–	+
M. umbellata Mart.	tt	r	f	o	r	r	c
Stylogyne ambigua (Mart.) Mez	st	–	–	o	–	–	+
MYRTACEAE							
Blepharocalyx salicifolius (Kunth) Berg	st	r	–	r	+	+	–
Calycorectes acutatus (Miq.) Toledo	st	r	+	c	–	o	o
Calyptranthes brasiliensis Sprengel	st	r	o	r	+	–	–
C. clusiaefolia (Miq.) Berg	st	f	c	r	r	c	f
C. lucida Mart.	tt	–	–	o	+	f	r
C. strigipes Berg	st	–	–	–	r	–	+
Campomanesia guazumifolia (Cambess.) Berg	st	–	–	r	r	–	r
C. pubescens (DC.) Berg	st	–	–	–	r	–	+
C. rufa (Berg) Nied.	sh	–	–	–	+	–	–
C. xanthocarpa Berg	st	–	–	–	r	–	–
Eugenia aurata Berg	st	–	+	+	–	–	+
E. blastantha (Berg) Legr.	st	r	o	+	–	–	f
E. florida DC.	st	–	r	r	f	o	–
E. involucrata DC.	tt	r	–	+	r	–	o
E. myrtifolia Cambess.	st	–	r	+	–	f	r
E. pluriflora DC.	st	–	–	r	r	–	+
E. punicifolia (Kunth) DC.	st	–	+	–	+	–	–
E. uniflora L.	st	–	–	r	–	–	+
Gomidesia affinis (Cambess.) Legr.	st	+	r	f	r	+	o
G. eriocalyx (DC.) Legr.	st	–	f	+	r	+	o
G. gaudichaudiana Berg	st	r	–	–	–	–	–
G. lindeniana Berg	st	–	–	–	r	+	r
G. velutina Berg	sh	–	+	–	–	–	–
Myrceugenia euosma (Berg) Legr.	st	–	r	–	–	–	–
M. miersiana (Gardn.) Legr. & Kaus.	st	–	–	–	–	r	–
Myrcia laruotteana Cambess.	tt	–	–	r	r	r	–
M. leptoclada DC.	st	–	–	+	r	o	–
M. multiflora (Lam.) DC.	tt	–	–	r	r	a	f
M. rostrata DC.	st	c	r	+	r	+	f
M. rufipes DC.	st	–	–	r	+	–	o
M. tomentosa (Aublet) DC.	st	r	–	r	o	+	o
M. velutina Berg	st	r	r	r	o	+	r
M. venulosa DC.	tt	r	–	r	c	+	a
Myrciaria ciliolata Cambess.	st	+	–	–	–	–	–
M. floribunda (West) Berg	st	–	–	–	–	–	+
M. tenella (DC.) Berg	sh	–	–	+	r	–	–
Pimenta pseudocaryophyllus (Gomes) Landrum	st	r	–	–	+	–	o
Psidium cattleianum Sab.	st	–	r	r	+	r	–
P. guajava L.f.	st	–	+	r	+	–	–
P. guineense Swartz	st	–	–	r	r	–	+
P. rufum Mart.	sh	–	+	+	–	–	+
Siphoneugena densiflora Berg	st	r	a	–	–	–	o

	Growth form	Study areas LV	PB	BS	IT	MD	TD
MYRTACEAE (contd)							
S. widgreniana (Berg) Burret	st	f	–	r	r	–	f
Syzygium jambos (L.) Alston	st	–	–	r	–	r	+
NYCTAGINACEAE							
Guapira noxia (Netto) Lundell	st	–	+	–	+	–	–
G. opposita (Vell.) Reitz	st	r	–	–	r	r	–
Pisonia ambigua Heimerl	tt	–	–	–	–	–	+
OCHNACEAE							
Ouratea semiserrata (Mart. & Nees) Engler	st	–	+	r	–	–	–
OLACACEAE							
Heisteria silviani Schwarke	st	r	–	+	–	–	+
OLEACEAE							
Chionanthus arboreus (Eichler) P.S.Green	tt	–	+	–	–	–	–
OPILIACEAE							
Agonandra engleri Hoehne	st	+	r	r	–	–	+
PIPERACEAE							
Ottonia leptostachya Kunth	sh	–	+	–	+	+	+
Piper aduncum L.	sh	+	+	+	+	+	r
P. arboreum Aublet	st	–	–	–	r	–	–
P. caracolanum C.DC.	sh	–	+	r	r	+	+
P. cernuum A.DC.	st	–	–	–	r	–	–
P. dilatatum L.C.Rich	sh	+	–	+	–	–	–
P. gaudichaudianum Kunth.	st	–	r	–	–	r	+
P. mollicomum Kunth.	sh	–	–	–	r	–	–
Pothomorphe umbellata (L.) Miq.	sh	–	+	+	–	+	r
POACEAE							
Merostachys neesii Rupr.	bb	–	+	–	–	+	–
PODOCARPACEAE							
Podocarpus lambertii Klotzsch	st	–	–	–	–	–	r
P. sellowii Klotzsch	st	–	+	–	–	–	–
POLYGONACEAE							
Coccoloba warmingii Meisner	tt	r	r	r	–	–	–
PROTEACEAE							
Euplassa incana (Klotzsch) Johnston	tt	+	r	–	–	r	+
E. rufa (Loesen) Sleumer	tt	–	–	r	r	–	r
Roupala brasiliensis Klotzsch	tt	r	+	o	r	r	o
R. longepetiolata Pohl	tt	–	r	–	–	–	+
R. montana Aublet	st	–	–	–	–	–	+
RHAMNACEAE							
Colubrina glandulosa Perkins	tt	–	–	–	+	–	+
Rhamnidium elaeocarpum Reisseck	st	+	–	r	–	–	+
Rhamnus sphaerosperma Swartz	st	–	–	–	+	–	+
ROSACEAE							
Prunus brasiliensis (Cham. & Schltdl.) D.Dietr.	st	–	–	+	–	+	–
P. sellowii Koehne	st	–	+	o	r	f	r
RUBIACEAE							
Alibertia concolor (Cham.) Schum.	sh	–	–	–	–	–	r
A. macrophylla Schum.	tt	r	–	r	o	r	o

	Growth form	Study areas LV	PB	BS	IT	MD	TD
RUBIACEAE (contd)							
A. sessilis (Vell.) Schum.	st	+	r	–	–	–	+
Amaioua guianensis Aublet	tt	a	f	r	r	c	f
Chomelia sericea Müll.Arg.	st	–	–	+	+	r	+
Coutarea hexandra (Jacquin) Schum.	st	–	–	r	r	–	r
Faramea cyanea Müll.Arg.	st	r	f	o	r	o	r
F. multiflora A.Rich.	st	–	r	–	–	–	+
Guettarda uruguensis Cham. & Schltdl.	st	–	–	r	r	–	–
G. viburnioides (Cham.) Schltdl.	st	–	–	+	o	+	+
Ixora warmingii Müll.Arg.	st	f	r	c	r	c	f
Ladenbergia hexandra (Pohl) Klotzsch	tt	–	r	–	–	–	–
Posoqueria latifolia (Rudge) Roem. & Schult.	st	–	+	–	–	–	–
Psychotria barbiflora DC.	sh	–	–	r	+	–	–
P. carthagenensis Jacquin	st	–	–	r	–	–	+
P. deflexa DC.	sh	–	–	+	–	r	–
P. hastisepala Müll.Arg.	sh	+	–	r	+	+	+
P. sessilis (Vell.) Müll.Arg.	st	+	f	r	r	+	o
P. suterella Müll.Arg.	sh	–	+	–	+	–	–
Randia nitida (Kunth) DC.	st	–	–	–	r	r	r
Rudgea viburnioides (Cham.) Benth.	sh	r	+	–	o	–	r
RUTACEAE							
Angostura pentandra (A.St.-Hil.) Albuquerque	tt	–	–	–	–	–	r
Dictyoloma vandellianum A.Juss.	st	–	+	–	–	–	–
Esenbeckia febrifuga (A.St.-Hil.) A.Juss.	st	–	–	o	r	–	r
E. grandiflora Mart.	st	+	+	–	–	–	–
Galipea multiflora Schult.	st	r	+	o	+	–	+
Metrodorea nigra A.St.-Hil.	tt	–	–	–	–	–	r
M. stipularis Mart.	tt	r	–	f	–	–	–
Pilocarpus pennatifolius Lemaire	tt	–	–	–	–	r	–
Zanthoxylum rhoifolium Lam.	tt	r	r	r	+	r	o
Z. riedelianum Engler	tt	–	–	–	r	–	–
Z. tingoassuiba A.St.-Hil.	tt	+	+	+	+	–	–
SABIACEAE							
Meliosma sellowii Urban	tt	–	r	–	–	–	+
SALICACEAE							
Salix humboldtiana Willd.	tt	–	–	–	–	c	–
SAPINDACEAE							
Allophyllus semidentatus (Miq.) Radlk.	st	–	–	r	–	–	–
Cupania oblongifolia Mart.	tt	–	–	–	–	–	+
C. racemosa (Vell.) Radlk.	tt	r	+	+	–	+	–
C. vernalis Cambess.	tt	+	–	c	f	r	f
Diatenopteryx sorbifolia Radlk.	st	r	–	–	r	–	–
Dilodendron bipinnatum Radlk.	st	–	–	–	–	–	+
Matayba elaeagnoides Radlk.	tt	–	f	–	–	r	o
M. guianensis Aublet	st	–	–	–	–	+	r
M. juglandifolia (Cambess.) Radlk.	tt	–	–	f	r	–	o
SAPOTACEAE							
Chrysophyllum gonocarpum (Mart. & Eichler) Engler	tt	–	–	r	–	–	–
C. marginatum (Hook & Arn.) Radlk.	st	–	–	+	r	–	r

	Growth form	Study areas LV	PB	BS	IT	MD	TD
SAXIFRAGACEAE							
Escallonia bifida Link. & Otto	sh	–	–	–	–	r	–
SIMAROUBACEAE							
Picramnia glazioviana Engler	tt	–	r	–	–	o	–
SOLANACEAE							
Brunfelsia brasiliensis (Sprengel) Smith & Downs	sh	+	+	–	+	–	+
Cestrum laevigatum Schltdl.	sh	+	–	–	+	+	+
C. sendtnerianum Mart.	sh	–	+	+	–	–	–
Sessea regnellii Taub.	tt	–	–	+	–	–	–
Solanum argenteum Dunal	tt	+	–	–	–	+	–
S. bullatum Vell.	tt	r	–	–	–	r	–
S. cernuum A.St.-Hil.	sh	–	+	–	–	–	–
S. erianthum D.Don	st	+	–	–	+	–	+
S. granuloso-leprosum Dunal	st	+	–	–	+	–	+
S. inaequale Vell.	tt	r	–	–	–	–	r
S. martii Sendt.	sh	+	–	–	+	–	+
S. swartzianum Roem. & Schult.	tt	+	–	–	–	+	–
STERCULIACEAE							
Helicteres ovata Lam.	sh	–	+	–	r	+	–
Guazuma ulmifolia L.	tt	r	r	f	r	+	r
STYRACACEAE							
Styrax camporum Pohl	tt	–	–	r	r	–	+
S. pohlii A.DC.	tt	f	r	o	–	r	r
SYMPLOCACEAE							
Symplocos celastrinea Mart.	st	–	–	–	–	–	+
S. lanceolata (Mart.) A.DC.	st	–	r	–	–	–	r
S. pubescens Klotzsch	st	–	–	r	r	–	+
THEACEAE							
Laplacea semiserrata Cambess.	tt	–	–	–	r	–	o
Ternstroemia alnifolia Wawra	tt	–	r	r	–	–	o
THYMELAEACEAE							
Daphnopsis brasiliensis Mart. & Zucc.	st	–	–	r	r	–	+
D. fasciculata (Meisner) Nevl.	st	–	r	r	r	r	r
TILIACEAE							
Luehea divaricata Mart. & Zucc.	tt	+	+	f	–	+	r
L. grandiflora Mart. & Zucc.	tt	r	+	+	+	+	o
L. paniculata Mart.	st	–	+	+	+	–	–
L. rufescens A.St.-Hil.	tt	–	–	–	f	+	–
ULMACEAE							
Celtis iguanea (Jacquin) Sargent	sh	r	+	+	–	–	+
Trema micrantha Blume	st	r	–	+	–	–	+
VERBENACEAE							
Aegiphila lhotzkiana Cham.	sh	+	+	+	+	–	+
A. sellowiana Cham.	st	+	+	–	r	+	o
Aloysia virgata (Ruiz & Pavon) A.Juss.	sh	–	–	–	–	–	r
Cytharexylum myrianthum Cham.	st	–	–	–	+	–	–
Lantana fucata Lindl.	sh	–	–	–	r	–	+
Vitex polygama Cham.	st	r	r	–	r	+	r

	Growth form	LV	PB	BS	IT	MD	TD
		Study areas					
VIOLACEAE							
Hybanthus atropurpureus (A.St.-Hil.) Taub.	sh	–	–	+	–	+	–
VOCHYSIACEAE							
Callisthene major Mart.	st	–	–	–	–	r	–
C. minor Mart.	st	–	+	–	–	–	–
Qualea dichotoma (Mart.) Warm.	tt	–	r	–	–	–	–
Q. multiflora Mart.	tt	r	r	r	+	r	r
Vochysia tucanorum Mart.	tt	r	r	r	r	r	f
WINTERACEAE							
Drimys brasiliensis Miers	st	–	r	–	–	–	–
Number of species found in the sample plots	–	136	119	157	176	118	–
Total number of species (found outside plots included)	456 (total)	184	219	241	256	192	277

[1]For LV, PB, BS, IT and MD, abundance estimates were based on the Importance Value Indices (IVI = CVI + relative frequency): a (> 10), c (5–10), f (2–5), o (1–2), r (< 1), + (found outside plots). For TD, these were based on field notes about the sample areas and the forest in general.