

# Tree species composition and environmental relationships in a Neotropical swamp forest in Southeastern Brazil

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**Abstract** We examined the relationships between topography, soil properties and tree species composition in a Neotropical swamp forest in southeastern Brazil. Plots were sampled in the forest, encompassing three different soil ground water regimes along the topographical declivity. All non-climbing plant individuals with trunk height >1.3 m were sampled. A canonical correspondence analysis—CCA—of the species–environmental relationships grouped tree species according to drainage and chemical soil conditions. A total of 86 species were found, being 77 species in the inferior, 40 species in the intermediate

and 35 species in the superior topographic section. Some species were among the 10 most abundant ones, both in the overall sampled area and in each topographical section, with alternation events occurring only with their abundance position. However, substantial differences in floristic composition between sections were detected in a fine spatial scale, due to higher number of species, diversity index ( $H'$ ) and species unique (exclusives) in the inferior topographic section. These higher values can be attributed to its higher spatial heterogeneity that included better drained and seasonally waterlogged soils, higher soil fertility and lower acidity. The increase of the soil water saturation and the uniform conditions derived from the superficial water layer has led to a lower number of species and an increase on the palm trees abundance in the intermediate and superior sections. Our results showed that at a small spatial scale niche differentiation must be an important factor related to the increase of the local diversity. The wide distribution of the most abundant species in the studied area and the increase of local diversity corroborate the pattern of distribution of species in larger scales of swamp forests, in which the most abundant species repeat themselves in high densities in different remnants. However, the floristic composition of each remnant is strongly variable, contributing to the increase of regional diversity.

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## Introduction

In riverine zones, tree species composition and distribution are affected by environmental factors such as soil texture and moisture content, nutrient status, tree gap dynamics, and the composition of neighbouring vegetation (Oliveira-Filho et al. 1990; Medley 1992; Felfili 1995). Riverine swamp forests contain almost permanently waterlogged soils in depressions, lowlands, headwaters and watercourse margins. In these forests, a few flood-tolerant plant species are often represented by many individuals (Scarano 2002; Koponen et al. 2004; Allen et al. 2005). Many species usually associated with well drained soils in surrounding forests also occur in swamp forests but are represented by only a few individuals, increasing species richness (Imbert et al. 2000; Scarano 2002). Nevertheless, tree species richness in swamp forests is generally lower than that of other forests on higher grounds, due to the exclusion of species that are intolerant to waterlogged soils (Lieberman et al. 1985; van Andel 2003).

Brazilian swamp forests are associated with different forest types according to the phytogeographic units in which they occur, and they can also vary within the same unit due to soil features. In the south and southeastern regions, swamp forests are mainly associated with the Atlantic Rain Forest domain. For example, in the coastal zone, freshwater swamp forests occur on sandy, mainly Quaternary alluvium-derived substrates (Scarano 2002), and peat forests occur on swampy peat soils (Sztutman and Rodrigues 2002; Dorneles and Waechter 2004). In southeastern regions, swamp forests are mainly associated with semi-deciduous forests of the Atlantic forest domain (Toniato et al. 1998; Rocha et al. 2005; Souza and Martins 2005). Gallery swamp forests are found in the Brazilian savannas (in the Cerrado domain) throughout central Brazil (Oliveira-Filho et al. 1990; Guarino and Walter 2005). The swamp forests in interior southeastern regions have a structural resemblance in between based on an important group of dominating species (Costa et al. 1997; Marques et al. 2003; Teixeira and Assis 2005;

Silva et al. 2007). Although these forests resemble each other in structure, their floras are variable, with a large number of unique species in each forest (Teixeira and Assis 2005).

Despite their ecological importance in the conservation of water resources, swamp forests are very small and fragile environments, extremely vulnerable to anthropogenic impacts, e.g., palm heart and tree extraction, canal building, embankment construction, highway activities, and urban expansion. They have been little studied but are gradually disappearing (Torres et al. 1994; Gomes et al. 2006). Because those forests are restricted to very small areas of the landscape where permanently waterlogged soils occur, they are naturally split into fragments surrounded by other kinds of vegetation. They occur mainly in bottom valleys in the inlands of southeastern Brazil, in areas that are useless for crops, which nevertheless surround them.

Micro-topography variations in swamp forests may promote a local drainage pattern variation (Scarano et al. 1997; Souza and Martins 2005), which can determine distinct patterns of spatial distribution for species, leading to different community structures (Koponen et al. 2004; Scarano 2006). Nevertheless, forest structure, dynamics and internal heterogeneity have received little attention in swamp forests (Souza and Martins 2005). Small scale studies on the relationships between environment and vegetation in Brazilian flood-prone forests have been carried out mainly in the Amazon basin (e.g. Wittmann et al. 2004), riverine forests within the Pantanal Matogrossense area (e.g. Damasceno-Junior et al. 2005), and in central and southeastern regions of Brazil (e.g. Oliveira-Filho et al. 1990; van den Berg and Oliveira-Filho 1999).

Souza and Martins (2005) evaluated spatial variation and dynamics of flooding, canopy openness, and structure relationships in a swamp forest in southeastern Brazil. However, these authors did not study the swamp forest floristic composition itself. We described the floristic and structural composition in a fine spatial scale of a swamp forest in the countryside of Brazil (São Paulo state, southeastern Brazil). This forest spreads over a topographical gradient of about 10%, which leads to its environmental heterogeneity in the local drainage pattern. This spatial environmental condition differentiates this forest from other swamp forests studied in central and southeastern Brazil,

which occur in more gentle slopes (e.g. Costa et al. 1997; Marimon et al. 2002; Nogueira and Schiavini 2003). Because of this unique feature, we assessed soil and topography features to explain variations on both structure and flora of the swamp forest.

## Methods

### Study site

The study area is located inside Sao José farm (22°22' S and 47°28' W), municipality of Rio Claro, Sao Paulo state (southeastern Brazil). The regional climate is Cwa type in Köppen's Classification (Setzer 1967), with a rainy season from October to March and a dry season from April to September. Data from 1994 to 2003 obtained at the Meteorological Station located 8 km from the study site indicated an average annual rainfall rate of 1,456 mm, from which 1,182 mm concentrate in the rainy season, and 274 mm in the dry months. The average temperature in the coldest month (June) was 18°C, whereas in the hottest month (January) it went up to 25°C.

The farm has an area of 5,900 ha. The native vegetation covered 2,250 ha until 1939. Since then, great part of the forest has been felled and replaced mainly with bean and corn fields (Pagano 1985). Nowadays, the forest encompasses three fragments with a total area of 580 ha. The remaining area is covered mainly with sugarcane, corn, orange and rubber trees. The present study was carried out in the highest forest remnant of the farm, which has an area of 230 ha of tropical forest (Atlantic Forest domain). This remnant comprises ca. 97% of seasonal semi-deciduous forest and 3% (ca. 8 ha) of swamp forest, which spreads over a topographical section with an average declivity of about 10%, between 650 and 630 m above sea level. This forest is established on many well drained hummocks ( $\leq 30$  cm-high, 2 m-wide) interspersed with natural drainage-ways that flow toward a small river (Ribeirão Claro). In the superior topographic section, the water table permanently outcrops to surface. In the inferior and intermediate sections, the water table lies close to the surface throughout the year and outcrops only in the rainy season (ca. six months per year), fulfilling the drainage channels. *Calophyllum brasiliense* and *Magnolia ovata* build the dominant canopy (average

height between 11 and 14 m), and they are also represented by emerging trees that exceed 20 m in height along with *Cedrela odorata*. Other species, such as *Dendropanax cuneatus*, *Calyptanthes concinna*, and the palm tree *Euterpe edulis* build the lower canopy (average height between 6 and 10 m). The understory stratum is characterized by *Costus spiralis*, the palm tree *Geonoma brevispatha*, the even lower rosette plant *Blechnum brasiliense*, and the shrub *Psychotria* spp. (Teixeira and Assis 2005). Lianas and epiphytes are not frequent and light entry is favoured by the fall of trunks and branches from the dominant canopy trees.

### Plant community survey

Fieldwork was carried out between September, 2002 and July, 2004. Three 0.15-ha sample plots were positioned along the topographical declivity. Plots were distanced ca. 40 m from each other to encompass different soil ground water regimes. Each plot was divided into 15 (10 × 10 m) contiguous quadrats. The first sample plot (P1) was placed in the inferior topographic section (ca. 632 m), on periodically waterlogged soils. The second sample plot (P2) was located at the intermediary topographic section (ca. 640 m), also on periodically waterlogged soils. The third sample plot (P3) was placed on the superior topographic section (ca. 648 m), on permanently waterlogged soils.

All non-climbing plant individuals with trunk height  $>1.3$  m were recorded in each quadrat. Each plant was identified, measured (circumference at breast height) and its total height was estimated with the aid of a pole of known length. Voucher specimens are deposited at the Herbário Rioclarense (HRCB). Species were classified into families according to the Angiosperm Phylogeny Group II system (APG II 2003).

### Topographical features, soil and drainage surveys

We obtained two topographic variables in each quadrat: (1) the average elevation, which was calculated with the corner altitude figures; and (2) the elevation range, which was calculated from the difference between the highest and the lowest corner altitude values (Oliveira-Filho et al. 1994).

Haplic Gleysols were found within the inferior and intermediary topographic sections, whereas Fluvisols were found within the superior topographic section. Soil classification followed the Brazilian soil taxonomy system (EMBRAPA 1999). We collected a 0.5-l sample soil from nine sub-samples randomly distributed in each quadrat (0–20 cm). Chemical analyses of these samples were carried out at Universidade Federal de São Carlos (Araras, São Paulo state, Brazil) following the procedures proposed by Raij (1983). The soil chemical properties obtained were pH, extractable P, exchangeable bases ( $K^+$ ,  $Ca^{2+}$ ,  $Mg^{2+}$  and  $Al^{3+}$ ), potential acidity ( $H + Al$ ), proportion of soil organic matter (O.M.), cation exchange capacity ( $CEC = K^+ + Ca^{2+} + Mg^{2+} + H + Al$ ), base saturation ( $V = 100 \cdot [(K^+ + Ca^{2+} + Mg^{2+}) \cdot CEC^{-1}]$ ) and aluminum saturation [ $m = 100 \cdot Al^{3+} \cdot (K^+ + Ca^{2+} + Mg^{2+} + Al^{3+})^{-1}$ ]. Base saturation and CEC were determined to specify total soil fertility.

We classified quadrats into seven drainage classes according to water logging period, drainage form, and waterlogged area. We attributed values to the following variables: permanently waterlogged (1) or periodically waterlogged (2); diffuse drainage (1) or drainage in channels (2); and quadrat area waterlogged between 76 and 100% (1), from 51 to 75% (2), from 26 to 50% (3), or from 1 to 25% (4). Values were added and a rank was set, so that quadrats with more deficient drainage (permanently waterlogged, with diffuse drainage throughout the quadrat area) received the lowest score (3). In the other extreme, higher values were given to drainage in channels that seasonally flood the small quadrat area (8); however, some non-flooded quadrats were observed and were given the highest values (9).

#### Data analyses

Relationships between species abundance, topography, soil chemical properties and drainage were explored with canonical correspondence analysis—CCA (ter Braak 1987). The species matrix consisted of the number of individual trees per species (variables), per quadrat (subjects), to which only 27 species with ten or more individuals were taken into consideration. The environmental data matrix included average elevation, elevation range, soil chemical properties and drainage rank (variables)

per quadrat (subject). Percentage environmental data ( $V$  and  $m$ ) were arc-sine transformed to approximate their distributions to the normal distribution (Zar 1996). We processed a preliminary analysis using all 14 variables and both multi-collinear (weighted correlations between variables  $\geq 0.7$ ) and lower related variables ( $r < 0.5$  with the CCA axis) were excluded. We chose  $H + Al$  and  $V$  to express soil acidity and fertility respectively, drainage, and CEC. The independence hypothesis between both specific abundance and environmental data matrixes was tested with Mantel test along with 1000 Monte Carlo's permutations (ter Braak 1987). We used the program PC-ORD version 4.0 (McCune and Mefford 1999). Data analysis was restricted to those two methods because the experimental design does not attend the theoretical assumptions needed to perform the traditional linear models (ANOVA).

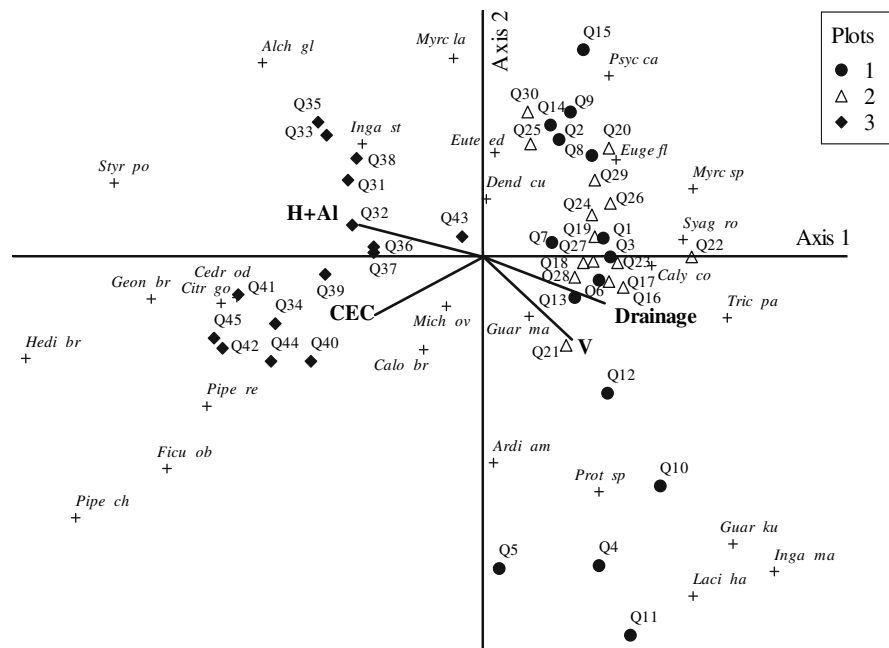
We calculated the species diversity [Shannon's index ( $H'$ ) and Pielou's evenness ( $J'$ )] (Brower and Zar 1984) for each sample plot. Jaccard's coefficient was used to compare the floristic similarity between plots (Müller-Dombois and Ellenberg 1974).

## Results

### Plant community versus environment correlation

The CCA ordination showed high correlations between species and environmental variables for the axis 1 (88.6%) and axis 2 (74%), and Mantel test carried out for the first two axes has shown that species were significantly correlated to the supplied variables ( $P = 0.001$ ). The CCA diagram distinguished three quadrat groups (Fig. 1) and pointed out a gradient from Gleysols to Neosols that increased in topographic elevation, soil water saturation and acidity, and decreased in fertility. Axis 1 segregated Gleysols (at the right side of axis 1) from Neosols (at the left side of axis 1). Gleysols were grouped into two subgroups, according to axis 2. One subgroup was made of 25 seasonally waterlogged quadrats (15 quadrats in plot 2 and 10 in plot 1), mainly at the superior quadrant. Five quadrats from plot 1 (Q4, Q5, Q10, Q11, and Q12) made up the other Gleysoil subgroup at the inferior quadrant, characterized by better drainage and highest fertility rates ( $V$ ). Though belonging to Gleysols, soil surface water saturation is not observed in these

**Fig. 1** Canonical correspondence analysis: ordination diagram for 45 quadrats based on the distribution of the 27 most abundant species (+) in three sample plots in the Neotropical swamp forest in southeastern Brazil, and their correlation with the four environmental variables used (arrows) in analyses. Quadrats are identified by numbers (Plot 1 ranges from 1 to 15, Plot 2 from 16 to 30, and Plot 3 from 31 to 45). Species names are abbreviated (full names given in Table 1)



quadrats, not even in the rainy months (January and February, for instance).

Amongst the 27 most abundant species, *Alchornea glandulosa*, *Cedrela odorata*, *Citronella gongonha*, *Geonoma brevispatha*, *Ficus obtusiuscula*, *Hedyosmum brasiliense*, *Inga striata*, *Piper cf. chimonanthifolium*, *P. regnellii*, and *Styrax pohlii* were associated with the permanently waterlogged and most acid Neosoils. *Calyptanthes concinna*, *Eugenia florida*, *Myrcogenia sp.*, *Psychotria carthaginensis*, *Syagrus romanzoffiana*, and *Trichilia pallida* were associated with 25 seasonally waterlogged quadrats on Gleysoils. *Ardisia ambigua*, *Guarea kunthiana*, *Inga marginata*, *Lacistema hasslerianum* and *Protium spruceanum* were found in the five quadrats with better drainage and highest fertility. *Calophyllum brasiliense*, *Dendropanax cuneatus*, *Euterpe edulis*, *Guarea macrophylla*, *Myrcia laruotteana*, and *Magnolia ovata* were concentrated at the central portion of the diagram, indicating that they were abundantly distributed throughout the swamp forest, independently of the gradient.

#### Plant community and soil conditions

We recorded a total amount of 3,467 individual plants in the three sample plots. These individuals were distributed into 86 species and 42 families (Table 1).

Overall palm trees (*Euterpe edulis*, *Geonoma brevispatha* and *Syagrus romanzoffiana*) represented 42% of the total individuals. The highest floristic similarity (Jaccard's coefficient) was found between plots 2 and 3 (0.47), followed by plots 1 and 2 (0.44), and plots 1 and 3 (0.35). Twenty three species (27% of total) were found in all three plots.

A sum of 1,100 individuals (29% of palm trees) belonging to 77 species (36 exclusives) and 38 families was found in plot 1. The Shannon's diversity index ( $H'$ ) for species was 2.81, whereas the Pielou's evenness index ( $J'$ ) was 0.64. The ten species with the highest abundance rate accounted for 80% of all individuals. The total basal area was 54.6 m<sup>2</sup> ha<sup>-1</sup> and the highest diameter value was found in *Calophyllum brasiliense* (58.6 cm). Ten percent of all individuals had diameter at breast height (DBH) higher than 15 cm. Soils with higher nutrient content, attesting higher fertility (base saturation, V values) and less acidity (expressed by potential acidity, H + Al values), were observed in this plot (Table 2). Whereas the ten seasonally waterlogged quadrats presented mean V values = 41.8 ± 8.5%, the five better drained quadrats presented V = 68.6 ± 13.4%. V values above 50% suggest eutrophic soils only to these five better drained quadrats.

A sum of 1,040 individuals (48% of palm trees) distributed in 40 species (three exclusives) and 21 families was found in plot 2. The diversity index ( $H'$ )

**Table 1** Abundance of the species with trunk height >1.3 m found in three sample plots in a Neotropical swamp forest in southeastern Brazil

Families	Species	Abbreviations	Plot 1	Plot 2	Plot 3	Total
Arecaceae	<i>Euterpe edulis</i> Mart.	<i>Eute ed</i>	295	483	476	1,254
Clusiaceae	<i>Calophyllum brasiliense</i> Cambess.	<i>Calo br</i>	171	118	257	546
Myrtaceae	<i>Calyptanthes concinna</i> DC.	<i>Caly co</i>	118	98	35	251
Magnoliaceae	<i>Magnolia ovata</i> A. St.-Hill	<i>Mich ov</i>	58	40	92	190
Arecaceae	<i>Geonoma brevispatha</i> Barb. Rodr.	<i>Geon br</i>	6	7	165	178
Burseraceae	<i>Protium spruceanum</i> (Benth.) Engl.	<i>Prot sp</i>	51	50	31	132
Araliaceae	<i>Dendropanax cuneatus</i> Decne & Planch.	<i>Dend cu</i>	48	28	51	127
Meliaceae	<i>Trichilia pallida</i> Sw.	<i>Tric pa</i>	63	42	1	106
Meliaceae	<i>Guarea kunthiana</i> C. DC.	<i>Guar ku</i>	34	36	1	71
Myrtaceae	<i>Eugenia florida</i> DC.	<i>Euge fl</i>	27	24	12	63
Meliaceae	<i>Guarea macrophylla</i> Vahl	<i>Guar ma</i>	20	15	18	53
Rubiaceae	<i>Psychotria carthaginensis</i> Jacq.	<i>Psyc ca</i>	10	21	7	38
Myrsinaceae	<i>Ardisia ambigua</i> Mart.	<i>Ardi am</i>	18	7	12	37
Moraceae	<i>Ficus obtusiuscula</i> (Miq.) Miq.	<i>Ficu ob</i>	4	1	27	32
Meliaceae	<i>Cedrela odorata</i> L.	<i>Cedr od</i>	3	4	24	31
Arecaceae	<i>Syagrus romanzoffiana</i> (Cham.) Glassman	<i>Syag ro</i>	15	9	1	25
Chlorantaceae	<i>Hedyosmum brasiliense</i> Mart. ex Miq.	<i>Hedy br</i>	–	–	24	24
Fabaceae	<i>Inga striata</i> Benth.	<i>Inga st</i>	8	2	10	20
Myrtaceae	<i>Myrcia laruotteana</i> Cambess.	<i>Myrc la</i>	7	7	9	20
Fabaceae	<i>Inga marginata</i> Willd.	<i>Inga ma</i>	16	3	–	19
Myrtaceae	<i>Myrceugenia</i> sp.	<i>Myrc sp</i>	11	6	1	18
Styracaceae	<i>Styrax pohlilii</i> A. DC.	<i>Styr po</i>	1	–	16	17
Lacistemataceae	<i>Lacistema hasslerianum</i> Chodat	<i>Laci ha</i>	5	5	1	11
Cardiopteridaceae	<i>Citronella gongonha</i> (Mart.) R.A. Howard	<i>Citr go</i>	2	–	8	10
Euphorbiaceae	<i>Alchornea glandulosa</i> Poepp.	<i>Alch gl</i>	1	1	8	10
Piperaceae	<i>Piper cf. chimonanthifolium</i> Kunth	<i>Pipe ch</i>	–	3	7	10
Piperaceae	<i>Piper regnellii</i> (Miq.) C. DC.	<i>Pipe re</i>	1	–	9	10
Meliaceae	<i>Trichilia clausenii</i> C. DC.	–	8	1	–	9
Anacardiaceae	<i>Tapirira guianensis</i> Aubl.	–	4	2	2	8
Urticaceae	<i>Cecropia pachystachya</i> Trecul	–	–	–	8	8
Bignoniaceae	<i>Tabebuia umbellata</i> (Sond.) Sandwith	–	5	–	1	6
Euphorbiaceae	<i>Croton piptocalyx</i> Müll. Arg.	–	2	3	1	6
Fabaceae	<i>Copaifera langsdorffii</i> Desf.	–	4	2	–	6
Meliaceae	<i>Trichilia casaretti</i> C. DC.	–	4	2	–	6
Lechytidaceae	<i>Cariniana estrellensis</i> (Raddi) Kuntze	–	1	4	–	5
Myrtaceae	<i>Myrciaria tenella</i> O. Berg	–	4	1	–	5
Olacaceae	<i>Ximenia americana</i> L.	–	4	1	–	5
Salicaceae	<i>Xylosma tweediana</i> (Clos) Eichler.	–	3	2	–	5
Fabaceae	<i>Andira anthelmia</i> (Vell.) J.F. Macbr.	–	4	–	–	4
Lauraceae	<i>Endlicheria paniculata</i> (Spreng.) J.F. Macbr.	–	4	–	–	4
Malvaceae	<i>Luehea divaricata</i> Mart.	–	3	1	–	4
Myrsinaceae	<i>Rapanea umbellata</i> (Mart.) Mex	–	1	–	3	4
Salicaceae	<i>Casearia sylvestris</i> Sw.	–	4	–	–	4
Euphorbiaceae	<i>Croton urucurana</i> Baill.	–	–	–	3	3



**Table 1** continued

Families	Species	Abbreviations	Plot 1	Plot 2	Plot 3	Total
Melastomataceae	<i>Miconia ligustroides</i> (DC.) Naudin	–	3	–	–	3
Myrsinaceae	<i>Cybianthus densicomus</i> Mart.	–	–	–	3	3
Myrtaceae	<i>Syzygium jambos</i> (L.) Auston	–	3	–	–	3
Rubiaceae	<i>Psychotria</i> sp.	–	1	2	–	3
Rubiaceae	<i>Chomelia obtusa</i> Cham. & Schl.	–	3	–	–	3
Sapotaceae	<i>Chrysophyllum gonocarpum</i> (Mart. & Eichler) Engl.	–	1	2	–	3
Solanaceae	<i>Cestrum</i> cf. <i>megalophyllum</i> Dunal	–	1	–	2	3
Euphorbiaceae	<i>Sebastiania</i> cf. <i>serrata</i> (Baill. ex Müll. Arg.) Müll. Arg.	–	–	2	–	2
Malvaceae	<i>Pseudobombax grandiflorum</i> (Cav.) A. Robyns	–	1	1	–	2
Meliaceae	<i>Trichilia catigua</i> A. Juss.	–	2	–	–	2
Monimiaceae	<i>Mollinedia widgrenii</i> A. DC.	–	2	–	–	2
Myrtaceae	<i>Eugenia blastantha</i> (O. Berg) D. Legrand	–	2	–	–	2
Myrtaceae	<i>Myrcia</i> cf. <i>diaphana</i> (O. Berg) N. Silveira	–	2	–	–	2
Nyctaginaceae	<i>Guapira opposita</i> (Vell.) Reitz	–	2	–	–	2
Oleaceae	<i>Chionanthus trichotomus</i> (Vell.) P.S. Green	–	2	–	–	2
Picramniaceae	<i>Picramnia sellowii</i> Planch.	–	2	–	–	2
Rubiaceae	<i>Ixora</i> cf. <i>venulosa</i> Benth.	–	–	2	–	2
Rutaceae	<i>Galipea jasminiflora</i> (A. St.-Hil.) Engl.	–	2	–	–	2
Salicaceae	<i>Casearia decandra</i> Jacq.	–	1	1	–	2
Siparunaceae	<i>Siparuna guianensis</i> Aubl.	–	2	–	–	2
Annonaceae	<i>Xylopia brasiliensis</i> (L.) Spreng.	–	–	–	1	1
Apocynaceae	<i>Aspidosperma cylindrocarpon</i> Müll. Arg.	–	1	–	–	1
Celastraceae	<i>Maytenus</i> cf. <i>floribunda</i> Reissek	–	–	1	–	1
Clusiaceae	<i>Clusia criuva</i> Cambess.	–	1	–	–	1
Combretaceae	<i>Terminalia brasiliensis</i> (Cambess.) Eichler	–	1	–	–	1
Euphorbiaceae	<i>Croton floribundus</i> Spreng.	–	1	–	–	1
Euphorbiaceae	<i>Pera obovata</i> (Klotzch) Baill.	–	1	–	–	1
Fabaceae	Fabaceae sp1.	–	1	–	–	1
Lauraceae	Lauraceae sp1.	–	1	–	–	1
Malvaceae	<i>Guazuma ulmifolia</i> Lam.	–	1	–	–	1
Moraceae	<i>Sorocea bomplandii</i> (Baill.) W.C. Burger, Lanj. & Wess. B.	–	1	–	–	1
Myrtaceae	<i>Eugenia dodoneifolia</i> Cambess.	–	1	–	–	1
Myrtaceae	<i>Eugenia</i> sp.	–	1	–	–	1
Myrtaceae	<i>Myrcia</i> sp.	–	1	–	–	1
Myrtaceae	<i>Myrciaria floribunda</i> (H. West ex Willd.) O. Berg	–	1	–	–	1
Phyllantaceae	<i>Phyllanthus</i> sp.	–	1	–	–	1
Phyllantaceae	<i>Savia dictyocarpa</i> Müll. Arg.	–	1	–	–	1
Polygonaceae	<i>Coccoloba</i> cf. <i>glaziovii</i> Lindau	–	1	–	–	1
Rosaceae	<i>Prunus myrtifolia</i> (L.) Urb.	–	1	–	–	1
Rubiaceae	<i>Palicourea marcgravii</i> A. St.-Hil.	–	1	–	–	1
Rutaceae	<i>Esenbeckia grandiflora</i> Mart.	–	1	–	–	1
Sapindaceae	<i>Matayba guianensis</i> Aubl.	–	1	–	–	1

Species abbreviations of the 27 most common species were used in a canonical correspondence analysis—CCA (Fig. 1). Each plot = 0.15 ha

**Table 2** Environmental data of the three sample plots in a Neotropical swamp forest in southeastern Brazil

Environmental data	Plot 1 Gleysoils	Plot 2 Gleysoils	Plot 3 Neosoils
Average elevation (m)	632.5 ± 1.2	640.0 ± 1.1	648.3 ± 1.5
H + Al (mmol <sub>c</sub> dm <sup>-3</sup> )	46.1 ± 9.6	52.9 ± 7.3	82.7 ± 10.5
CEC (mmol <sub>c</sub> dm <sup>-3</sup> )	97.2 ± 15.3	93.8 ± 4.6	117.9 ± 10.6
V (%)	50.8 ± 14.4	43.7 ± 6.4	29.8 ± 7.0

*N* = 15 quadrats per plot

for species was 2.13, and the Pielou's evenness index (*J'*) was 0.58. The ten highest abundant species accounted for 90% of all individuals. The total basal area was 50.4 m<sup>2</sup> ha<sup>-1</sup> and the highest diameter value (54.8 cm) was found in *Cedrela odorata*. 7.3% of all individuals had DBH > 15 cm. Intermediate values of V and H + Al were registered in this plot.

A sum of 1,327 individuals (tree palms represented 48% of the total) belonging to 35 species (five exclusives) and 22 families was found in plot 3. The diversity index (*H'*) was 2.22, and the Pielou's evenness index (*J'*) was 0.62. The ecological dominance was also higher, so the ten highest density species represented 89% of all individuals. The total basal area was 49.1 m<sup>2</sup> ha<sup>-1</sup> and the highest diameter was obtained with *Magnolia ovata* (47.8 cm). 5.6% of all individuals had DBH > 15 cm. From those most abundant sampled species (*n* > 100 individuals), excluding palms, *Calophyllum brasiliense*, *Calypttranthes concinna*, *Protium spruceanum*, *Dendropanax cuneatus*, and *Trichilia pallida* were represented by individuals with lower diameter in this plot than in the other plots. *Magnolia ovata* showed similar diameter distribution between plots (Fig. 2). Although CTC was higher than Gleysoils due to the content of organic matter and conveyed clay, base saturation was lower, and potential acidity was higher, thus making such plot soils less fertile and more acidified.

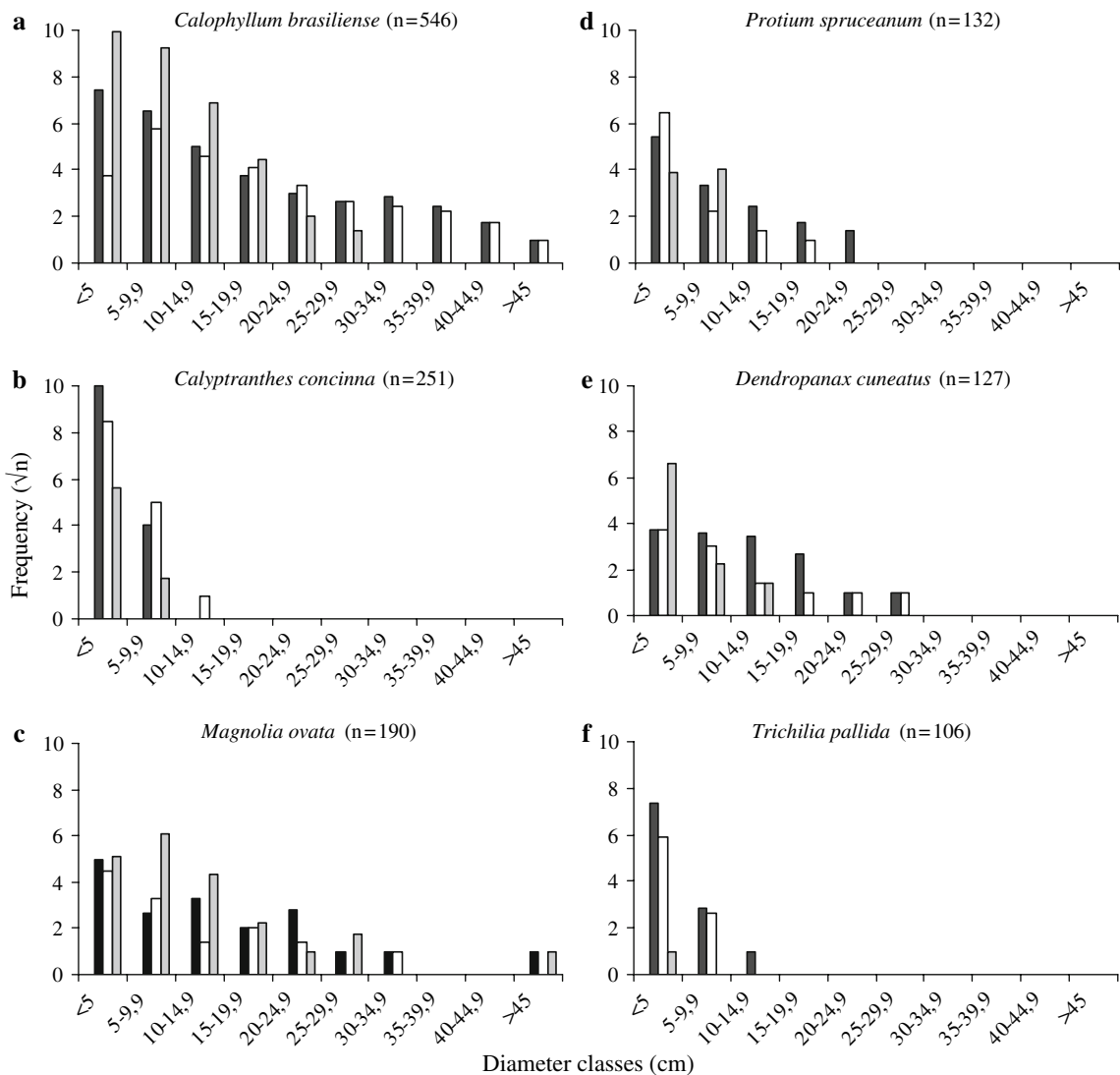
## Discussion

Although some species were amongst the 10 most abundant ones, both in the overall sample area and in each sample plot, with alternation events occurring only in their abundance position among plots, substantial differences in floristic composition between them were detected in a fine spatial scale. The periodically waterlogged plot 1 presented about

twice as many species and families than the other sample plots. The highest number of species in plot 1 (47% unique) and few shared species in all three plots proved that swamp forest specific composition is spatially heterogeneous within a scale of few meters (40 m). A mosaic of situations created by micro topography variations including well drained hummocks, permanently flooded pits and natural drainage channels is a common feature in Brazilian swamp forests (Scarano et al. 1997; Toniato et al. 1998; Souza and Martins 2005). However, the most accentuated topographic ruggedness in comparison with the other swamp forests determined the existence of different drainage patterns in distinct topographic sectors of the studied forest. Differences in soil drainage probably modified soil chemical properties of the studied area. The flooding regime has been pointed out to be the primary agent in determining chemical, physical and biological soil status of the riverine forests (Hughes 1990; Veneklaas et al. 2005).

The higher spatial heterogeneity within the inferior topographic section (including better drained and higher soil fertility) allows the coexistence of a high amount of hygrophilous species, and those ones found on better drained soils within a very small area (77 species in 0.15 ha), characterizing a swamp-semi-deciduous forest ecotone. For instance, *Aspidosperma cylindrocarpon*, *Casearia sylvestris*, *Croton floribundus*, *Eugenia dodoneifolia*, *Galipea jasminiflora*, *Mollinedia widgrenii*, *Pseudobombax grandiflorum*, *Siparuna guianensis*, *Terminalia brasiliensis* and *Trichilia catigua* are tree species constantly sampled in semi-deciduous and eventual flooded riverine forests. These species were sampled only in the inferior section. On the other side, the soil surface homogeneity in the superior and intermediate topographic sections might have determined their lowest number of species and diversity. Whereas a variety of habitats and microsites mixed in small continuous areas can increase





**Fig. 2** Diameter classes distributions for tree species with trunk height >1.3 m in three sample plots in the swamp forest in southeastern Brazil. ■ Plot 1; □ Plot 2; ▒ Plot 3

plant diversity within flooded remnants (Ferreira and Stohlgren 1999; Cattanio et al. 2002; Koponen et al. 2004), niche differentiation may be further reduced by uniform conditions imposed by the superficial water layer (Duivenvoorden 1996). Besides soil evenness, partial or total lack of oxygen supply determined by water saturation is a strongly selective factor on species establishment (Joly 1991).

Our results show that niche differentiation must be an important factor related to the increase of local diversity. Besides the increase in specific richness and diversity inside the inferior topographic section, we

observed that the environmental heterogeneity among plots provided an increase in the total number of species found in the forest remnant (86 species). Regarding the fact that comparisons between different remnants of swamp forests studied in Brazil in terms of number of species are not precise because of both different sampled areas (from 0.1 to 1.0 ha) and different criteria for species inclusion (from 1.3 m of height in this study to DBH > 5 cm) (see Silva et al. 2007), the species number found in the present study was relatively high. The number of species in the swamp forests of southeastern and central Brazil

regions ranged mainly from 30 to 60 species (e.g. Torres et al. 1994; Ivanauskas et al. 1997; Toniato et al. 1998; Marques et al. 2003; Nogueira and Schiavini 2003; Guarino and Walter 2005; Scarano 2006).

Regarding palm species, *Syagrus romanzoffiana* occurred predominantly in plot 1, but *Euterpe edulis* and *Geonoma brevispatha* had an increase in density as soil water saturation went up. The higher ecological dominance of palm trees in more flooded environments is a common fact in Neotropical forests (Kahn and Mejia 1990; van Andel 2003). Whereas *S. romanzoffiana* has a more generalist habitat, *G. brevispatha* is restricted to swamp forests in central and southeastern South America (Henderson et al. 1995), and the threatened *E. edulis* occurs in the Atlantic rainforest as well as along riverine forests in the Brazilian countryside (Reis et al. 2000).

Besides floristic changes, we observed structural differences within the studied forest. Regarding trees, higher abundance and lower DBH were found along with the increase of soil water saturation. Higher plant density seems to reflect the natural dynamics of flooded ecosystems, where there is some compensation for space occupation with reduced individual sizes, though with higher densities. Souza and Martins (2005) have stated that swamp forests present similar architectures as those ones found in tree fall gaps in surrounding non-flooded vegetation because of the low stature and high density.

Under fine spatial scale approaches, we can observe that floristic and structural variations within a particular swamp forest can be related to different soil conditions. Even though the most abundant species were the same in each forest plot, the floristic differences were noticeable and contributed to the increase of local diversity. Concerning the small scale of the survey (i.e., internal variation of an 8-ha remnant), our results agree with the spatial species distribution pattern observed in large scales of swamp forests, in which the most abundant species (e.g. *C. brasiliense*, *M. ovata*, *P. spruceanum* and *D. cuneatus*) repeat themselves at high density rates in the different remnants. However, the floristic composition of each remnant is strongly variable, contributing to the increase of the regional diversity.

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