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Articles

Structure and phytogeographic relationships of swamp forests of Southeast Brazil

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ABSTRACT

Swamp forests are associated with soils that are saturated or inundated because of a high water table. In Brazil, little is known about the plant ecology of such forests. In this paper, we aimed to describe the phytosociological structure of the tree layer of swamp forests in Restinga de Jurubatiba National Park, in the northern part of the state of Rio de Janeiro, and to evaluate the floristic similarities between these forests and some other possibly related types of vegetation formations in Brazil. The sampling included 84 species, within 62 genera and 34 families. The Shannon diversity index was 3.42, and the Shannon evenness index was 0.77. The forests studied showed an oligarchic structure; *Tapirira guianensis*, *Calophyllum brasiliense* and *Protium icicariba* were the most important species. Oligarchy, or monodominance, and relatively low species richness are the norm in the swamp forests of southeastern Brazil and result from the strong selective character of the saturated/inundated soils. In comparison with local areas of *restinga* (coastal woodland), Atlantic Forest *sensu stricto*, other swamp forests and flooded riparian forests, the similarity was low (Jaccard similarity coefficient < 0.25). In addition to the similar ecological conditions, geographic proximity was a key factor determining the patterns of similarity found. Our results indicate that the swamp forests of southeastern Brazil do not represent a distinguishable floristic unit, due to sources of local variation, notably migration and the establishment of adaptive species from neighboring vegetation formations (some 70% of the species surveyed).

Key words: Atlantic Forest biome, Jaccard similarity coefficient, phytogeography, phytosociology, coastal sand plain

Introduction

Swamp forests comprise vegetation that develops on soils saturated or inundated by the water table (WCMC 1992; Scarano 2006). In Brazil, such forests are known by a variety of local names (Dorneles & Waechter 2004). These forests are naturally fragmented and are associated with hydromorphic soils, occurring near springs, on the banks of rivers or lakes and within natural topographic depressions (Ivanauskas *et al*. 1997; Toniato *et al*. 1998; Jacomine 2004). They are widely distributed throughout the neotropics and present interfaces with various types of vegetation formations, including different types of forests and grasslands (Teixeira & Assis 2011).

Until recently, little was known about the plant ecology of swamp forests in Brazil. However, in the last 20 years, many local surveys have been conducted in the southeastern, southern and central-west regions of Brazil (Teixeira & Assis 2011; Tab. 1). This increase of local floristic data has made it possible to conduct a number of large-scale phytogeographic analyses, in which swamp forests have been compared with flooded riparian forests (Rodrigues & Nave 2004; Silva *et al*. 2007) or with each other (Teixeira & Assis 2011). However, the authors of such studies have focused their analyses on swamp forests located on the Brazilian Highlands, evaluating only two areas of swamp forest in the coastal plains, where a number of local surveys have already been conducted (Tab. 1).

A number of studies have defined the overall structural and floristic patterns of Brazilian swamp forests: low diversity; the predominance of one or a few species—including the flooded-forest specialist species *Calophyllum brasiliense* Cambess., *Symphonia globulifera* L.f. and *Tabebuia cassinoides* (Lam.) DC., in areas of the coastal plain of the state of

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Table 1. Quantitative parameters of the tree/shrub-tree layer of swamp forests in southern and southeastern Brazil.

Code	Area	IC	A/P	N	S	H'	J'	D	BA	Reference
Coastal plains										
JU1	Restinga de Jurubatiba National Park, RJ	DBH ≥ 5 cm	1.44	2164	84	3.42	0.77	1503	24.9	This study
JU2	Restinga de Jurubatiba National Park, RJ	DBH ≥ 5 cm	0.5	938	45	2.79	0.73	1876	32.9	Oliveira (2000)
JU3	Restinga de Jurubatiba National Park, RJ	DBH ≥ 5 cm	0.52	827	49	2.76	0.71	1590	13.9	Barros (2000)
PA1	Poço das Antas Biological Reserve, RJ	DBH ≥ 10 cm; height ≥ 10 m	1	486	97	3.98	0.87	486	23.8	Guedes-Bruni *et al.* (2006a)
PA2	Poço das Antas Biological Reserve, RJ	DBH ≥ 10 cm	0.72	628	31	1.75* 1.99*	0.57* 0.66*	1003* 742*	36.5* 37.0*	Carvalho *et al.* (2006b)
PA3	Poço das Antas Biological Reserve, RJ	DBH ≥ 3.5 cm	0.5	1744	59	1.30	-	3488	-	Scarano (2006)
CE1	Campina do Encantado State Park, SP (shallow peat forest)	DBH ≥ 4.8 cm	0.3	519	46	2.98	0.78	1730	27.7	Sztutman & Rodrigues (2002)
CE2	Campina do Encantado State Park, SP (deep peat forest)	DBH ≥ 4.8 cm	0.2	546	5	0.82	0.51	2730	19.2	Sztutman & Rodrigues (2002)
ICA	Ilha do Cardoso, Cananéia, SP (site II)	DBH ≥ 1.6 cm	0.1	867	30	2.44	0.71	8670	23.3	Sugiyama (1998)
IM1	Ilha do Mel, Paranaguá, PR	DBH ≥ 5 cm	0.56	1510	53	3.22	0.81	2696	45.4	Silva *et al.* (1994)
IM2	Ilha do Mel Ecological Station, PR (periodically flooded swamp)	DBH ≥ 4.8 cm	0.3	500	54	3.22	0.81	1667	36.9	Menezes-Silva (1998)
IM3	Ilha do Mel Ecological Station, PR (permanently flooded swamp)	DBH ≥ 4.8 cm	0.4	607	60	3.21	0.78	1518	54.4	Menezes-Silva (1998)
PST	Passa-Sete, Morretes, PR	DBH ≥ 10 cm	0.26	419	13	-	-	1610	31.5	Galvão *et al.* (2002)
BAT	Batuva, Guaraqueçaba, PR	DBH ≥ 10 cm	0.16	312	13	-	-	1951	36.4	Galvão *et al.* (2002)
CAB	Cabaraquara, Matinhos, PR	DBH ≥ 10 cm	0.32	443	26	-	-	1384	48.7	Galvão *et al.* (2002)
ATA	Atami, Pontal do Paraná, PR	DBH ≥ 10 cm	0.2	410	28	-	-	2050	38.6	Galvão *et al.* (2002)
ALE	Alexandra-Matinhos, Matinhos, PR	DBH ≥ 10 cm	0.2	337	36	-	-	1685	49.7	Galvão *et al.* (2002)
GT1	Guaratuba 1, Guaratuba, PR	DBH ≥ 10 cm	0.3	400	26	-	-	1333	27.5	Galvão *et al.* (2002)
GT2	Guaratuba 2, Guaratuba, PR	DBH ≥ 10 cm	0.4	434	78	-	-	1085	40.1	Galvão *et al.* (2002)
TOR	Torres, RS	DBH ≥ 2.5 cm	0.2	706	60	-	-	3530	34.4	Kindel (2002)
LPE	Lagoa do Peixe National Park, RS	DBH ≥ 5 cm	60	240	21	2.60	0.85	3479	-	Dorneles & Waechter (2004)
TAI	Taim, RS	DBH ≥ 10 cm	30	120	12	1.89	0.76	791	-	Waechter & Jarenkow (1998)
Highlands										
COQ	Coqueiral, MG	DBH ≥ 5 cm	0.32	585	99	3.50	0.76	1828	36.1	Rocha *et al.* (2005)
SRC	Santa Rita de Caldas, MG	DBH ≥ 5 cm	1	2982	110	2.98	0.63	2982	45.4	Loures *et al.* (2007)
CA1	Campinas, SP	DBH ≥ 3.2 cm	0.2	904	55	2.80	0.70	4520	29.0	Toniato *et al.* (1998)
CA2	Campinas Experimental Center, SP	DBH ≥ 5 cm	0.87	930	33	2.45	0.70	1069	-	Torres *et al.* (1994)
BR1	Brotas, SP	DBH ≥ 5 cm	0.36	735	51	2.81	0.71	2042	-	Marques *et al.* (2003)
BR2	Brotas, SP	DBH ≥ 4.8 cm	0.2	498	33	2.52	0.72	2490	-	Costa *et al.* (1997)
ITA	Itatinga, SP	DBH ≥ 4.8 cm	1	1242	39	2.75	0.75	1242	17.3	Ivanauskas *et al.* (1997)
AGU	Agudos, SP	DBH ≥ 4.8 cm	0.22	989	34	2.60	0.74	4496	-	Paschoal & Cavassan (1999)
RCL	Rio Claro, SP	DBH ≥ 4.8 cm	0.45	1651	49	2.10	0.54	3669	48.4	Teixeira & Assis (2005)
BRA	Brasília National Park, DF	DBH ≥ 3 cm	0.8	2763	60	2.99	0.73	3454	44.4	Guarino & Walter (2005)
SUC	Sucupira farm, DF	DBH ≥ 3 cm	0.8	2667	53	2.84	0.71	3334	33.5	Guarino & Walter (2005)

IC – inclusion criterion; A/P – sample area (ha)/number of points; N – number of live trees surveyed; S – number of species; H' – Shannon diversity index; J' – Shannon evenness index; D – total density (trees.ha^{-1}); BA – basal area (m^2.ha^{-1}); RJ – (state of) Rio de Janeiro; DBH – diameter at breast height; SP – (state of) São Paulo; PR – (state of) Paraná; RS – (state of) Rio Grande do Sul; MG – (state of) Minas Gerais; DF – *Distrito Federal* (Federal District) of Brasília.
*Values for the two sites studied.

Rio de Janeiro (Scarano *et al.* 1997); and flora that is heavily influenced by the surrounding vegetation (*e.g.*, Teixeira & Assis 2011). However, in comparison with other vegetation formations in Brazil, little is known about these wetlands. As previously mentioned, the few large-scale comparisons conducted to date have focused mainly on the swamp forests of the Brazilian Highlands. Therefore, there is a need for not only additional local surveys but also for further phytogeographic analyses that include swamp forests on the coastal plain.

Within the Atlantic Forest biome, especially in the coastal plains, many swamp forests have been cleared or disturbed by changes in the flooding regime, timber extraction or fire (Ivanauskas *et al.* 1997; Galvão *et al.* 2002; Carvalho *et al.* 2006b; Scarano 2006). This poor conservation status is not surprising, given that the biome as a whole has been reduced to 11.4-16.0% of its original size (Ribeiro *et al.* 2009). Unfortunately, although the Atlantic Forest is internationally recognized as a biodiversity hotspot (Myers *et al.* 2000; Mittermeier *et al.* 2005) and now benefits from a number of conservation initiatives and policies (Aguiar *et al.* 2003; Rocha *et al.* 2006), its marginal habitats (*sensu* Scarano 2002), such as the swamp forests, are not always treated with such care (Scarano 2009, Ribeiro *et al*. 2011).

Our paper focuses on a particular set of swamp forests in southeast Brazil, namely those that appear on marine sand deposits within areas of *restinga* (coastal woodland), which are ecosystems associated with the Atlantic Forest (Scarano 2009). These Quaternary deposits are covered by a mosaic of vegetation, ranging from sparse herbaceous to dense forest vegetation (Araujo *et al*. 1998).

The objective of this study was to describe the phytosociological structure of the tree layer of the swamp forests in southeastern Brazil, as well as to determine the extent to which they are floristically similar to local areas of open *restinga*, Atlantic Forest *sensu stricto*, other swamp forests, and flooded riparian forests. We also sought to determine whether those swamp forests presented phytogeographic relationships with the other vegetation formations.

Material and methods

Study area

Our study area was within Restinga de Jurubatiba National Park (22°08'-22°19'S; 41°17'-41°43'W), which is located on the northern coast of the state of Rio de Janeiro, in southeastern Brazil (Fig. 1). The park encompasses portions of the municipalities of Macaé, Carapebus and Quissamã, covering an area of 14,839 ha, and preserves one of the most important remnants of the *restinga* ecosystem in Brazil (Esteves 1998; Rocha *et al*. 2004).

The study area is in the southern portion of an extensive Quaternary coastal plain, the origin of which is closely related to the evolution of the Paraíba do Sul River delta. This portion of the plain is composed mainly of Pleistocene marine sands; Holocene marine deposits are scarce and limited to a narrow strip near what is now the shoreline. The Pleistocene terraces are limited inwards by Tertiary sediments of the Barreiras Formation (Martin *et al*. 1993). This great coastal plain has been extensively drained and inhabited by humans since the seventeenth century. An extensive network of artificial canals—initially constructed to transport agricultural products and timber but subsequently used in order to increase the amount of arable land—lowered the water table level and dried up many local lagoons and swamps. In addition, levees were built along the Paraíba do Sul River to prevent flooding on part of the plain (Martin *et al*. 1993; Soffiati 1998).

Restinga de Jurubatiba National Park is also a research station for the Brazilian Long-Term Ecological Research Program (Barbosa *et al*. 2004; Rocha *et al*. 2004). In recent years, a number of plant ecology studies have been

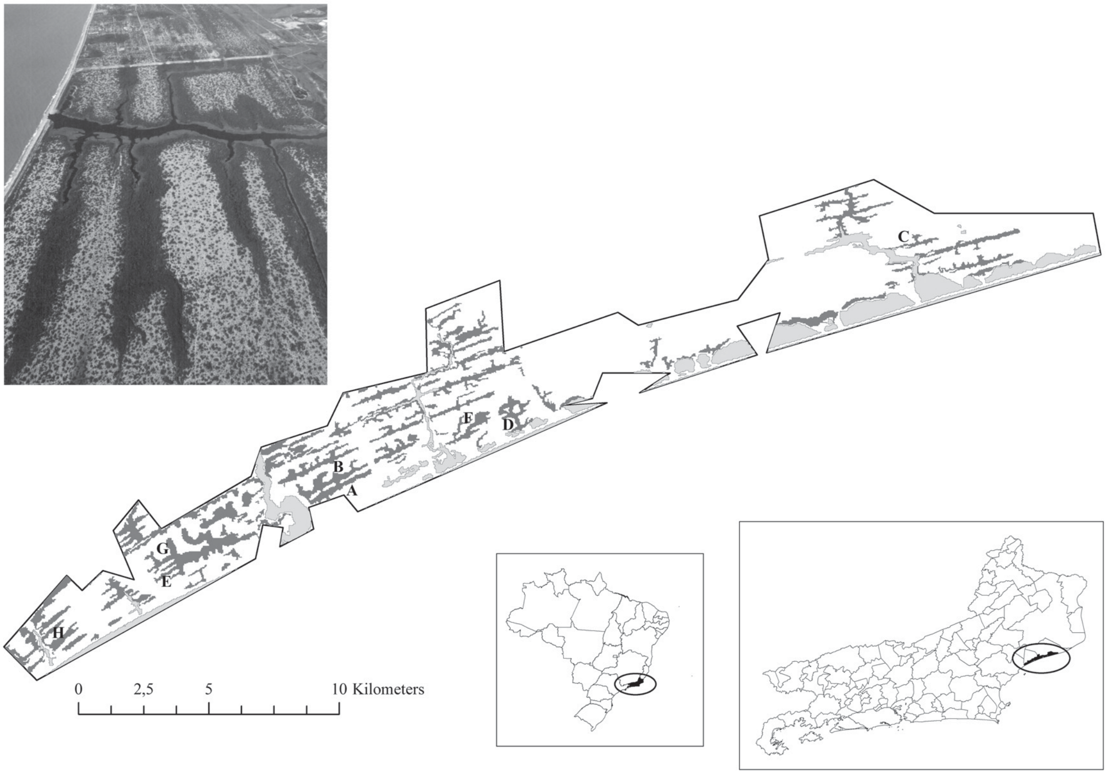

Figure 1. Map of Restinga de Jurubatiba National Park, in the state of Rio de Janeiro, Brazil, showing coastal lagoons and the Atlantic Ocean (light gray); forest formations (dark gray); and the eight swamp forest study sites (A-H). In the detail, aerial photograph of the southwestern edge of the park, showing the swamp forests associated with the Jurubatiba lagoon (photo: Romulo Campos).

conducted within the park (Scarano *et al*. 2004). Mean annual precipitation is 1164 mm and rainfall is strongly seasonal, with monthly averages ranging from 41 mm in winter (June) to 189 mm in summer (December). The mean annual temperature is 22.6°C, with monthly averages ranging from a maximum of 29.7°C, in January, to a minimum of 20.0°C, in July (Henriques *et al*. 1986).

The swamp forests studied are among some ten types of vegetation formations found in the study area (Araujo *et al*. 1998) and occur in swales between successive ancient beach ridges, expanding over branches of local lagoons. The swamp forests are subjected to flooding due to a rise in the water table during the rainy season (October-March). The most typical shape of such forests is that of long strips parallel to the coastline, varying in width (but mostly narrow), abruptly or gradually giving way to areas of open *restinga* on either side (Fig. 1). Although the *restinga* studied was formed predominantly during the Pleistocene, the conditions did not become conducive to swamp formation until more recently, a result of the silting of lagoons formed by Holocene marine sand damming of waters (Martin *et al*. 1993). These swamp forests are subjected to two flooding gradients related to variations in topography. First, there is a gradient over the cross section, in which the forest bottom (i.e., the center, which is topographically lower) is more intensely flooded than are the edges, which seldom flood, and there are changes in physico-chemical characteristics of the soil, the hydromorphic conditions resulting in increased accumulation of organic matter (> 2 m thick in the bottom, Araujo *et al*. 1998). Second, there is a flooding gradient related to the distance from the lagoons. These flooding gradients are responsible for physiognomic and structural variation within short distances (< 100 m). At the canopy level (a height of approximately 20 m), the most common tree species are *Tapirira guianensis* Aubl., *Calophyllum brasiliense* and *Symphonia globulifera*. The understory is typically not very dense. The main understory species are *Protium icicariba* (DC.) Marchand and *Geonoma schottiana* Mart., which proliferate along the forest edges and bottoms, respectively. The trees within swamp forest often have slender trunks, with diameters that rarely exceed 50 cm.

According to local inhabitants, these swamp forests were intensively exploited in the past, mainly for the collection of firewood. In addition, some tree species were extracted for their timber or other products, such as hearts of palm from *Euterpe edulis* Mart. The interviewees reported that the extraction was more pronounced on the firm ground along the forest edges than on the unstable peaty soil of the bottoms. Nevertheless, some of the swamps have been completely deforested. Until recently, there were reports of illegal burning of swamp forests, which during dry periods destroyed a significant area of those forests, mainly due to the difficulties in controlling the burning of dry peat. As a result, the local swamp forests are now a mosaic of different successional stages.

Sampling

The study was conducted between 2002 and 2004 at eight randomly chosen sites of periodically flooded swamp forests associated with different lagoons (Fig. 1). Aiming to include a wide range of environmental conditions, we established three sets of three 4 × 50 m quadrats at each site: one set at each edge and one in the bottom. Therefore, we established a total of 72 quadrats (nine per site), corresponding to a total sampling area of 1.44 ha. Edges and bottoms were distinguished by topographic, edaphic and physiognomic characteristics. We measured diameter at breast height (DBH, 1.3 m above the ground) and sampled only those trees with a DBH ≥ 5 cm. For trees that forked or branched below 1.3 m, only the branches with a DBH ≥ 5 cm were measured. We used the elongated quadrats in order to match the long, narrow shape of the swamps (the longer side followed the main axis of the swamps). The dimensions of the quadrats were adapted, from Gentry (1982), to our inclusion criterion.

The botanical material was identified on the basis of the specialized literature, by comparison with specimens in the collections of the Herbarium of the Research Institute of the Rio de Janeiro Botanical Garden (code, RB) and, when possible, through consultation with specialists. Voucher specimens were deposited in the RB. Species were classified in accordance with the Angiosperm Phylogeny Group III guidelines (APG III 2009), and the classification of genera by family followed Souza and Lorenzi (2008).

Phytosociological structure

For each species, we calculated the relative values of density, frequency, dominance and importance value (Mueller-Dombois & Ellenberg 1974). The Shannon diversity and evenness indices (H' and J', respectively), using the natural logarithm, followed Zar (1996). The calculations were performed with the FITOPAC program, version 1.6 (Shepherd 2006).

Phytogeographic relationships

The Jaccard similarity coefficient (Magurran 1988) was used for floristic comparisons between the swamp forests within the study area and other vegetation formations described in previous studies conducted in Brazil. These comparisons included two categories: neighboring vegetation formations (areas of dry *restinga* and Atlantic Forest); and floodplain forests (other swamp forests and flooded riparian forests). We do not intend, obviously, to include all studies of such vegetation formations, but rather to select those considered appropriate for the establishment of phytogeographic patterns. Phytosociological surveys were the main sources of data (Tab. 2). Unidentified species were excluded, as were allochthonous species. According to Mueller-Dombois & Ellenberg (1974), Jaccard similarity coefficients > 0.25 indicate floristic similarity between the units compared. The names of all species were reviewed in accordance with the List of Species of the Brazilian Flora (Lista de Espécies da Flora do Brasil 2012) or by consulting specialists. In addition, we calculated the percentages of species within the study area that had also been registered in the same types of vegetation formations used for comparison by the Jaccard similarity coefficient.

Results

Phytosociological structure

We surveyed 2164 live trees, belonging to 84 species, 62 genera and 34 families (Tab. 3). Of those 84 species, six (7.1%) accounted for nearly half (48.8%) of the individuals surveyed. Those six species were *Tapirira guianensis*, *Protium icicariba*, *Geonoma schottiana*, *Euterpe edulis*, *Calophyllum brasiliense* and *Tabebuia cassinoides*. The most important was *T. guianensis*, which, together with *C. brasiliense* and *P. icicariba*, accounted for ≈34% of total importance value. Conversely, 15 (17.9%) of the 84 species (including *Elaeis guineensis*, an exotic palm species of African origin), were represented by a single individual. The H' was 3.42, and the J' was 0.77.

Of the 84 species surveyed, 40 (47.6%) belonged to one of six families: Myrtaceae (n = 14); Lauraceae (n = 7); Clusiaceae (n = 6); Arecaceae (n = 5); Annonaceae (n = 4); and Moraceae (n = 4). As can be seen in Tab. 3, the most species-rich genera were *Myrcia* (7 species); *Eugenia* (4 species), *Ficus* (4 species), *Ocotea* (3 species) and *Protium* (3 species).

Table 2. Jaccard similarity coefficients between the swamp forests studied in Restinga de Jurubatiba National Park, in the state of Rio de Janeiro, and other vegetation formations in Brazil.

Habitat/area	Alt.	Dist.	IC	S	I	Jaccard	Reference
Open *restinga*							
Restinga de Jurubatiba National Park, RJ (*Clusia* scrub)	< 12	-	height ≥ 0.5 m	61	59	0.21	Araujo *et al.* (2004)
Restinga de Jurubatiba National Park, RJ (*Clusia* scrub)	< 12	-	woody vegetation	35	31	0.17	Zaluar (1997)
Restinga de Jurubatiba National Park, RJ (Ericaceae scrub)	< 12	-	CD ≥ 0.5 m	43	34	0.15	Montezuma (1997)
Atlantic Forest *sensu stricto*							
Poço das Antas Biological Reserve, RJ	12-200	86	DBH ≥ 10 cm; height ≥ 10 m	169	129	0.11	Guedes-Bruni *et al.* (2006b)
Bacia do Rio São João/Mico Leão Dourado Environmental Protection Area, RJ	30-400	106	DBH ≥ 5 cm	161	141	0.06	Carvalho *et al.* (2006a)
Itatiaia National Park, RJ	1067	319	DBH ≥ 10 cm; height ≥ 10 m	150	114	0.06	Guedes-Bruni (1998)
Praia do Sul State Biological Reserve, RJ (25-year-old forest)	140	307	DBH ≥ 2.5 cm; height ≥ 2 m	70	61	0.06	Oliveira (2002)
Paraíso State Ecological Station, RJ	200	146	DBH ≥ 5 cm	138	115	0.06	Kurtz & Araujo (2000)
Praia do Sul State Biological Reserve, RJ (50-year-old forest)	260	292	DBH ≥ 2.5 cm; height ≥ 2 m	63	50	0.06	Oliveira (2002)
Campos dos Goytacazes, RJ	50	49	DBH ≥ 10 cm	125	95	0.05	Moreno *et al.* (2003)
Tijuca Mountain, RJ	500-700	199	DBH ≥ 2.5 cm; height ≥ 2 m	203	169	0.05	Oliveira *et al.* (1995)
Santa Lúcia Biological Station, ES (mountaintop)	820-855	271	DBH ≥ 6.4 cm	238	107	0.05	Thomaz & Monteiro (1997)
Santa Lúcia Biological Station, ES (valley bottom)	650-660	271	DBH ≥ 6.4 cm	228	116	0.05	Thomaz & Monteiro (1997)
Macaé de Cima Ecological Reserve, RJ (30-year-old forest)	1000	104	DBH ≥ 5 cm	155	122	0.05	Pessoa *et al.* (1997)
Campos dos Goytacazes, RJ	250	49	DBH ≥ 10 cm	145	109	0.04	Moreno *et al.* (2003)
Magé, RJ (disturbed forest)	30	160	DBH ≥ 5 cm	90	70	0.04	Guedes (1988)
Santa Lúcia Biological Station, ES (mountainside)	675-700	271	DBH ≥ 6.4 cm	221	107	0.04	Thomaz & Monteiro (1997)
Serra da Capoeira Grande Environmental Protection Area, RJ	60-150	234	DBH ≥ 4.8 cm	69	63	0.04	Peixoto *et al.* (2004)
Ilha Grande State Park, RJ (climax forest)	280	292	DBH ≥ 2.5 cm; height ≥ 2 m	134	101	0.03	Oliveira (2002)

Continues

Table 2. Continuation.

Habitat/area	Alt.	Dist.	IC	S	I	Jaccard	Reference
Macaé de Cima Ecological Reserve, RJ (preserved forest)	1100	104	DBH ≥ 5 cm	189	172	0.02	Guedes-Bruni *et al.* (1997)
Swamp forests							
Restinga de Jurubatiba National Park, RJ	< 12	9.8*	DBH ≥ 5 cm	45	37	0.39	Oliveira (2000)
Restinga de Jurubatiba National Park, RJ	< 12	12.5*	DBH ≥ 5 cm	49	39	0.38	Barros (2000)
Campina do Encantado State Park, SP (shallow peat forest)	< 15	695	DBH ≥ 4.8 cm	46	45	0.18	Sztutman & Rodrigues (2002)
Poço das Antas Biological Reserve, RJ	10	86	DBH ≥ 10 cm; height ≥ 10 m	97	81	0.17	Guedes-Bruni *et al.* (2006a)
Ilha do Mel, Paranaguá, PR	< 5	783	DBH ≥ 5 cm	53	50	0.16	Silva *et al.* (1994)
Guaratuba 2, Guaratuba, PR	5	835	DBH ≥ 10 cm	78	59	0.16	Galvão *et al.* (2002)
Ilha do Mel Ecological Station, PR (periodically flooded swamp)	< 5	783	DBH ≥ 4.8 cm	54	52	0.16	Menezes-Silva (1998)
Ilha do Mel Ecological Station, PR (permanently flooded swamp)	< 5	783	DBH ≥ 4.8 cm	60	55	0.15	Menezes-Silva (1998)
Poço das Antas Biological Reserve, RJ	10	86	DBH ≥ 10 cm	31	29	0.13	Carvalho *et al.* (2006b)
Torres, RS	< 20	1140	DBH ≥ 2.5 cm	60	50	0.12	Kindel (2002)
Alexandra-Matinhos, Matinhos, PR	5	816	DBH ≥ 10 cm	36	29	0.11	Galvão *et al.* (2002)
Ilha do Cardoso, Cananéia, SP (site II)	< 14	725	DBH ≥ 1.6 cm	30	30	0.11	Sugiyama (1998)
Atami, Pontal do Paraná, PR	3	791	DBH ≥ 10 cm	29	19	0.1	Galvão *et al.* (2002)
Guaratuba 1, Guaratuba, PR	5	829	DBH ≥ 10 cm	26	22	0.1	Galvão *et al.* (2002)
Lagoa do Peixe National Park, RS	< 15	1367	DBH ≥ 5 cm	21	21	0.09	Dorneles & Waechter (2004)
Cabaraquara, Matinhos, PR	2-3	820	DBH ≥ 10 cm	27	23	0.08	Galvão *et al.* (2002)
Itatinga, SP	570	740	DBH ≥ 4.8 cm	39	35	0.07	Ivanauskas *et al.* (1997)
Poço das Antas Biological Reserve, RJ	10	86	DBH ≥ 3.5 cm	59	23	0.07	Scarano (2006)
Rio Claro, SP	630-650	612	DBH ≥ 4.8 cm	49	43	0.07	Teixeira & Assis (2005)
Brasília National Park, DF	990-1040	1013	DBH ≥ 3 cm	60	45	0.07	Guarino & Walter (2005)
Agudos, SP	550	763	DBH ≥ 4.8 cm	34	32	0.06	Paschoal & Cavassan (1999)
Taim, RS	< 10	1582	trees	19	19	0.05	Waechter & Jarenkow (1998)
Campinas, SP	590-610	578	DBH ≥ 3.2 cm	55	49	0.05	Toniato *et al.* (1998)
Passa-Sete, Morretes, PR	10	825	DBH ≥ 10 cm	13	12	0.04	Galvão *et al.* (2002)
Brotas, SP	620-680	677	DBH ≥ 5 cm	51	40	0.04	Marques *et al.* (2003)
Sucupira farm, DF	1100-1200	977	DBH ≥ 3 cm	53	44	0.04	Guarino & Walter (2005)
Coqueiral, MG	810-840	425	DBH ≥ 5 cm	99	99	0.04	Rocha *et al.* (2005)
Campina do Encantado State Park, SP (deep peat forest)	< 15	695	DBH ≥ 4.8 cm	5	5	0.04	Sztutman & Rodrigues (2002)
Batuva, Guaraqueçaba, PR	70	752	DBH ≥ 10 cm	13	12	0.03	Galvão *et al.* (2002)
Santa Rita de Caldas, MG	1158-1204	498	DBH ≥ 5 cm	110	107	0.03	Loures *et al.* (2007)
Campinas Experimental Centre, SP	660	576	DBH ≥ 5 cm	33	21	0.03	Torres *et al.* (1994)
Brotas, SP	710-740	662	DBH ≥ 4.8 cm	33	26	0.03	Costa *et al.* (1997)
Flooded riparian forests							
Madre de Deus de Minas, MG (alluvial bed and slope)	900-950	305	DGL ≥ 5 cm	116	115	0.08	Vilela *et al.* (2000)
Mogi Guaçu, SP (Mariana forest)	610-630	581	DBH ≥ 2.5 cm	101	101	0.06	Mantovani *et al.* (1989)
Bom Sucesso, MG	825	368	DGL ≥ 5 cm	157	154	0.06	Carvalho *et al.* (1995)
Mogi Guaçu, SP	580-590	583	DBH ≥ 10 cm	59	47	0.06	Gibbs & Leitão-Filho (1978); Gibbs *et al.* (1980)
Chaves, PA	< 5	2583	DBH ≥ 10 cm	36	36	0.04	Almeida *et al.* (2004)
Bocaina de Minas, MG	1135	303	height ≥ 3 m	81	81	0.04	Pereira *et al.* (2006)
Mogi Guaçu, SP (Figueira forest)	570-590	583	DBH ≥ 2.5 cm	36	33	0.03	Mantovani *et al.* (1989)
Barcarena, PA	15-25	2423	DBH ≥ 10 cm	78	78	0.03	Almeida *et al.* (2004)

Continues

Table 2. Continuation.

Habitat/area	Alt.	Dist.	IC	S	I	Jaccard	Reference
Poconé, MT (Cuiabá River)	110-130	1682	DBH ≥ 3.2 cm	31	28	0.02	Guarim-Neto *et al.* (1996)
Mogi Guaçu, SP (Português forest)	580-590	577	DBH ≥ 2.5 cm	40	37	0.02	Mantovani *et al.* (1989)
Poconé, MT (Bento Gomes River)	120-150	1714	DBH ≥ 3.2 cm	25	23	0.01	Guarim-Neto *et al.* (1996)
Xingu River, PA	70-100	2342	DBH ≥ 10 cm	40	24	0.01	Campbell *et al.* (1986)
Tapajós River, PA	10-30	2618	DBH ≥ 5 cm	36	33	0.01	Ferreira & Prance (1998)
Senador José Porfírio, PA	< 5	2439	DBH ≥ 10 cm	42	36	0.01	Almeida *et al.* (2004)
Afuá, PA	< 10	2626	DBH ≥ 10 cm	60	51	0.01	Almeida *et al.* (2004)
Corumbá, MS	80-100	1694	DBH ≥ 4.8 cm	37	34	0	Damasceno-Junior *et al.* (2005)
Negro River, AM	10-30	2921	height ≥ 1 m	54	33	0	Keel & Prance (1979)
Madre de Deus de Minas, MG (alluvial bed)	900-950	305	DGL ≥ 5 cm	8	8	0	Vilela *et al.* (2000)

Alt. – approximate altitude (meters above sea level); Dist. – approximate distance from the park (km); IC – inclusion criterion; S – number of species; I – identified species used for Jaccard calculation; RJ – (state of) Rio de Janeiro; CD – crown diameter; DBH – diameter at breast height; ES – (state of) Espírito Santo; SP – (state of) São Paulo; PR – (state of) Paraná; RS – (state of) Rio Grande do Sul; DF – *Distrito Federal* (Federal District) of Brasília; MG – (state of) Minas Gerais; DGL – diameter at ground level; PA – (state of) Pará; MT – (state of) Mato Grosso; MS – (state of Mato Grosso do Sul); AM – (state of) Amazonas.
* Mean distance to the eight swamp forests studied.

The total density and basal area were 1503 trees.ha^{-1} and 24.9 m^2.ha^{-1}, respectively. Although we identified a few trees of considerable size (possible remnants of the original structure of the local swamp forests)—including *Calophyllum brasiliense* (height/diameter, 30 m/53 cm), *Ficus organensis* (28 m/88 cm), *Tapirira guianensis* (28 m/51 cm), *Symphonia globulifera* (28 m/37.7 cm) and *Tabebuia cassinoides* (23 m/60.5 cm)—the mean height and diameter were relatively low (9.4 ± 4.4 m and 11.8 ± 8.5 cm, respectively). In addition, 16.5% of the individuals surveyed (concentrated at the edges) were forked or branched below 1.3 m, which is partly the result of past cuts. We also surveyed 211 dead, still standing trees (8.9% of the total), which collectively had a basal area of 2.6 m^2.ha^{-1}.

Phytogeographic relationships

The swamp forests studied were found to bear little similarity to the types of vegetation formations used for comparison (Tab. 2). In most cases, the Jaccard similarity coefficients were lower than 0.25; as expected, the highest values were obtained only when our data were compared with those of two other surveys conducted in swamp forests within our study area (Jaccard, 0.39 and 0.38, respectively).

Our swamp forests were more similar to, or at least as similar as, open *restinga* formations within the park, such as the so-called *Clusia* scrub (Jaccard of 0.21-0.17) and Ericaceae scrub (Jaccard, 0.15), as they were to other swamp forests of the coastal plains of the states of Rio de Janeiro, São Paulo and Paraná (Jaccard, 0.18-0.03). Conversely, the swamp forests in our study area presented very low similarity to other swamp forests, including those in the Brazilian Highlands (in the Federal District of Brasilia, the state of Minas Gerais and the state of São Paulo: Jaccard, 0.07-0.03) and those in the coastal plains from the southernmost Brazilian state of Rio Grande do Sul (Jaccard, 0.12-0.05), especially in the southernmost portion of those plains (Taim wetland: Jaccard, 0.05). The Jaccard similarity coefficients for comparisons between our swamp forests and areas of Atlantic Forest *sensu stricto* in the states of Rio de Janeiro and Espírito Santo or various flooded riparian forests in Brazil were consistently quite low (0.11-0.02 and 0.08-0, respectively).

Despite the low Jaccard similarity coefficients, many of the species surveyed in the swamp forests of Restinga de Jurubatiba National Park were also registered in the types of vegetation formations used for comparison (Tab. 3 and 4). Some 70% of the species were shared with neighboring vegetation formations, including open *restinga* within the park (33.3%) and the Atlantic Forest *sensu stricto* in the states of Rio de Janeiro and Espírito Santo (53.1%). Considering the floodplain forests, many species were common to other swamp forests (54.3%) and flooded riparian forests (37%). In addition, excluding the flooded-forest specialist species *Calophyllum brasiliense*, *Symphonia globulifera* and *Tabebuia cassinoides*, the great majority (78%) of the species common to other swamp forests also occurred in the Atlantic Forest *sensu stricto*. In the case of species common to flooded riparian forests, the percentage was also very high (78.6%, Tab. 3).

Discussion

Phytosociological structure

The results indicated an oligarchic structure in the swamp forests studied. In addition to the known flooded-forest specialist species (*Calophyllum brasiliense*, *Symphonia globulifera* and *Tabebuia cassinoides*), some species common to neighboring areas of dry *restinga* (*Tapirira guianensis* and *Protium icicariba*) and areas of Atlantic Forest (*Euterpe edulis*

Table 3. Tree species (diameter at breast height ≥ 5 cm) surveyed in swamp forests of Restinga de Jurubatiba National Park, in the state of Rio de Janeiro, Brazil, ordered by importance value, phytosociological parameters and occurrence (1/0) in some other vegetation formations in Brazil (based on the surveys presented in Tab. 2).

Family	Species	N	RD	RDo	RF	IV	ORP	ATF	SWF*	FRF
ANACARDIACEAE	*Tapirira guianensis* Aubl.	356	16.45	31.05	8.91	18.80	1	1	1	1
CLUSIACEAE	*Calophyllum brasiliense* Cambess.	103	4.76	15.16	5.13	8.35	0	0	1	1
BURSERACEAE	*Protium icicariba* (DC.) Marchand	203	9.38	4.82	5.94	6.71	1	0	0	0
ARECACEAE	*Euterpe edulis* Mart.	143	6.61	2.50	3.10	4.07	0	1	1	1
CLUSIACEAE	*Symphonia globulifera* L.f.	84	3.88	4.41	3.91	4.07	0	0	1	1
ARECACEAE	*Geonoma schottiana* Mart.	150	6.93	1.04	4.18	4.05	0	1	1	1
BIGNONIACEAE	*Tabebuia cassinoides* (Lam.) DC.	101	4.67	3.56	2.70	3.64	0	0	1	0
PERACEAE	*Pera glabrata* (Schott) Poepp. ex Baill.	61	2.82	3.07	3.51	3.13	1	1	1	1
ELAEOCARPACEAE	*Sloanea guianensis* (Aubl.) Benth.	74	3.42	2.60	2.97	3.00	0	1	1	0
MYRTACEAE	*Calyptranthes brasiliensis* Spreng.	70	3.23	1.42	4.05	2.90	1	0	1	1
HUMIRIACEAE	*Humiria balsamifera* (Aubl.) J. St.-Hil.	51	2.36	3.89	1.89	2.71	1	0	0	1
LAURACEAE	*Persea aurata* Miq.	48	2.22	1.43	3.10	2.25	0	0	0	0
MYRTACEAE	*Myrcia ilheosensis* Kiaersk.	68	3.14	1.08	2.16	2.13	1	0	1	0
MALVACEAE	*Pseudobombax grandiflorum* (Cav.) A. Robyns	42	1.94	2.01	2.16	2.04	0	1	1	1
MYRTACEAE	*Blepharocalyx salicifolius* (Kunth) O. Berg	39	1.80	1.32	2.02	1.72	0	0	1	1
MELASTOMATACEAE	*Miconia cinnamomifolia* (DC.) Naudin	38	1.76	0.91	2.29	1.65	0	1	1	1
MALPIGHIACEAE	*Byrsonima sericea* DC.	27	1.25	1.28	1.62	1.38	1	0	0	0
LAURACEAE	*Ocotea notata* (Nees) Mez	31	1.43	1.05	1.48	1.32	1	0	0	0
NYCTAGINACEAE	*Guapira opposita* (Vell.) Reitz	27	1.25	0.87	1.48	1.20	1	1	1	1
FABACEAE	*Andira nitida* Mart. ex Benth.	16	0.74	1.06	1.62	1.14	0	0	0	0
SIMAROUBACEAE	*Simarouba amara* Aubl.	15	0.69	1.36	1.35	1.13	0	1	1	1
AQUIFOLIACEAE	*Ilex theezans* Mart. ex Reissek	26	1.20	0.73	1.35	1.09	1	1	1	1
APOCYNACEAE	*Aspidosperma ramiflorum* Müll. Arg.	23	1.06	0.72	1.48	1.09	0	1	0	1
MORACEAE	*Ficus organensis* (Miq.) Miq.	8	0.37	1.85	0.94	1.06	0	1	1	0
APOCYNACEAE	*Aspidosperma pyricollum* Müll. Arg.	20	0.92	0.57	1.21	0.90	0	0	0	1
LAURACEAE	*Aniba firmula* (Nees & Mart.) Mez	17	0.79	0.86	0.94	0.86	0	1	1	1
MYRSINACEAE	*Myrsine rubra* M.F. Freitas & Kin.-Gouv.	15	0.69	0.46	1.21	0.79	0	0	0	0
ANNONACEAE	*Xylopia sericea* A. St.-Hil.	14	0.65	0.46	1.21	0.77	0	1	1	0
RUBIACEAE	*Amaioua intermedia* Mart.	15	0.69	0.25	1.35	0.76	1	1	1	1
ARECACEAE	*Bactris setosa* Mart.	16	0.74	0.10	1.35	0.73	0	0	1	0
MYRTACEAE	*Myrcia multiflora* (Lam.) DC.	11	0.51	0.50	1.08	0.69	1	1	1	1
EUPHORBIACEAE	*Alchornea triplinervia* (Spreng.) Müll. Arg.	12	0.55	0.25	1.21	0.67	0	1	1	1
FABACEAE	*Ormosia arborea* (Vell.) Harms	9	0.42	0.52	0.81	0.58	1	1	1	1
MYRTACEAE	*Eugenia bahiensis* DC.	11	0.51	0.28	0.94	0.58	0	0	0	0
LAURACEAE	*Ocotea lobbii* (Meisn.) Rohwer	11	0.51	0.31	0.81	0.54	0	0	0	0
SAPINDACEAE	*Cupania emarginata* Cambess.	9	0.42	0.24	0.94	0.53	1	1	0	0
MORACEAE	*Ficus clusiifolia* Schott	4	0.18	0.99	0.40	0.53	0	1	1	0
CLUSIACEAE	*Clusia criuva* Cambess.	11	0.51	0.31	0.67	0.50	0	0	1	0
BURSERACEAE	*Protium heptaphyllum* (Aubl.) Marchand	10	0.46	0.16	0.81	0.48	1	1	1	1
BIGNONIACEAE	*Jacaranda bracteata* Bureau & K. Schum.	10	0.46	0.28	0.67	0.47	0	1	0	0
RUTACEAE	*Esenbeckia grandiflora* Mart.	17	0.79	0.19	0.40	0.46	0	0	0	0
BURSERACEAE	*Protium brasiliense* (Spreng.) Engl.	9	0.42	0.15	0.67	0.41	0	0	0	0
SAPINDACEAE	*Matayba guianensis* Aubl.	6	0.28	0.13	0.81	0.41	0	1	1	1
FABACEAE	*Inga laurina* (Sw.) Willd.	4	0.18	0.58	0.40	0.39	0	0	1	1
LAURACEAE	*Nectandra psammophila* Nees	7	0.32	0.26	0.54	0.37	0	0	0	0
PERACEAE	*Chaetocarpus myrsinites* Baill.	7	0.32	0.12	0.67	0.37	1	0	0	0
CLUSIACEAE	*Tovomita fructipendula* (Ruiz & Pav.) Cambess.	8	0.37	0.06	0.67	0.37	0	1	0	1
MYRTACEAE	*Myrcia recurvata* O. Berg	5	0.23	0.09	0.67	0.33	0	1	0	0
AQUIFOLIACEAE	*Ilex pseudobuxus* Reissek	6	0.28	0.14	0.54	0.32	0	0	1	0
MYRSINACEAE	*Myrsine guianensis* (Aubl.) Kuntze	6	0.28	0.13	0.54	0.32	0	1	1	0

Continues

Table 3. Continuation.

Family	Species	N	RD	RDo	RF	IV	ORP	ATF	SWF*	FRF
ARECACEAE	*Syagrus romanzoffiana* (Cham.) Glassman	4	0.18	0.20	0.54	0.31	0	1	1	1
APOCYNACEAE	*Tabernaemontana* sp.	3	0.14	0.45	0.27	0.29	-	-	-	-
LAURACEAE	*Rhodostemonodaphne macrocalyx* (Meisn.) Rohwer ex Madriñán	4	0.18	0.11	0.54	0.28	0	1	0	0
CLUSIACEAE	*Garcinia brasiliensis* Mart.	4	0.18	0.22	0.40	0.27	1	1	0	1
MYRTACEAE	*Psidium cattleyanum* Sabine	4	0.18	0.09	0.54	0.27	1	1	1	1
SAPOTACEAE	*Manilkara subsericea* (Mart.) Dubard	4	0.18	0.20	0.40	0.26	1	0	0	0
RUBIACEAE	*Posoqueria longiflora* Aubl.	4	0.18	0.05	0.54	0.26	0	0	0	0
PHYLLANTHACEAE	*Hieronyma oblonga* (Tul.) Müll. Arg.	7	0.32	0.10	0.27	0.23	0	1	1	0
MYRTACEAE	*Myrcia bergiana* O. Berg	5	0.23	0.04	0.40	0.23	0	0	0	0
MYRTACEAE	*Myrcia* sp.	4	0.18	0.08	0.40	0.22	-	-	-	-
LAURACEAE	*Ocotea pulchella* (Nees) Mez	4	0.18	0.05	0.40	0.21	0	0	1	1
BONNETIACEAE	*Bonnetia stricta* (Nees) Nees & Mart.	6	0.28	0.08	0.27	0.21	0	0	0	0
MYRTACEAE	*Myrcia vittoriana* Kiaersk.	3	0.14	0.04	0.40	0.20	1	0	0	0
ANNONACEAE	*Annona acutiflora* Mart.	3	0.14	0.02	0.40	0.19	0	0	0	0
MYRTACEAE	*Eugenia rostrata* O. Berg	4	0.18	0.06	0.27	0.17	0	0	0	0
ERICACEAE	*Agarista revoluta* (Spreng.) Hook. f. ex Nied.	3	0.14	0.06	0.27	0.16	1	0	0	0
MYRTACEAE	*Eugenia excelsa* O. Berg	5	0.23	0.10	0.13	0.16	0	1	0	1
URTICACEAE	*Cecropia lyratiloba* Miq.	2	0.09	0.07	0.27	0.15	0	1	1	0
CLUSIACEAE	*Clusia hilariana* Schltdl.	2	0.09	0.03	0.27	0.13	1	0	0	0
ARECACEAE	*Elaeis guineensis* Jacq. (exótica)	1	0.05	0.10	0.13	0.09	-	-	-	-
THEACEAE	*Laplacea fructicosa* (Schrad.) Kobuski	1	0.05	0.03	0.13	0.07	0	1	1	0
MYRTACEAE	*Eugenia umbelliflora* O. Berg	1	0.05	0.03	0.13	0.07	1	0	1	0
MALVACEAE	*Eriotheca pentaphylla* (Vell.) A. Robyns	1	0.05	0.03	0.13	0.07	0	1	1	0
SAPOTACEAE	*Pouteria caimito* (Ruiz & Pav.) Radlk.	1	0.05	0.03	0.13	0.07	0	1	1	0
SOLANACEAE	*Aureliana fasciculata* (Vell.) Sendtn.	1	0.05	0.02	0.13	0.07	0	1	0	0
ANNONACEAE	*Annona glabra* L.	1	0.05	0.01	0.13	0.07	1	0	0	0
MYRTACEAE	*Myrcia racemosa* (O. Berg) Kiaersk.	1	0.05	0.01	0.13	0.06	0	1	1	0
MORACEAE	*Ficus gomelleira* Kunth & C.D. Bouché ex Kunth	1	0.05	0.01	0.13	0.06	0	1	1	0
MORACEAE	*Ficus pulchella* Schott	1	0.05	0.01	0.13	0.06	0	1	1	0
CELASTRACEAE	*Maytenus obtusifolia* Mart.	1	0.05	0.01	0.13	0.06	1	1	0	0
SOLANACEAE	*Solanum caavurana* Vell.	1	0.05	0.01	0.13	0.06	0	0	0	0
MELIACEAE	*Trichilia casaretti* C. DC.	1	0.05	0.01	0.13	0.06	0	1	1	0
RUTACEAE	*Pilocarpus spicatus* A. St.-Hil.	1	0.05	0.01	0.13	0.06	1	1	0	0
ANNONACEAE	*Xylopia ochrantha* Mart.	1	0.05	0.01	0.13	0.06	1	0	0	0

N – number of trees surveyed; RD – relative density; RDo – relative dominance; RF – relative frequency; IV – importance value (%); ORP – open *restinga* within the park; ATF – Atlantic Forest *sensu stricto* (in the states of Rio de Janeiro and Espírito Santo); SWF – swamp forests in southern and southeastern Brazil; FRF – flooded riparian forests.

*The surveys of Barros (2000) and Oliveira (2000) conducted in swamp forests within the park were excluded.

Table 4. Percentage of species in the swamp forests of Restinga de Jurubatiba National Park, in the state of Rio de Janeiro, that were also registered in other vegetation formations in Brazil and the corresponding Jaccard similarity coefficient intervals.

Vegetation formation	N	Jaccard	%
Neighboring vegetation formation	20	0.21-0.02	70.4
Open *restinga* within the park	3	0.21-0.15	33.3
Atlantic Forest *sensu stricto* of RJ and ES	17	0.11-0.02	53.1
Swamp forests of southern and southeastern Brazil*	30	0.18-0.03	54.3
Flooded riparian forests	18	0.08-0	37.0

N – number of surveys used in the analysis.

*The surveys of Barros (2000) and Oliveira (2000) conducted in swamp forests within the park were excluded.

and *Geonoma schottiana*) showed high densities and are very important to the structure of the forests studied (Tab. 3). This indicates the generalist character of these species in relation to the water content of the soil.

In a swamp forest, the saturation or inundation of the soil, caused by a rise in the water table, exerts strong selective pressure (Marques *et al*. 2003; Rocha *et al*. 2005; Toniato 2006), determining the floristic composition and structure of the forest. The saturated soil restricts the number and abundance of shrub and tree species that are able to establish themselves, whereas it favors occupation by flooded-forest specialists, as well as some generalist species (Marques *et al*. 2003). A higher degree and longer duration of saturation in the superficial soil layers translates to greater selective pressure. As a result, swamp forests frequently show oligarchy, or monodominance (Araujo *et al*. 1998; Galvão *et al*. 2002; Scarano 2006), which are common in habitats subjected to extreme environmental conditions (Richards 1979; Scarano 2002). In fact, species richness, diversity and evenness are lower in swamp forests than in adjacent or nearby forests located on drier soils and thereby spared the direct influence of the water table level (Ivanauskas *et al*. 1997; Sztutman & Rodrigues 2002; Carvalho *et al*. 2006b).

In our study area, the species richness and diversity were relatively high when compared with those of other swamp forests (Tab. 1), which is attributable to the broad range of environmental conditions included in our sample, especially as regards the phreatic flooding regime (from none up to several months) as a result of small topographic variations. This situation enabled the establishment of species with different ecological requirements—from flooded-forest specialists to generalists, and even species common to the drier soils present in neighboring vegetation formations (see below). However, the considerable differences in abundance of these species led to the low evenness value.

The total density and basal area were low when compared with those reported in other studies using identical or comparable inclusion criteria (Tab. 1); even studies using the more rigid inclusion criterion of DBH ≥ 10 cm (Galvão *et al.* 2002; Carvalho *et al.* 2006b) indicated values for basal area much higher. Some other swamp forests (IM1, IM2 and IM3) located in areas of *restinga*, like those studied here, also showed values for basal area that were higher than that found in our study area. These results are possibly related to the history of use of our swamp forests, as mentioned earlier, although some of their equivalents used for comparison have also been subjected to explotation (*e.g.*, PA2, PST and BAT).

The number of dead trees we found represented only a small part of the renewal dynamics of the local swamps, given that our analysis did not include fallen trees that were still alive nor mass mortalities caused by sporadic events. These seem to be particularly applicable to swamp forests. As an example, soon after the end of our survey, an extremely strong wind that lasted for only a few minutes was responsible for a sharp decline in the number of trees at site E. This was attributable to the instability of peaty soils and the shallow root systems of the trees, in response to the proximity of the water table. Trees located along the upper stretches of the forest edge, where there is less accumulation of peat, were less affected. On the other hand, the combination of heavy rains and the fact that the sandbar separating the Preta lagoon from the sea failed to open subjected site C and the neighboring swamps to an exceptional high water level and long-term flooding (2005-2006), coinciding with the massive death of trees.

These examples illustrate the great fragility of swamp forests, as has been reported (e.g. Scarano *et al*. 1998; Jacomine 2004). They are particularly sensitive to changes in the flood regime, and when these occur due to human activity and become permanent, in addition to rapid degradation, the forests show no natural recovery (Scarano *et al*. 1998). In fact, the narrowing of river channels, the construction of embankments and the installation of drainage systems have been responsible for the virtual disappearance of the swamps on the coastal plains in the state of Rio de Janeiro. Fortunately, since the establishment of Restinga de Jurubatiba National Park in 1998, the human activities that were damaging the local swamp forests (cutting, burning and hunting) have diminished and are currently almost nonexistent.

Phytogeographic relationships

The floodplain forests of Brazil (including flooded riparian forests and swamp forests) occur under a variety of ecological conditions—including those related to climate, geology, geomorphology, soil, water, flooding and adjacent floras—which induce variations in their floristic composition, physiognomy, structure and dynamics (Prance 1979; Mantovani 1989; Ivanauskas *et al*. 1997; Parolin *et al*. 2004; Rodrigues & Shepherd 2004; Scarano 2006). Studies using multivariate techniques have further indicated that swamp forests differ floristically from flooded riparian forests, mainly due to differences in flooding regimes (Rodrigues & Nave 2004; Silva *et al*. 2007). Even within a single site, differences in topography, flooding intensity and soil conditions affect the spatial distribution of species and promote phytosociological variation (Keel & Prance 1979; Vilela *et al*. 2000; Sztutman & Rodrigues 2002; Damasceno-Junior *et al*. 2005; Scarano 2006; Teixeira *et al*. 2008). The floristic differences related to this great heterogeneity of ecological conditions were responsible for the low similarity between various Brazilian floodplain forests and the swamp forest studied here, as well as for the relatively high species richness found in our study area, in comparison with other swamps (Tab. 1).

Our results indicate that the swamp forests in our study area bear a stronger floristic resemblance to their closest neighbors (areas of dry, open *restinga* within the same park) and to a few other swamp forests than to the adjacent Atlantic Forest *sensu stricto* in the mountain chains and flooded riparian forests at the regional or national level. Therefore, like ecological conditions, geographic proximity represents a key determinant of floristic composition. In addition, despite the low similarity between our swamp forests and areas of Atlantic Forest *sensu stricto*, a high proportion (53.1%) of species we found is shared with this forest. Furthermore, in comparison with other swamp forests, those studied here were found to be most similar to those located in the coastal plains of southeast Brazil (in the states of Rio de Janeiro, São Paulo and Paraná), which are geographically and climatically more similar than are swamp forests elsewhere. Moreover, in those coastal plains, the similarity decreased in relation to swamp forests that showed lower species richness, which are often degraded or early successional forests, such as the Passa-Sete and Batuva locations studied by Galvão *et al.* (2002), or related to specific edaphic conditions, such as those observed in the deep peat forest studied by Sztutman & Rodrigues (2002). All of this leads to the assumption that the swamp forests of southeastern Brazil do not consist of a distinguishable floristic unit. We argue that this is related to potential sources of local variation, notably migration and establishment of adaptive species from neighboring vegetation formations. Topographic variations at the local level and successional stage would control the establishment of these species at a given site.

Our results clearly indicate that the floristic composition of the studied swamp forests is largely related to the surrounding vegetation, i.e., areas of dry *restinga* and Atlantic Forest (≈70% of the species surveyed are shared with those vegetation formations). A similar pattern has often been reported for other floodplain forests in Brazil (Gibbs & Leitão-Filho 1978; Ivanauskas *et al.* 1997; Marques *et al.* 2003; Rodrigues & Shepherd 2004; Carvalho *et al.* 2006b; Scarano 2006; Teixeira & Assis 2011). This calls attention to the ecological plasticity of some tree species that occur in the surroundings of floodplain forests. Marques *et al.* (2011) studied the coastal lowland vegetation of southern and southeastern Brazil. Using detrended correspondence analysis, the authors showed that swamp forests did not form a distinct group and tended to be more similar to neighboring terra firme forests and scrublands. This result supports our previous assumption that the swamp forests of southeastern Brazil do not consist of a distinguishable floristic unit.

Another interesting result of the present study is that a high proportion (78%) of the species shared with other swamp forests also occurred in the Atlantic Forest *sensu stricto*. This clearly indicates that the floristic connection between the swamp forests studied here and their equivalents in southern and southeastern Brazil is primarily attributable to Atlantic Forest species.

The fact that the flora of our study area, like those of other swamp forests (B.C. Kurtz, unpublished data), did not consist predominantly of flooded-forest specialists (even in the more severely flooded bottoms) is at first surprising. Higher plants, like any other aerobic organism, need an adequate supply of oxygen for the performance of vital functions, such as cell division (Hendry & Crawford 1994). However, even terrestrial plants, such as trees, are capable of surviving under conditions of a partial or total lack of oxygen, and there is considerable interspecific variation regarding the length of time they can do so, ranging from hours to years (Crawford 1992). In order to colonize a floodplain habitat, a given plant must first overcome the hazards of dispersal, germination and youth, resorting to biochemical, physiological, morphological or anatomic mechanisms in order to tolerate or avoid the deleterious effects of oxygen deprivation during growth (Scarano 2006).

The wide range of environmental conditions in our study area, particularly in relation to the phreatic flooding regime conditioned by topographic variations, allowed for the establishment of species with different ecological requirements—including generalist species from the neighboring areas of dry *restinga* or Atlantic Forest (*e.g.*, *Tapirira guianensis*, *Protium icicariba*, *Euterpe edulis*, *Geonoma schottiana*, *Pera glabrata*, *Sloanea guianensis*, *Calyptranthes brasiliensis*, *Pseudobombax grandiflorum*, *Miconia cinnamomifolia*, *Simarouba amara*, *Ficus organensis*, *Aniba firmula*, *Xylopia sericea*, *Myrcia multiflora* and *Alchornea triplinervia*)—and contributed decisively to the high local species richness. Even apparently flood-intolerant species (*Jacaranda bracteata*, *Clusia hilariana* and *Eugenia excelsa*) were established on the seldom-flooded or unflooded patches along the forest edges. In fact, some studies evaluating broad flooding regimes, related to topographic variations, also showed high species richness in Brazilian floodplain forests, including swamps (Rocha *et al.* 2005; Guedes-Bruni *et al.* 2006a; Teixeira *et al.* 2008) and flooded riparian forests (e.g. Carvalho *et al.* 1995; Vilela *et al.* 2000).

The ecological succession in swamp forests, which is controlled by the phreatic flooding regime, is also responsible for floristic changes. This can be observed on the coastal plain of southeastern Brazil, where early successional stages, which correspond to permanently flooded sites, are frequently dominated by *Tabebuia cassinoides* (Gentry 1992; Araujo *et al.* 1998; Scarano 2006). This species typically forms pure stands (Gentry 1992). However, in the more advanced stages (as in our study area), the soils are subjected only to periodic flooding, which, together with the occurrence of subtle topographic variations, creates a local mosaic of flooded and unflooded patches that varies over the years depending upon the amount of rainfall (see Scarano *et al.* 1997). As previously mentioned, these conditions promote higher species richness. Therefore, throughout the successional process, the influence of neighboring vegetation formations (areas of Atlantic Forest or *restinga*, depending on the location) will be progressively stronger. Galvão *et al.* (2002) showed profound changes in composition, diversity and structure over the course of the successional process of swamp forests in the coastal plains of the state of Paraná.

These changes included a decline in *T. cassinoides* dominance and an increase in the importance of other tree species, especially *Calophyllum brasiliense*.

Despite recent advances, knowledge of the ecology of swamp forests in Brazil continues too limited, and there is a need for additional information on their floristic composition, dynamics and phytogeographic relationships. Further local surveys should be encouraged, especially in the northern and northeastern regions, for which there is total lack of quantitative data. Such surveys will enable new phytogeographic analyses including various sets of sites.

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References

Aguiar, A.P.; Chiarello, A.G.; Mendes, S.L. & Matos, E.N. 2003. The Central and Serra do Mar corridors in the Brazilian Atlantic forest. Pp. 118-132. In: Galindo-Leal, C. & Câmara, I.G. (Eds.). **The Atlantic forest of South America: biodiversity status, threats and outlook**. Washington D.C., Island Press.

Almeida, S.S.; Amaral, D.D. & Silva, A.S.L. 2004. Análise florística e estrutura de florestas de várzea no estuário amazônico. **Acta Amazonica 34**: 513-524.

APG III. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. **Botanical Journal of the Linnean Society 161**: 105-121.

Araujo, D.S.D.; Scarano, F.R.; Sá, C.F.C.; Kurtz, B.C.; Zaluar, H.L.T.; Montezuma, R.C.M. & Oliveira, R.C. 1998. Comunidades vegetais do Parque Nacional da Restinga de Jurubatiba. Pp. 39-62. In: Esteves, F.A. (Ed.). **Ecologia das lagoas costeiras do Parque Nacional da Restinga de Jurubatiba e do município de Macaé (RJ)**. Rio de Janeiro, Universidade Federal do Rio de Janeiro.

Araujo, D.S.D.; Pereira, M.C.A. & Pimentel, M.C.P. 2004. Flora e estrutura de comunidades na restinga de Jurubatiba – síntese dos conhecimentos com enfoque especial para a formação aberta de *Clusia*. Pp. 59-76. In: Rocha, C.F.D.; Esteves, F.A. & Scarano, F.R. (Orgs.). **Pesquisas de longa duração na Restinga de Jurubatiba: ecologia, história natural e conservação**. São Carlos, RiMa.

Barbosa, F.A.R.; Scarano, F.R.; Sabará, M.G. & Esteves, F.A. 2004. Brazilian LTER: ecosystem and biodiversity information in support of decision-making. **Environmental Monitoring and Assessment 90**: 121-133.

Barros, M.J. 2000. **Estrutura de uma mata inundável de restinga do Parque Nacional da Restinga de Jurubatiba, município de Carapebus, Rio de Janeiro**. Dissertação de Mestrado, Rio de Janeiro, Universidade Federal do Rio de Janeiro.

Campbell, D.G.; Daly, D.C.; Prance, G.T. & Maciel, U.N. 1986. Quantitative ecological inventory of terra firme and várzea tropical forest on the Rio Xingu, Brazilian Amazon. **Brittonia 38**: 369-393.

Carvalho, D.A.; Oliveira-Filho, A.T.; Vilela, E.A.V. & Gavilanes, M.L. 1995. Estrutura fitossociológica de mata ripária do alto rio Grande (Bom Sucesso, estado de Minas Gerais). **Revista Brasileira de Botânica 18**: 39-49.

Carvalho, F.A.; Nascimento, M.T. & Braga, J.M.A. 2006a. Composição e riqueza florística do componente arbóreo da Floresta Atlântica submontana na região de Imbaú, município de Silva Jardim, RJ. **Acta Botanica Brasilica 20**: 727-740.

Carvalho, F.A.; Nascimento, M.T.; Braga, J.M.A. & Rodrigues, P.J.F.P. 2006b. Estrutura da comunidade arbórea da Floresta Atlântica de baixada periodicamente inundada na Reserva Biológica de Poço das Antas, Rio de Janeiro, Brasil. **Rodriguésia 57**: 503-518.

Costa, F.R.C.; Schlittler, F.H.M.; Cesar, O. & Monteiro, R. 1997. Aspectos florísticos e fitossociológicos de um remanescente de mata de brejo no município de Brotas, SP. **Arquivos de Biologia e Tecnologia 40**: 263-270.

Crawford, R.M.M. 1992. Oxygen availability as an ecological limit to plant distribution. **Advances in Ecological Research 23**: 93-185.

Damasceno-Junior, G.A.; Semir, J.; Santos, F.A.M. & Leitão-Filho, H.F. 2005. Structure, distribution of species and inundation in a riparian forest of Rio Paraguai, Pantanal, Brazil. **Flora 200**: 119-135.

Dorneles, L.P.P. & Waechter, J.L. 2004. Fitossociologia do componente arbóreo na floresta turfosa do Parque Nacional da Lagoa do Peixe, Rio Grande do Sul, Brasil. **Acta Botanica Brasilica 18**: 815-824.

Esteves, F.A. (Ed.). 1998. **Ecologia das lagoas costeiras do Parque Nacional da Restinga de Jurubatiba e do município de Macaé (RJ)**. Rio de Janeiro, Universidade Federal do Rio de Janeiro.

Ferreira, L.V. & Prance, G.T. 1998. Structure and species richness of low-diversity floodplain forest on the Rio Tapajós, Eastern Amazonia, Brazil. **Biodiversity and Conservation 7**: 585-596.

Galvão, F.; Roderjan, C.V.; Kuniyoshi, Y.S. & Ziller, S.R. 2002. Composição florística e fitossociologia de caxetais do litoral do estado do Paraná - Brasil. **Floresta 32**: 17-39.

Gentry, A.H. 1982. Patterns of Neotropical plant species diversity. Pp. 1-84. In: Hecht, M.K.; Wallace, B. & Prance, G.T. (Eds.). **Evolutionary biology**, vol. 15. New York, London, Plenum Press.

Gentry, A.H. 1992. Bignoniaceae – Part II (Tribe Tecomeae). In: **Flora Neotropica**. Monograph 25(2). New York, The New York Botanical Garden.

Gibbs, P.E. & Leitão-Filho, H.F. 1978. Floristic composition of an area of gallery forest near Mogi Guaçu, state of São Paulo, S.E. Brazil. **Revista Brasileira de Botânica 1**: 151-156.

Gibbs, P.E.; Leitão-Filho, H.F. & Abbott, R.J. 1980. Application of the point-centred quarter method in a floristic survey of an area of gallery forest at Mogi-Guaçu, SP, Brazil. **Revista Brasileira de Botânica 3**: 17-22.

Guarim-Neto, G.; Guarim, V.L.M.S.; Moraes, E.C.C. & Ferreira, L.A.D. 1996. Fitossociologia de matas ciliares no Pantanal mato-grossense. **Boletim do Museu Paraense Emílio Goeldi, Série Botânica 12**: 251-263.

Guarino, E.S.G. & Walter, B.M.T. 2005. Fitossociologia de dois trechos inundáveis de matas de galeria no Distrito Federal, Brasil. **Acta Botanica Brasilica 19**: 431-442.

Guedes, R.R. 1988. Composição florística e estrutura de um trecho de mata perturbada de baixada no município de Magé, Rio de Janeiro. **Archivos do Jardim Botânico do Rio de Janeiro 29**: 155-200.

Guedes-Bruni, R.R. 1998. **Composição, estrutura e similaridade florística de dossel em seis unidades fisionômicas de Mata Atlântica no Rio de Janeiro**. Tese de Doutorado, São Paulo, Universidade de São Paulo.

Guedes-Bruni, R.R.; Pessoa, S.V.A. & Kurtz, B.C. 1997. Florística e estrutura do componente arbustivo-arbóreo de um trecho preservado de floresta montana na Reserva Ecológica de Macaé de Cima. Pp. 127-145. In: Lima, H.C. & Guedes-Bruni, R.R. (Eds.). **Serra de Macaé de Cima: diversidade florística e conservação em Mata Atlântica**. Rio de Janeiro, Instituto de Pesquisas Jardim Botânico do Rio de Janeiro.

Guedes-Bruni, R.R.; Silva Neto, S.J.; Morim, M.P. & Mantovani, W. 2006a. Composição florística e estrutura de trecho de Floresta Ombrófila Densa Atlântica aluvial na Reserva Biológica de Poço das Antas, Silva Jardim, Rio de Janeiro, Brasil. **Rodriguésia 57**: 413-428.

Guedes-Bruni, R.R.; Silva Neto, S.J.; Morim, M.P. & Mantovani, W. 2006b. Composição florística e estrutura de dossel em trecho de Floresta Ombrófila Densa Atlântica sobre morrote mamelonar na Reserva Biológica de Poço das Antas, Silva Jardim, Rio de Janeiro, Brasil. **Rodriguésia 57**: 429-442.

Hendry, G.A.F. & Crawford, R.M.M. 1994. Oxygen and environmental stress in plants - an overview. **Proceedings of the Royal Society of Edinburgh 102B**: 1-10.

Henriques, R.P.B.; Araujo, D.S.D. & Hay, J.D. 1986. Descrição e classificação dos tipos de vegetação da restinga de Carapebus, Rio de Janeiro. **Revista Brasileira de Botânica 9**: 173-189.

Ivanauskas, N.M.; Rodrigues, R.R. & Nave, A.G. 1997. Aspectos ecológicos de um trecho de floresta de brejo em Itatinga, SP: florística, fitossociologia e seletividade de espécies. **Revista Brasileira de Botânica 20**: 139-153.

Jacomine, P.K.T. 2004. Solos sob matas ciliares. Pp. 27-31. In: Rodrigues, R.R. & Leitão-Filho, H.F. (Eds.). **Matas Ciliares: conservação e recuperação**. 2 ed. São Paulo, Editora da Universidade de São Paulo, FAPESP.

Keel, S.H.K. & Prance, G.T. 1979. Studies of the vegetation of a white-sand black-water igapó (Rio Negro, Brazil). **Acta Amazonica 9**: 645-655.

Kindel, A. 2002. **Diversidade e estratégias de dispersão de plantas vasculares da floresta paludosa do Faxinal, Torres – RS**. Tese de Doutorado, Porto Alegre, Universidade Federal do Rio Grande do Sul.

Kurtz, B.C. & Araujo, D.S.D. 2000. Composição florística e estrutura do componente arbóreo de um trecho de Mata Atlântica na Estação Ecológica Estadual do Paraíso, Cachoeiras de Macacu, Rio de Janeiro, Brasil. **Rodriguésia 51**: 69-111.

Lista de Espécies da Flora do Brasil. 2012. In: http://floradobrasil.jbrj.gov.br/2012 (consulted in March 2012).

Loures, L.; Carvalho, D.A.; Machado, E.L.M. & Marques, J.J.G.S.M. 2007. Florística, estrutura e características do solo de um fragmento de floresta paludosa no sudeste do Brasil. **Acta Botanica Brasilica 21**: 885-896.

Magurran, A.E. 1988. **Ecological diversity and its measurement**. Princeton, Princeton University Press.

Mantovani, W. 1989. Conceituação e fatores condicionantes. Pp. 11-19. In: Barbosa, L.M. (Coord.). **Anais do Simpósio sobre Mata Ciliar**. Campinas, Fundação Cargill.

Mantovani, W.; Rossi, L.; Romaniuc-Neto, S.; Assad-Ludewigs, I.Y.; Wanderley, M.G.L.; Melo, M.M.R.F. & Toledo, C.B. 1989. Estudo fitossociológico de áreas de mata ciliar em Mogi-Guaçu, SP, Brasil. Pp. 235-267. In: Barbosa, L.M. (Coord.). **Anais do Simpósio sobre Mata Ciliar**. Campinas, Fundação Cargill.

Marques, M.C.M.; Silva, S.M. & Salino, A. 2003. Florística e estrutura do componente arbustivo-arbóreo de uma floresta higrófila da bacia do rio Jacaré-Pepira, SP, Brasil. **Acta Botanica Brasilica 17**: 495-506.

Marques, M.C.M.; Swaine, M.D. & Liebsch, D. 2011. Diversity distribution and floristic differentiation of the coastal lowland vegetation: implications for the conservation of the Brazilian Atlantic Forest. **Biodiversity and Conservation 20**: 153-168.

Martin, L.; Suguio, K. & Flexor, J.M. 1993. As flutuações de nível do mar durante o quaternário superior e a evolução geológica de "deltas" brasileiros. **Boletim do Instituto de Geociências-USP 15**: 1-186.

Menezes-Silva, S. 1998. **As formações vegetais da planície litorânea da Ilha do Mel, Paraná, Brasil: composição florística e principais características estruturais**. Tese de Doutorado, Campinas, Universidade Estadual de Campinas.

Mittermeier, R.A.; Gil, P.R.; Hoffman, M.; Pilgrim, J.; Brooks, T.; Mittermeier, C.G.; Lamoreux, J. & Fonseca, G.A.B. 2005. **Hotspots revisited: Earth's biologically richest and most endangered terrestrial ecoregions**. Chicago, The University of Chicago Press.

Montezuma, R.C.M. 1997. **Estrutura da vegetação de uma restinga de Ericaceae no município de Carapebus – RJ**. Dissertação de Mestrado, Rio de Janeiro, Universidade Federal do Rio de Janeiro.

Moreno, M.R.; Nascimento, M.T. & Kurtz, B.C. 2003. Estrutura e composição florística do estrato arbóreo em duas zonas altitudinais na Mata Atlântica de encosta da região do Imbé, RJ. **Acta Botanica Brasilica 17**: 371-386.

Mueller-Dombois, D. & Ellenberg, H. 1974. **Aims and methods of vegetation ecology**. New York, John Wiley & Sons.

Myers, N.; Mittermeier, R.A.; Mittermeier, C.G.; Fonseca, G.A.B. & Kent, J. 2000. Biodiversity hotspots for conservation priorities. **Nature 403**: 853-858.

Oliveira, R.C. 2000. **Estrutura do componente arbóreo da mata periodicamente inundada do Parque Nacional da Restinga de Jurubatiba, Rio de Janeiro, Brasil**. Dissertação de Mestrado, Rio de Janeiro, Universidade Federal do Rio de Janeiro.

Oliveira, R.R. 2002. Ação antrópica e resultantes sobre a estrutura e composição da Mata Atlântica na Ilha Grande, RJ. **Rodriguésia 53**: 33-57.

Oliveira, R.R.; Zaú, A.S.; Lima, D.F.; Silva, M.B.R.; Vianna, M.C.; Sodré, D.O. & Sampaio, P.D. 1995. Significado ecológico da orientação de encostas no maciço da Tijuca, Rio de Janeiro. Pp. 523-541. In: Esteves, F.A. (Ed.). **Estrutura, funcionamento e manejo de ecossistemas brasileiros**. Oecologia Brasiliensis, vol 1. Rio de Janeiro, PPGE-UFRJ.

Parolin, P.; De Simone, O.; Haase, K.; Waldhoff, D.; Rottenberger, S.; Kuhn, U.; Kesselmeier, J.; Kleiss, B.; Schmidt, W.; Piedade, M.T.F. & Junk, W.J. 2004. Central Amazonian floodplain forests: tree adaptations in a pulsing system. **Botanical Review 70**: 357-380.

Paschoal, M.E.S. & Cavassan, O. 1999. A flora arbórea da mata de brejo do ribeirão do Pelintra, Agudos – SP. **Naturalia, São Paulo 24**: 171-191.

Peixoto, G.L.; Martins, S.V.; Silva, A.F. & Silva, E. 2004. Composição florística do componente arbóreo de um trecho de Floresta Atlântica na Área de Proteção Ambiental da Serra da Capoeira Grande, Rio de Janeiro, RJ, Brasil. **Acta Botanica Brasilica 18**: 151-160.

Pereira, I.M.; Oliveira-Filho, A.T.; Botelho, S.A.; Carvalho, W.A.C.; Fontes, M.A.L.; Schiavini, I. & Silva, A.F. 2006. Composição florística do compartimento arbóreo de cinco remanescentes florestais do maciço do Itatiaia, Minas Gerais e Rio de Janeiro. **Rodriguésia 57**: 103-126.

Pessoa, S.V.A.; Guedes-Bruni, R.R. & Kurtz, B.C. 1997. Composição florística e estrutura do componente arbustivo-arbóreo de um trecho secundário de floresta montana na Reserva Ecológica de Macaé de Cima. Pp. 147-167. In: Lima, H.C. & Guedes-Bruni, R.R. (Eds.). **Serra de Macaé de Cima: diversidade florística e conservação em Mata Atlântica**. Rio de Janeiro, Instituto de Pesquisas Jardim Botânico do Rio de Janeiro.

Prance, G.T. 1979. Notes on the vegetation of Amazonia III. The terminology of Amazonian forest types subject to inundation. **Brittonia 31**: 26-38.

Ribeiro, M.C.; Metzger, J.P.; Martensen, A.C.; Ponzoni, F.J. & Hirota, M.M. 2009. The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. **Biological Conservation 142**: 1141-1153.

Ribeiro, M.C.; Martensen, A.C.; Metzger, J.P.; Tabarelli, M.; Scarano, F. & Fortin, M.J. 2011. The Brazilian Atlantic Forest: a shrinking biodiversity hotspot. Pp. 405-434. In: Zachos, F.E. & Habel, J.C. (Eds.). **Biodiversity Hotspots: distribution and protection of conservation priority areas**. Heidelberg, Springer.

Richards, P.W. 1979. **The tropical rain forest: an ecological study**. Cambridge, Cambridge University Press.

Rocha, C.F.D.; Esteves, F.A. & Scarano, F.R. (Orgs.). 2004. **Pesquisas de longa duração na Restinga de Jurubatiba: ecologia, história natural e conservação**. São Carlos, RiMa.

Rocha, C.F.D.; Bergallo, H.G.; Van Sluys, M.; Alves, M.A.S. & Jenkins, C. 2006. Corredores ecológicos e conservação da biodiversidade: um estudo de caso na Mata Atlântica. Pp. 317-342. In: Rocha, C.F.D.; Bergallo, H.G.; Van Sluys, M. & Alves, M.A.S. (Eds.). **Biologia da conservação: essências**. São Carlos, RiMa.

Rocha, C.T.V.; Carvalho, D.A.; Fontes, M.A.L.; Oliveira-Filho, A.T.; Van Den Berg, E. & Melo-Marques, J.J.G.S. 2005. Comunidade arbórea de um continuum entre floresta paludosa e de encosta em Coqueiral, Minas Gerais, Brasil. **Revista Brasileira de Botânica 28**: 203-218.

Rodrigues, R.R. & Nave, A.G. 2004. Heterogeneidade florística das matas ciliares. Pp. 45-71. In: Rodrigues, R.R. & Leitão-Filho, H.F. (Eds.). **Matas ciliares: conservação e recuperação**. 2 ed. São Paulo, Editora da Universidade de São Paulo, FAPESP.

Rodrigues, R.R. & Shepherd, G.J. 2004. Fatores condicionantes da vegetação ciliar. Pp. 101-107. In: Rodrigues, R.R. & Leitão-Filho, H.F. (Eds.). **Matas ciliares: conservação e recuperação**. 2 ed. São Paulo, Editora da Universidade de São Paulo, FAPESP.

Scarano, F.R. 2002. Structure, function and floristic relationships of plant communities in stressful habitats marginal to the Brazilian Atlantic rainforest. **Annals of Botany 90**: 517-524.

Scarano, F.R. 2006. Plant community structure and function in a swamp forest within the Atlantic rain forest complex: a synthesis. **Rodriguésia 57**: 491-502.

Scarano, F.R. 2009. Plant communities at the periphery of the Atlantic rain forest: rare-species bias and its risks for conservation. **Biological Conservation 142**: 1201-1208.

Scarano, F.R.; Ribeiro, K.T.; Moraes, L.F.D. & Lima, H.C. 1997. Plant establishment on flooded and unflooded patches of a freshwater swamp forest in southeastern Brazil. **Journal of Tropical Ecology 14**: 793-803.

Scarano, F.R.; Rios, R.I. & Esteves, F.A. 1998. Tree species richness, diversity and flooding regime: case studies of recuperation after anthropic impact in Brazilian flood-prone forests. **International Journal of Ecology and Environmental Sciences 24**: 223-235.

Scarano, F.R.; Cirne, P.; Nascimento, M.T.; Sampaio, M.C.; Villela, D.M.; Wendt, T. & Zaluar, H.L.T. 2004. Ecologia vegetal: integrando ecossistema, comunidades, populações e organismos. Pp. 77-97. In: Rocha, C.F.D.; Esteves, F.A. & Scarano, F.R. (Orgs.). **Pesquisas de longa duração na Restinga de Jurubatiba: ecologia, história natural e conservação**. São Carlos, RiMa.

Shepherd, G.J. 2006. **FitopacShell 1.6.4. Manual, versão preliminar**. Departamento de Botânica, Universidade Estadual de Campinas.

Silva, A.C.; Van Den Berg, E.; Higuchi, P. & Oliveira-Filho, A.T. 2007. Comparação florística de florestas inundáveis das regiões Sudeste e Sul do Brasil. **Revista Brasileira de Botânica 30**: 257-269.

Silva, S.M.; Britez, R.M.; Souza, W.S. & Joly, C.A. 1994. Fitossociologia do componente arbóreo da floresta de restinga da Ilha do Mel, Paranaguá, PR. Pp. 33-48. In: **Anais do III Simpósio de Ecossistemas da Costa Brasileira: subsídios a um gerenciamento ambiental**, vol. 3. São Paulo, ACIESP.

Soffiati, A. 1998. Aspectos históricos das lagoas do norte do estado do Rio de Janeiro. Pp. 3-35. In: Esteves, F.A. (Ed.). **Ecologia das lagoas costeiras do Parque Nacional da Restinga de Jurubatiba e do município de Macaé (RJ)**. Rio de Janeiro, UFRJ.

Souza, V.C. & Lorenzi, H. 2008. **Botânica sistemática: guia ilustrado para identificação das famílias de Fanerógamas nativas e exóticas no Brasil, baseado em APG II**. 2 ed. Nova Odessa, Instituto Plantarum.

Sugiyama, M. 1998. Estudo de florestas da restinga da Ilha do Cardoso, Cananéia, São Paulo, Brasil. **Boletim do Instituto de Botânica 11**: 119-159.

Sztutman, M. & Rodrigues, R.R. 2002. O mosaico vegetacional numa área de floresta contínua da planície litorânea, Parque Estadual da Campina do Encantado, Pariquera-Açu, SP. **Revista Brasileira de Botânica 25**: 161-176.

Teixeira, A.P. & Assis, M.A. 2005. Caracterização florística e fitossociológica do componente arbustivo-arbóreo de uma floresta paludosa no município de Rio Claro (SP), Brasil. **Revista Brasileira de Botânica 28**: 467-476.

Teixeira, A.P.; Assis, M.A.; Siqueira, F.R. & Casagrande, J.C. 2008. Tree species composition and environmental relationships in a Neotropical swamp forest in Southeastern Brazil. **Wetlands Ecology and Management 16**: 451-461.

Teixeira, A.P. & Assis, M.A. 2011. Floristic relationships among inland swamp forests of Southeastern and Central-Western Brazil. **Revista Brasileira de Botânica 34**: 91-101.

Thomaz, L.D. & Monteiro, R. 1997. Composição florística da Mata Atlântica de encosta da Estação Biológica de Santa Lúcia, município de Santa Teresa – ES. **Boletim do Museu de Biologia Mello Leitão, Nova Série 7**: 3-48.

Toniato, M.T.Z. 2006. O regime hidrológico em matas de brejo: reflexos na estrutura e diversidade. Pp. 385-387. In: Mariath, J.E.A. & Santos, R.P. (Orgs.). **Os avanços da Botânica no início do século XXI: morfologia, fisiologia, taxonomia, ecologia e genética**. Porto Alegre, Sociedade Botânica do Brasil.

Toniato, M.T.Z.; Leitão-Filho, H.F. & Rodrigues, R.R. 1998. Fitossociologia de um remanescente de floresta higrófila (mata de brejo) em Campinas, SP. **Revista Brasileira de Botânica 21**: 197-210.

Torres, R.B.; Matthes, L.A.F. & Rodrigues, R.R. 1994. Florística e estrutura do componente arbóreo de mata de brejo em Campinas, SP. **Revista Brasileira de Botânica 17**: 189-194.

Vilela, E.A.; Oliveira-Filho, A.T.; Carvalho, D.A.; Guilherme, F.A.G. & Appolinário, V. 2000. Caracterização estrutural de floresta ripária do alto rio Grande, em Madre de Deus de Minas, MG. **Cerne 6**: 41-54.

Waechter, J.L. & Jarenkow, J.A. 1998. Composição e estrutura do componente arbóreo nas matas turfosas do Taim, Rio Grande do Sul. **Biotemas 11**: 45-69.

WCMC – World Conservation Monitoring Centre. 1992. **Global biodiversity: status of the Earth's living resources**. London, Chapman & Hall.

Zaluar, H.L.T. 1997. **Espécies focais e a formação de moitas na restinga aberta de Clusia, Carapebus, RJ**. Dissertação de Mestrado, Rio de Janeiro, Universidade Federal do Rio de Janeiro.

Zar, J.H. 1996. **Biostatistical analysis**. 3 ed. New Jersey, Prentice Hall.