

ARE THE NEOTROPICAL SWAMP FORESTS A DISTINGUISHABLE FOREST TYPE? PATTERNS FROM SOUTHEAST AND SOUTHERN BRAZIL

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This work synthesises information about plant diversity of 37 sites of coastal and inland swamp forests of southeast and southern Brazil and investigates floristic similarities and differences among them. Swamp forests often show low species richness, diversity and evenness, which are associated with the selective character of oxygen deprivation caused by soil waterlogging. However, our results pointed out some degree of site-level variation ($S_{\text{obs}} = 5$ to 110; $S_{\text{jack1}} = 6$ to 151; $H' = 0.82$ to 3.98; $J' = 0.51$ to 0.87) related to local ecological conditions. Two major phytogeographical patterns emerged from our work: the strong influence of the neighbouring non-flooded vegetation on the flora of swamp forests and its high spatial heterogeneity. At least 85.9% of the 518 species sampled are found in neighbouring non-flooded vegetation. A correspondence analysis consistently separated swamp forests of the coastal plain from those of the plateau. A Mantel test indicated a significant correlation between floristic and geographical distances among sites ($r = 0.45$; $p = 0.001$), and highlighted the main effect of regional-scale changes in the flora of swamp forests. We conclude that swamp forests of southeast and southern Brazil cannot be considered a distinguishable floristic unit.

Keywords. Atlantic Forest complex, Cerrado, phytogeography, plant diversity, wetlands.

INTRODUCTION

Brazil is a mega-diverse country that harbours the world's richest flora (more than 45,800 known species; Lista de Espécies da Flora do Brasil, 2014), with a very high percentage (~46%) of endemics (Forzza *et al.*, 2012). The magnitude of the threat to this extraordinary patrimony is shown by the fact that Brazil is home to two out of 35 hotspots of biodiversity – the Atlantic Forest and the Cerrado (Brazilian savannas) – for their exceptional concentrations of endemic species and rates of habitat loss (Mittermeier *et al.*, 2005; Ribeiro *et al.*, 2011).

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Habitat degradation has also affected swamp forests, a type of vegetation that grows on soils saturated or inundated by water table movements (WCMC, 1992; Scarano, 2006). These forests show naturally fragmented distribution and are related to hydromorphic soils, occurring by springs, riverbanks or oxbow lakes and natural depressions of the terrain (Ivanauskas *et al.*, 1997; Toniato *et al.*, 1998; Jacomine, 2004). They are widely distributed in the Neotropics and show interfaces with different types of vegetation, including rainforests, such as the Atlantic Forest, and grasslands, such as the Cerrado (Teixeira & Assis, 2011).

The overall structural and floristic patterns of Brazilian swamp forests have been described as having low diversity at local scale, dominance by one or few species, and species composition strongly influenced by the surrounding vegetation (Teixeira & Assis, 2011; Kurtz *et al.*, 2013). Similar patterns are also found in other swamp forests across the tropics (e.g. Richards, 1979; Phillips *et al.*, 1997; Pitman *et al.*, 1999; Posa *et al.*, 2011). However, there are only a few large-scale phytogeographical comparisons among Brazilian swamp forests (Rodrigues & Nave, 2004; Silva *et al.*, 2007; Teixeira & Assis, 2011), and hardly any have addressed coastal plain swamps. The only large-scale comparison including swamp forests of the coastal plain was carried out by Kurtz *et al.* (2013). These authors evaluated the floristic similarities among a set of coastal swamp forests and some other, possibly related, types of vegetation in Brazil. The results indicated an overall low similarity pattern, even with other swamp forests, and a strong influence of the neighbouring vegetation on the floristic composition of the swamp forests studied. Consequently, the authors proposed that swamp forests of southeast Brazil might not comprise a distinguishable floristic unit and attributed this to potential sources of local variation, notably migration and establishment of adaptable species from the neighbouring vegetation types. Here, we enhance the sampling universe both numerically and geographically to verify whether swamp forests in southeast and southern Brazil comprise a discrete floristic unit.

In this paper we compare the floristic and diversity patterns at 37 swamp forest sites. Our aims are (i) to synthesise information about plant diversity of swamp forests in southeast and southern Brazil, including sites of the coastal plain and inland plateau, and (ii) to investigate floristic similarities and differences among these swamp forests. Considering that these two sets of forests are subject to different physiographic conditions and, consequently, are surrounded and affected by different types of vegetation, we expect that the swamp forests of the coastal plain will be more similar to each other than to their counterparts on the inland plateau.

MATERIAL AND METHODS

Data source

We include in the analyses 28 phytosociological studies conducted in swamp forests of southeast and southern Brazil, in a total of 37 sites surveyed: 24 sites located in the coastal plain between Rio de Janeiro and Rio Grande do Sul states, and 13 sites

located in the inland plateau of Brazil (Table 1; Fig. 1). The sampling effort (number of individuals surveyed) was different between surveys, depending on the inclusion criteria and sample size (Table 1). However, because of the low number of studies conducted so far, this was not considered a restriction for comparing surveys.

Data analysis

We obtained from each site the following: species numbers, species list, Shannon diversity index (H') and evenness (J), the latter two parameters being calculated with natural logarithms (Zar, 1996). We also obtained, whenever possible, the number of sampling units per site and the number of species occurring in only one sampling unit. These data were used to compute the non-parametric richness estimator Jackknife 1 (first-order Jackknife; see Colwell & Coddington, 1994). This incidence-based estimator has shown good performance and its use has been recommended in biodiversity studies (Hortal *et al.*, 2006; Willie *et al.*, 2012).

To assess floristic heterogeneity of the swamp forests analysed, we created a binary matrix of species from all sites. For this, plant names were reviewed according to Lista de Espécies da Flora do Brasil (2014), or by specialists. Species not identified at this level and exotic species were excluded from the analyses. This species matrix included 518 trees and shrubs (Kurtz *et al.*, 2014). To verify the occurrence of these species in the neighbouring non-flooded vegetation, i.e. Atlantic Forest, Cerrado and/or *Restinga* (vegetation on sandy coastal plains), we compiled data from the literature (available from authors by request). The higher the percentage of shared species, the higher the influence of these non-flooded vegetation types on the flora of the swamp forests. A very high percentage means that swamp forests of southeast and southern Brazil might not comprise a distinguishable floristic unit.

Considering that our aim was searching for overall phytogeographical patterns for swamp forests, we excluded from multivariate analyses species sampled in just one site (exclusive species). This resulted in a new matrix with 250 species. We used a simple correspondence analysis (CA; Greenacre, 1984). The strength of CA is that the ordinations of species and samples are obtained simultaneously, allowing an examination of the relationships between them in a single analysis (Valentin, 2000). The calculations were performed with STATISTICA 8.0 (StatSoft, 2007). To confirm our initial expectation, i.e. that swamp forests of the coastal plain are more similar to each other than to their counterparts on the inland plateau, these sets of forests should be separated in the CA diagram.

We also tested the correlation between floristic and geographical distances among sites. The geographical distances were calculated with the tool 'Point distances' from Geospatial Modelling Environment 0.7.3.0 (Beyer, 2012), in ArcGIS 10.2.1 (ESRI, 2013). To assess floristic similarity, we used the Sørensen distance (see McCune & Mefford, 2011) on the matrix of 250 species. To verify the correlation between the matrices of floristic and geographical distances, we used the Mantel test (see Sokal,

TABLE 1. Phytosociological surveys of the woody layer of swamp forests from southeast and southern Brazil

Code	Site ^a	Altitude	Climate	IC	<i>A/P</i>	<i>N</i>	<i>S</i> _{obs}	<i>S</i> _{jack1}	<i>I</i>	<i>NE</i>	<i>H'</i>	<i>J'</i>	Reference
Coastal plain													
JU1	Restinga de Jurubatiba National Park, RJ	< 12	Aw	DBH ≥ 5 cm	1.44	2164	84	100	81	58	3.42	0.77	Kurtz <i>et al.</i> (2013)
JU2	Restinga de Jurubatiba National Park, RJ	< 12	Aw	DBH ≥ 5 cm	0.5	938	45	61	37	36	2.79	0.73	Oliveira (2000)
JU3	Restinga de Jurubatiba National Park, RJ	< 12	Aw	DBH ≥ 5 cm	0.52	827	49	59	39	37	2.76	0.71	Barros (2000)
PA1	Poço das Antas Biological Reserve, RJ	10	Aw	DBH ≥ 10 cm; height ≥ 10 m	1	486	97	134	81	50	3.98	0.87	Guedes-Bruni <i>et al.</i> (2006)
PA2	Poço das Antas Biological Reserve, RJ	10	Aw	DBH ≥ 10 cm	0.72	628	31	—	29	24	1.75 ^b 1.99 ^b	0.57 ^b 0.66 ^b	Carvalho <i>et al.</i> (2006)
PA3	Poço das Antas Biological Reserve, RJ	10	Aw	DBH ≥ 3.5 cm	0.5	1744	59	—	23	15	1.30	—	Scarano (2006)
IAN	Ilha Anchieta State Park, SP (site F)	4	Af	DBH ≥ 1.6 cm	?	363	38	—	37	29	3.13	0.84	Reis-Duarte (2004)
BER	Bertioga, SP	10	Af	DBH ≥ 3.2 cm	0.24	476	65	81	58	48	3.50	0.84	Guedes <i>et al.</i> (2006)
CE1	Campina do Encantado State Park, SP (shallow peat forest)	< 15	Cfa	DBH ≥ 4.8 cm	0.3	519	46	57	45	40	2.98	0.78	Sztutman & Rodrigues (2002)
CE2	Campina do Encantado State Park, SP (deep peat forest)	< 15	Cfa	DBH ≥ 4.8 cm	0.2	546	5	6	5	5	0.82	0.51	Sztutman & Rodrigues (2002)
ICA	Ilha do Cardoso, Cananéia, SP (site II)	< 14	Af	DBH ≥ 1.6 cm	0.1	867	30	35	30	27	2.44	0.71	Sugiyama (1998)
IM1	Ilha do Mel, Paranaguá, PR	< 5	Af	DBH ≥ 5 cm	0.56	1510	53	60	50	47	3.22	0.81	Silva <i>et al.</i> (1994)

TABLE 1. (Cont'd)

IM2	Ilha do Mel Ecological Station, PR (periodically flooded swamp)	< 5	Af	DBH \geq 4.8 cm	0.3	500	54	69	52	52	3.22	0.81	Menezes-Silva (1998)
IM3	Ilha do Mel Ecological Station, PR (permanently flooded swamp)	< 5	Af	DBH \geq 4.8 cm	0.4	607	60	75	55	52	3.21	0.78	Menezes-Silva (1998)
PST	Passa-Sete, Morretes, PR	10	Af	DBH \geq 10 cm	0.26	419	13	16	12	12	—	—	Galvão <i>et al.</i> (2002)
BAT	Batuva, Guaraqueçaba, PR	70	Af	DBH \geq 10 cm	0.16	312	13	16	12	12	—	—	Galvão <i>et al.</i> (2002)
CAB	Cabaraquara, Matinhos, PR	2–3	Af	DBH \geq 10 cm	0.32	443	27	37	23	23	—	—	Galvão <i>et al.</i> (2002)
ATA	Atami, Pontal do Paraná, PR	3	Af	DBH \geq 10 cm	0.2	410	29	40	19	18	—	—	Galvão <i>et al.</i> (2002)
ALE	Alexandra-Matinhos, Matinhos, PR	5	Af	DBH \geq 10 cm	0.2	337	36	48	29	29	—	—	Galvão <i>et al.</i> (2002)
GT1	Guaratuba 1, Guaratuba, PR	5	Af	DBH \geq 10 cm	0.3	400	26	38	22	22	—	—	Galvão <i>et al.</i> (2002)
GT2	Guaratuba 2, Guaratuba, PR	5	Af	DBH \geq 10 cm	0.4	434	78	105	59	50	—	—	Galvão <i>et al.</i> (2002)
TOR	Torres, RS	< 20	Cfa	DBH \geq 2.5 cm	0.2	706	60	—	50	45	—	—	Kindel (2002)
LPE	Lagoa do Peixe National Park, RS	< 15	Cfa	DBH \geq 5 cm	60	240	21	26	21	21	2.60	0.85	Dorneles & Waechter (2004)
TAI	Taim, RS	< 10	Cfa	DBH \geq 10 cm	30	120	12	16	19 ^c	13	1.89	0.76	Waechter & Jarenkow (1998)
Inland plateau													
UBE	Uberlândia, MG	860	Aw	DBH \geq 4.8 cm	0.62	2189	33	39	29	24	2.27	0.65	Nogueira & Schiavini (2003)
COQ	Coqueiral, MG	810–840	Cwb	DBH \geq 5 cm	0.32	585	99	136	99	61	3.50	0.76	Rocha <i>et al.</i> (2005)
SRC	Santa Rita de Caldas, MG	1158–1204	Cfb	DBH \geq 5 cm	1	2982	110	151	107	64	2.98	0.63	Loures <i>et al.</i> (2007)

TABLE 1. (Cont'd)

Code	Site ^a	Altitude	Climate	IC	<i>A/P</i>	<i>N</i>	<i>S</i> _{obs}	<i>S</i> _{jack1}	<i>I</i>	<i>NE</i>	<i>H'</i>	<i>J'</i>	Reference
CRP	Cristais Paulista, SP	945–1000	Cwb	DBH ≥ 3.2 cm	0.6	2036	61	76	82 ^c	71	2.71	0.66	Teixeira & Assis (2009)
CA1	Campinas, SP	590–610	Cwa	DBH ≥ 3.2 cm	0.2	904	55	74	49	41	2.80	0.70	Toniato <i>et al.</i> (1998)
CA2	Campinas Experimental Centre, SP	660	Cwa	DBH ≥ 5 cm	0.87	930	33	—	21	16	2.45	0.70	Torres <i>et al.</i> (1994)
BR1	Brotas, SP	620–680	Cwa	DBH ≥ 5 cm	0.36	735	51	68	40	30	2.81	0.71	Marques <i>et al.</i> (2003)
BR2	Brotas, SP	710–740	Cwa	DBH ≥ 4.8 cm	0.2	498	33	46	26	26	2.52	0.72	Costa <i>et al.</i> (1997)
ITA	Itatinga, SP	570	Cwa	DBH ≥ 4.8 cm	1	1242	39	—	35	31	2.75	0.75	Ivanauskas <i>et al.</i> (1997)
AGU	Agudos, SP	550	Cwa	DBH ≥ 4.8 cm	0.22	989	34	—	32	27	2.60	0.74	Paschoal & Cavassan (1999)
RCL	Rio Claro, SP	630–650	Cwa	DBH ≥ 4.8 cm	0.45	1651	49	64	43	38	2.10	0.54	Teixeira & Assis (2005)
BRA	Brasília National Park, DF	990–1040	Aw	DBH ≥ 3 cm	0.8	2763	60	70	45	41	2.99	0.73	Guarino & Walter (2005)
SUC	Sucupira farm, DF	1100–1200	Aw	DBH ≥ 3 cm	0.8	2667	53	61	44	37	2.84	0.71	Guarino & Walter (2005)

Altitude: approximate altitude (metres above sea level); Climate: according to Köppen classification; IC: inclusion criteria (DBH = diameter at breast height); *A/P*: sample area (ha)/number of points; *N*: number of live individuals sampled; *S*_{obs}: observed number of species; *S*_{jack1}: estimated number of species; *I*: identified species; *NE*: non-exclusive species used in the multivariate analyses; *H'*: Shannon diversity index (nat.ind.⁻¹); *J'*: evenness.

^aSites may be at different successional stages or have different conservation status, but since this information was not consistently provided by the authors it was not included in the table.

^bValues of *H'* and *J'* for the two fragments surveyed.

^cNumber of species in the floristic survey.

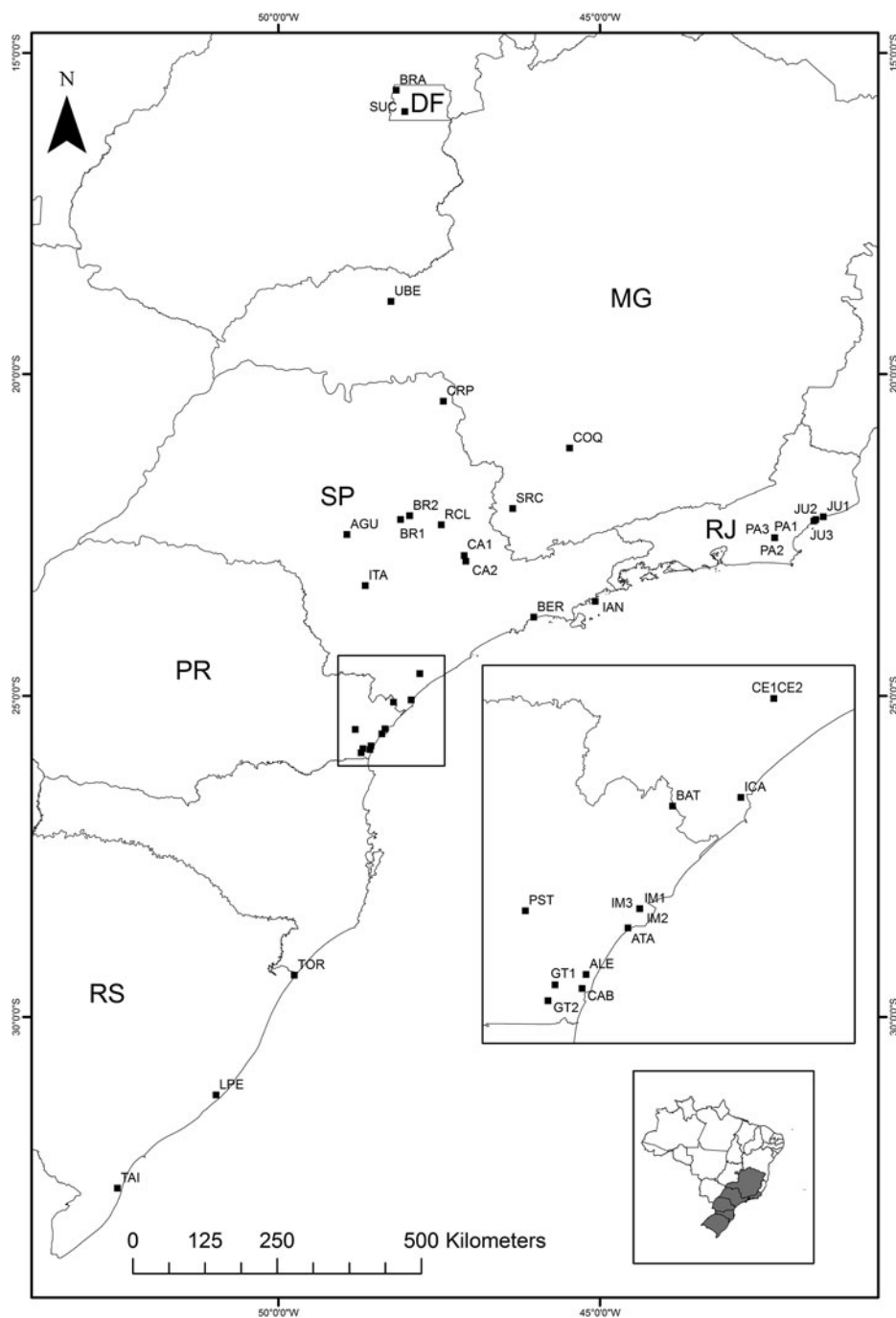


FIG. 1. Map of southeast and southern Brazil, showing the location of the 37 swamp forests analysed. DF: Distrito Federal; MG: Minas Gerais; SP: São Paulo; RJ: Rio de Janeiro; PR: Paraná; RS: Rio Grande do Sul (see Table 1 for details and references).

1979). The significance was verified with the Monte Carlo test, with 1000 randomised runs. The calculations were performed with PC-ORD 6.0 (McCune & Mefford, 2011).

RESULTS

Species richness, diversity and evenness

The swamp forests analysed showed a general pattern of low species richness, diversity and evenness (Table 1); monodominance or oligarchy at a local scale was frequent. Even the richness estimates were relatively low, rarely exceeding a hundred species per site. The percentage of species observed at each site relative to the estimated number of species was higher than 70% (except for site GT1; 68.4%), reaching 88.3% at site IM1.

Some sites had extreme values for the parameters analysed. Swamp forests degraded or at initial successional stage (PST and BAT), or located at higher latitudes (LPE and TAI, Rio Grande do Sul state), showed very low species richness. The extreme case was a forest on deep peat (> 5 m) on the coastal plain of São Paulo (CE2), which showed only five species ($S_{\text{jack1}} = 6$) and strong co-dominance of *Ilex pseudobuxus* Reissek and *Ternstroemia brasiliensis* Cambess. These two species accounted for 97.3% of individuals sampled, resulting in extremely low diversity and evenness ($H' = 0.82$; $J' = 0.51$). These results contrast with those found for a shallower section of the same peat (~1.5 to 3 m deep; CE1: $S_{\text{obs}} = 46$; $S_{\text{jack1}} = 57$; $H' = 2.98$; $J' = 0.78$).

On the other hand, an area located on the coastal plain of Rio de Janeiro (PA1) and another on the plateau of Minas Gerais (COQ) had high species richness ($S_{\text{obs}} = 97$ and 99; $S_{\text{jack1}} = 134$ and 136, respectively) and relatively high diversity ($H' = 3.98$ and 3.50, respectively). PA1 also had the highest evenness ($J' = 0.87$). Site SRC, located on the plateau of Minas Gerais, showed the highest species richness ($S_{\text{obs}} = 110$; $S_{\text{jack1}} = 151$), but low diversity ($H' = 2.98$) and evenness ($J' = 0.63$). This fact reflects an oligarchic structure, where *Myrsine leuconeura* Mart., *Myrceugenia ovata* (Hook. & Arn.) O.Berg, and *Sebastiania brasiliensis* Spreng. together constituted almost half (48.4%) of individuals sampled.

Intermediate values of species richness can also be associated with very low values of diversity and/or evenness. This occurred as a consequence of the dominance of *Tabebuia cassinoides* (Lam.) DC. in a permanently flooded swamp forest on the coastal plain of Rio de Janeiro (PA3: $S_{\text{obs}} = 59$; $H' = 1.30$), and oligarchy of *Euterpe edulis* Mart., *Calophyllum brasiliense* Cambess. and *Magnolia ovata* (A.St.-Hil.) Spreng. in a swamp forest on the plateau of São Paulo (RCL: $S_{\text{obs}} = 49$; $S_{\text{jack1}} = 64$; $H' = 2.10$; $J' = 0.54$).

Phytogeographical relationships

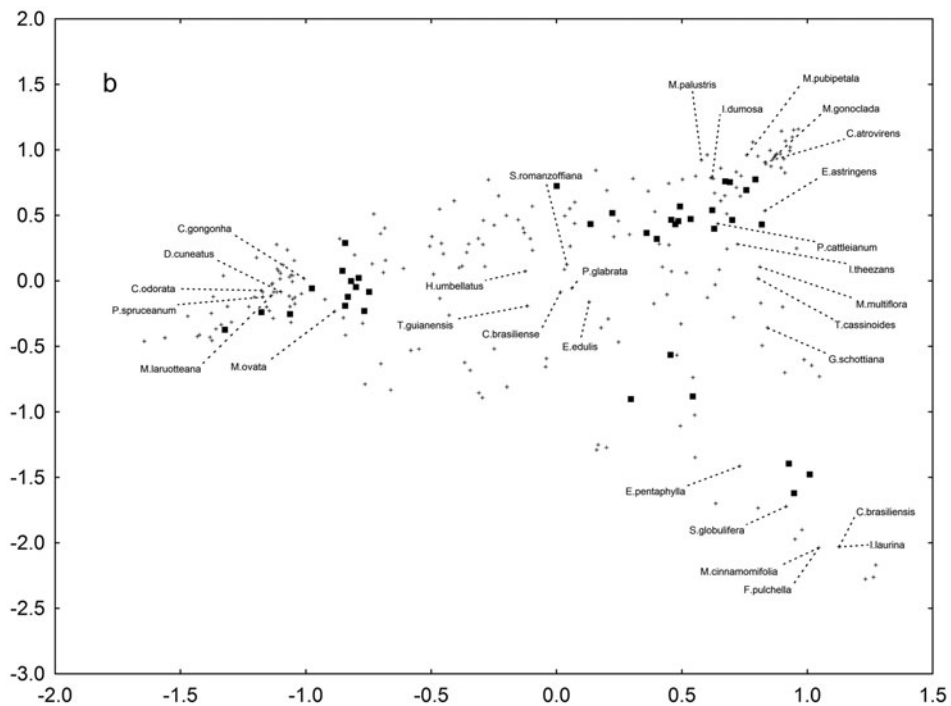
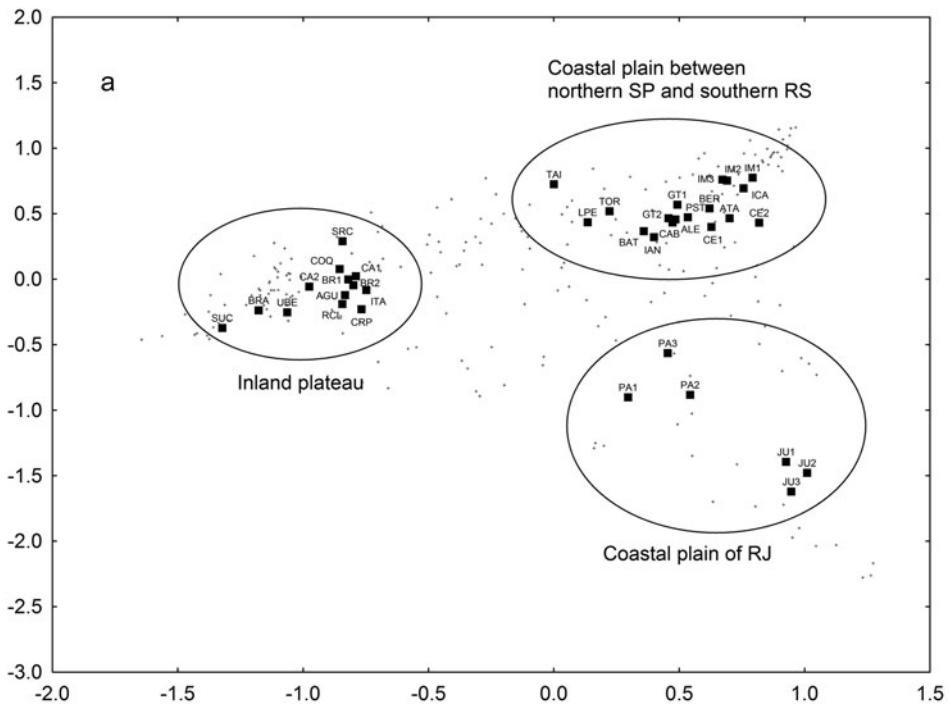
Considering all species identified at the 37 sites ($S = 518$), 268 (51.7%) were sampled at only one site, and 349 (67.4%) at up to two sites. On the other hand, only six species

(1.2%) were sampled at more than half the sites: *Calophyllum brasiliense* (30), *Tapirira guianensis* Aubl. (25), *Pera glabrata* (Schott) Poepp. ex Baill. (23), *Alchornea triplinervia* (Spreng.) Müll.Arg. (20), *Euterpe edulis* and *Tabebuia cassinoides* (19 sites each). Of these 518 species, at least 445 (85.9%) were recorded in the neighbouring non-flooded vegetation. Conversely, only 24 species (4.6%) seem to be restricted or occur preferentially on soils subjected to flooding (data available from authors by request).

Species often sampled on the coastal plain were: *Tabebuia cassinoides*, *Calophyllum brasiliense*, *Alchornea triplinervia*, *Psidium cattleianum* Sabine, *Myrcia multiflora* (Lam.) DC., *Pera glabrata*, *Clusia criuva* Cambess., *Tapirira guianensis*, *Euterpe edulis*, *Ocotea pulchella* (Nees & Mart.) Mez and *Myrcia racemosa* (O.Berg) Kiaersk. On the inland plateau, *Dendropanax cuneatus* (DC.) Decne. & Planch., *Magnolia ovata*, *Calophyllum brasiliense*, *Tapirira guianensis*, *Cecropia pachystachya* Trécul, *Protium spruceanum* (Benth.) Engl., *Guarea macrophylla* Vahl, *Pera glabrata*, *Handroanthus umbellatus* (Sond.) Mattos, *Citronella gongonha* (Mart.) R.A.Howard, *Cedrela odorata* L., *Myrcia laruotteana* Cambess. and *Styrax pohlii* A.DC. were frequent. Some of these species may have great phytosociological importance at a local scale.

In the swamp forests of the coastal plain, 304 species were sampled in total, and in those located on the inland plateau, the total was 313 species, indicating very similar figures. Only 99 species (19.1%) were common to both sets of swamps. Although the number of sites surveyed on the coastal plain was almost twice that of the inland plateau (24 vs. 13), the effort in terms of total individuals sampled was greater on the plateau (20,171 vs. 15,996).

The CA evidenced three groups of swamp forests (Fig. 2a). The first axis separated swamp forests of the coastal plain (right side of diagram) from those of the inland plateau (left side). The second axis separated the swamp forests of the coastal plain: sites of Rio de Janeiro, below, and sites located between northern São Paulo and southern Rio Grande do Sul, above. Considering the difficulty of adequately representing all 250 species analysed in a single diagram, we highlight in Fig. 2b some frequent species that illustrate different associations with those groups of swamp forests. This does not mean these species are necessarily exclusive to a specific group. Thus, some species are related to the coastal plain where they are widely distributed (e.g. *Psidium cattleianum*, *Myrcia multiflora*, *Ilex theezans* Mart. ex Reissek, *Geonoma schottiana* Mart. and *Tabebuia cassinoides*; the latter did not occur in Rio Grande do Sul). Other species are associated with one or another of the two sections of coastal plain discriminated in the analysis, i.e. Rio de Janeiro (e.g. *Symphonia globulifera* L.f., *Inga laurina* (Sw.) Willd., *Eriotheca pentaphylla* (Vell. & K.Schum.) A.Robyns, *Miconia cinnamomifolia* (DC.) Naudin, *Ficus pulchella* Schott and *Calyptanthes brasiliensis* Spreng.) and São Paulo to Rio Grande do Sul (e.g. *Ilex dumosa* Reissek, *Eugenia astringens* Cambess., *Maytenus gonoclada* Mart., *Cyathea atrovirens* (Langsd. & Fisch.) Domin, *Myrcia palustris* DC. and *Myrcia pubipetala* Miq.). In fact, many species that occur on the coastal plain, independently of the occurrence on the inland plateau, have their southern limits in swamps of Paraná or of the north-central portion of Rio Grande do Sul. In turn, *Magnolia ovata*, *Dendropanax cuneatus*, *Protium*



spruceanum, *Citronella gongonha*, *Cedrela odorata* and *Myrcia laruotteana* are related to the inland plateau. Finally, some species show no apparent preference for the plateau or coastal plain, and they occur indiscriminately in both situations. These species (e.g. *Calophyllum brasiliense*, *Tapirira guianensis*, *Pera glabrata*, *Euterpe edulis*, *Handroanthus umbellatus* and *Syagrus romanzoffiana* (Cham.) Glassman) are placed in the centre of the diagram. The eigenvalues for the first two axes were 0.58 (axis 1) and 0.44 (axis 2).

The Mantel test indicated a significant correlation between floristic and geographical distances among sites ($r = 0.45$; $p = 0.001$).

DISCUSSION

Species richness, diversity and evenness

The overall low diversity and evenness in swamp forests is often associated with the intense selective character of oxygen deprivation caused by soil waterlogging (e.g. Scarano, 2006). Our results indicate, however, some degree of site-level variation in richness ($S_{\text{obs}} = 5$ to 110; $S_{\text{jack1}} = 6$ to 151), diversity ($H' = 0.82$ to 3.98) and evenness ($J' = 0.51$ to 0.87) of swamp forests, which may be related to climate (Waechter & Jarenkow, 1998; Dorneles & Waechter, 2004), topography and flooding regime (e.g. Rocha *et al.*, 2005; Scarano, 2006; Kurtz *et al.*, 2013), water quality (Sztutman & Rodrigues, 2002), successional stage (Galvão *et al.*, 2002), and history of human disturbance (Galvão *et al.*, 2002). These frequently operate in an integrated way.

Swamp forests are composed of (i) flooding specialists, (ii) generalists (i.e. species apparently indifferent to the content of water in the soil), and (iii) low tolerance species (species with a preference for drier soils) (see Ivanauskas *et al.*, 1997; Marques *et al.*, 2003; Dorneles & Waechter, 2004; Carvalho *et al.*, 2006; Kurtz *et al.*, 2013). The relative contribution of these three groups to the structure of a specific site can vary considerably in response to the sources of local variation mentioned above. In general, flooding specialists (e.g. *Tabebuia cassinoides*, *Calophyllum brasiliense*, *Symphonia globulifera*, *Protium spruceanum* and/or *Magnolia ovata*) and some generalists (especially *Tapirira guianensis*) are notable in the structure (e.g. Toniato *et al.*, 1998; Galvão *et al.*, 2002; Sztutman & Rodrigues, 2002; Marques *et al.*, 2003; Rocha *et al.*, 2005; Teixeira & Assis, 2005, 2009; Carvalho *et al.*, 2006; Kurtz *et al.*, 2013), while other generalists and species with preference for drier soils promote richness and diversity at a given site. These latter species have low density and phytosociological importance, and have only one or a few individuals in the surveys.

Even at a given site, small topographic variations produce differences in the intensity of water saturation in very close patches of soil, promoting environmental



FIG. 2. Scatter plots showing the position of 37 swamp forests of southeast and southern Brazil (a) and their non-exclusive woody species (b) in relation to the first two axes of the correspondence analysis (see Table 1 for details and references).

heterogeneity and allowing the establishment of species with different ecological requirements (Scarano, 2006). Indeed, surveys by other authors that comprised wide flooding regime amplitude related to topographic variations showed higher species richness (JU1, PA1, COQ and SRC). Thus, the different types of neighbouring vegetation are the primary sources of generalists and species of drier soil (e.g. Costa *et al.*, 1997; Ivanauskas *et al.*, 1997; Marques *et al.*, 2003; Teixeira & Assis, 2005; Carvalho *et al.*, 2006; Toniato, 2006; Kurtz *et al.*, 2013).

On the coastal plain of southeast Brazil, forests subjected to permanent flooding are typically dominated by *Tabebuia cassinoides* (e.g. PA3, PST and BAT; see also Araujo *et al.*, 1998; Menezes & Araujo, 2005). This species is highly resistant to flooding and direct light, and shows pronounced asexual reproduction via roots and fallen trunks, which favours its predominance in areas affected by rising groundwater level (Scarano *et al.*, 1998; Scarano, 2006) or recurrent logging (Galvão *et al.*, 2002). Eventually, and with no apparent reason, *Tabebuia cassinoides* is absent from certain sites (CE1 and CE2), within its natural range.

Throughout the process of ecological succession controlled by the water table flooding regime, there are profound changes in physiognomy, composition, diversity and structure of the coastal swamp forests. With reduction in the intensity and duration of flooding, there is a decline of *Tabebuia cassinoides* and an increase in other tree species, including the flooding specialist *Calophyllum brasiliense* (e.g. Galvão *et al.*, 2002) and many other species from the surrounding vegetation. Differences in species richness ($S_{\text{obs}} = 59$ vs. 97), diversity ($H' = 1.30$ vs. 3.98) and structure (monodominance of *Tabebuia cassinoides* vs. high evenness) of areas subjected to permanent (PA3) and periodic flooding (PA1) of a swamp forest in Rio de Janeiro illustrate these changes (see also Araujo *et al.*, 1998; Menezes & Araujo, 2005).

Regarding the inland plateau, some studies have established, at a local scale, correlations between flooding regime and canopy openness, and species distributions (Teixeira *et al.*, 2008, 2011; Teixeira & Assis, 2009), but so far there is no consistent information about the dynamics of primary succession of swamp forests there.

Some authors have described differences in tree composition, diversity and structure in swamp forests that occur in dome-shaped peat grounds in the tropics (e.g. Phillips *et al.*, 1997; Page *et al.*, 1999; Posa *et al.*, 2011). These phasic communities occur in concentric zones from the periphery to the top of the dome, and their distribution at a local scale has been related to gradients in hydrology, nutrient availability, thickness of peat (Phillips *et al.*, 1997; Page *et al.*, 1999) and, presumably, the availability of species within dispersal distance (Posa *et al.*, 2011). Here the primary succession does not always mean an increase in richness and diversity of tree species, as outlined above for coastal swamp forests in southeastern Brazil. Instead, the process of peat accumulation produces increasingly oligotrophic conditions towards the top portion of the dome, eventually conditioning the development of species-poor, stunted forests (e.g. Phillips *et al.*, 1997).

Phytogeographical relationships

Two major phytogeographical patterns emerge from our analyses. First, there is a strong influence of the neighbouring non-flooded vegetation on the flora of swamp forests of southeast and southern Brazil. Detrended correspondence analysis including the coastal lowland vegetation in the same region (Marques *et al.*, 2011) showed a similar pattern, i.e. swamp forests did not form a distinct group in the diagram and they tended to be closer to neighbouring unflooded forests and scrubs. Thus, swamp forests of southeast and southern Brazil cannot be considered a distinguishable floristic unit, reinforcing the conclusion of Kurtz *et al.* (2013). The influence of neighbouring vegetation types has also been described for other tropical swamp forests (e.g. Pitman *et al.* 1999, for the Peruvian Amazon). Posa *et al.* (2011) indicated in their literature review that only some 11% of plants recorded in peat swamp forests of southeast Asia were restricted to that habitat. This figure is close to ours, and suggests that the influence of surrounding vegetation on the flora of swamp forests could be a pattern throughout the tropics.

Second, the floras of swamp forests of southeast and southern Brazil show high spatial heterogeneity, with the great majority of species sampled being restricted to one or a few of the 37 sites analysed (see Kurtz *et al.*, 2014). Considering the influence discussed above, this floristic heterogeneity largely reflects the heterogeneity of the vegetation domains in which the swamp forests occur, i.e. Atlantic Forest (Oliveira-Filho & Fontes, 2000) and Cerrado (Ratter *et al.*, 1996). Posa *et al.* (2011) argued that there is no single peat swamp forest vegetation across southeast Asia, and that the ecological and floristic heterogeneity found there suggests that each swamp is distinct.

The geographical location of each site, and its associated climate and neighbouring vegetation types, seem to be the determining factors behind the similarity relationships indicated in the CA. This analysis clearly differentiated swamp forests located on the coastal plain from those of the inland plateau, thus confirming our initial expectation. The analysis further separated swamp forests of the coastal plain of Rio de Janeiro (subject to a dry winter: Aw climate type) from the other coastal swamp forests (without dry season: Af or Cfa). Indeed, the correlation between floristic and geographical distances among sites, indicated by the Mantel test, highlights the main effect of regional-scale changes in species composition of swamp forests.

Swamp forests of the coastal plain, between Rio de Janeiro and northern Rio Grande do Sul, occur within the Atlantic Forest *sensu stricto* (*s.s.*; i.e. rainforests) or in areas of *Restinga*, the flora of which is strongly influenced by the Atlantic Forest (see Araujo, 2000). Oliveira-Filho & Fontes (2000) indicated that the decrease in temperature and increase in annual precipitation along the coast between northern Rio de Janeiro and southern São Paulo were responsible for variations in composition of the tree component of the Atlantic Forest *s.s.* Although they did not include swamp forests (nor the latitudinal variation included here) in their analyses, our results

strongly suggest that these climatic variations are also determining the composition of swamp forests, either directly or through the influence of the neighbouring Atlantic Forest *s.s.*

The Atlantic Forest *s.s.*, which has its meridional limit on the northern coast of Rio Grande do Sul (Joly *et al.*, 1991), exerts less influence on the southernmost swamp forests due to the dilution of tropical forest species that occurs southwards (Waechter & Jarenkow, 1998). However, this was not sufficient to separate sites LPE and TAI in the CA from their counterparts located further north.

In turn, swamp forests of the inland plateau are located in areas subject to a dry season of varying duration (prevailing climate Cwa or Aw). In southeast Brazil, changes in the rainfall pattern (i.e. decrease of annual means and increase in seasonality) in the E–W direction, related to distance from the Atlantic Ocean, promote the transition between rainforests and semideciduous forests (plateau forests; Leitão-Filho, 1987; Oliveira-Filho & Fontes, 2000). These changes, in addition to factors such as fire and soil fertility, also promote the transition of semideciduous forests to the Cerrado (Oliveira-Filho & Ratter, 1995; Oliveira-Filho & Fontes, 2000). Thus, climatic conditions and the influence of semideciduous forests and/or Cerrado seem to lead to the separation of the swamp forests of the inland plateau from their counterparts on the coastal plain.

Dispersal limitation could also potentially contribute to site differences. We believe that this is less relevant to the overall pattern since many of the species present in such sites have long distance mechanisms of dispersal. However, this awaits further elucidation.

Finally, despite recent advances, the ecology of swamp forests in Brazil is still poorly known. New local surveys are encouraged, especially in the North and Northeast regions, where there are so far no quantitative data. An increase in local surveys would allow new phytogeographical analyses at a larger spatial scale.

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