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Structure of the tree stratum of three swamp forest communities in southern Brazil under different soil conditions

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ABSTRACT

Restinga forests are commonly known to be plant communities rather poor in tree species. This study aimed to describe and explain the association between the floristic-structural similarities and the environmental conditions in three Swamp *Restinga* Forest communities in southern Brazil. In 13 plots of 100 m^2 each, we sampled all individual trees (circumference at breast height >12 cm and height ≥3 m). We collected soil samples in each plot for chemical and textural analyses. Phytosociological parameters were calculated and different structural variables were compared between areas. The density of individuals did not differ between areas; however, the maximum height and abundance of species differed between the site with Histosols and the other two sites with Gleysols. Further, a canonical correspondence analysis based on a matrix of vegetation and that of environmental characteristics explained 31.5% of the total variation. The high floristic and environmental heterogeneity indicate that swamp-forests can shelter many species with low frequency. Most species were generalists that were not exclusive to this type of forest. Overall, our study showed that swamp-forests within the same region can show considerable differences in composition and structure and can include species-rich communities, mostly due to the presence of species with a broader distribution in the Atlantic Rainforest domain on sites with less stressful environmental conditions and without waterlogged conditions.

Keywords: Atlantic rainforest, diversity, floristic, *Restinga*, soil

Introduction

The forest cover in southern Brazil has been greatly reduced, principally due to the expansion of agricultural lands and settlements. At present, only 7.3% of the original forest area in Rio Grande do Sul (RS) and only 23.4% in Santa Catarina (SC) remain (Fundação SOS Mata Atlântica *et al.* 2010). Particularly in the lowland Atlantic Rainforest region, large parts of the natural vegetation have been substituted by pastures, croplands, and settlement areas (MMA 2008). Only a few forest fragments remain, many of them smaller than 50 ha (Ribeiro *et al.* 2009). One of the lowland formations in the South Brazilian coastal region are the *Restinga* Forests (RF), for which transformation to other types of land use have been particularly high (Assumpção & Nascimento 2000). *Restingas* occur in areas of the coastal plain with consolidated sandy deposits (Gomes 1995), and their vegetation comprises mosaics of different communities under marine, fluvial-marine, and continental influence (Waechter 1985). *Restinga* ecosystems are primarily determined by local soil conditions, topography, and depth of the water table (Waechter 1985; Silva 1999; Mantovani 2003). They have been shown to be clearly distinct from Ombrophilous Forests in terms of floristic composition in a study using a large set of data from southern and southeastern Brazil (Marques *et al.* 2011). Waechter (1985) subdivided the RF formations into two types: *Restinga* on sandy soils (Sandy *Restinga* Forest, SARF) and *Restinga* in areas with swampy, peaty or waterlogged soils (Swamp *Restinga* Forest, SWRF). SWRF form a set of forest formations restricted to hydromorphic soils and are characterized by a groundwater table close to the surface or by periodic flooding. They include many species that are tropical and hygromorphic, some megaphyllous and malacophyllous species, and species with strategies that allow them to survive under conditions of water saturation and, in some cases high salinity (Waechter 1985; Oliveira & Joly 2010). In contrast, SARFs are characterized by a lower richness of tree species (6–48 species found per site in different studies, e.g., Dillenburg *et al.* 1992; Hentschel 2008; Scherer *et al.* 2009), species that are xeromorphic, sclerophyllous, and microphyllous, and some succulent species (Waechter 1985, Scherer *et al.* 2009).

A number of studies conducted in SWRFs of southern Brazil have shown considerable floristic richness, particularly of the tree community (26–81 tree species) (Kindel 2002; Hentschel 2008; Santos *et al.* 2012; Martins

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et al. 2013). Nevertheless, knowledge on these forests is still scarce, and there are no detailed and comparative discussions of the composition, structure, and functional characteristics of the South Brazilian SWRF.

The aim of this study was to evaluate the structural floristic patterns of the tree stratum in three SWRF areas in the coastal plain in northern RS and southern SC. We expected that species richness and diversity would be lower under more stressful site conditions. On the other hand, a greater variation in both the hydrological regime and the physical and chemical soil conditions at a site should result in local-scale differences in species composition and structure, resulting in increased species richness and diversity (Oliveira-Filho *et al.* 1994; Teixeira & Assis 2009; Martins *et al.* 2013).

Material and Methods

Location area

The study was performed in three SWRF areas in the lowland Atlantic Rainforest region of southern Brazil (IBGE 1992). The study areas were located in Morrinhos do Sul (MDS) in RS and in Içara (IÇA) and Balneário Arroio do Silva (BAS), both in SC (Tab. 1). The climate in the region is type Cfa according to the Köppen–Geiger classification: humid temperate with hot summers (Peel *et al.* 2007). The coastal plain *Restingas* in southern Brazil are situated on Pleistocene and Holocene sediments, with rare outcrops of ancient rocks, such as Triassic sandstone and Jurassic basalt in Torres and Itapeva (Suguio & Tessler 1984; Waechter 1985).

The three study areas had not been clearcut in the last 50 years. Signs of selective cutting of some individuals of heart of palm (palmito juçara, *Euterpe edulis* Mart.) were found in MDS. The fragment in MDS is located on the edge of the Morro do Forno Lake, in the Mampituba River basin, approximately 1 km from the slopes of the Serra Geral. MDS presents a considerable internal topographical variation from the wider area, resulting in a variety of soil conditions and water saturation areas throughout the year. The BAS forest fragment is located at the edge of the Caverá lagoon. Its substrate is peat (2.5–3.5 m deep) that remains waterlogged at the ground level for almost the whole year, and it has little internal topographic variation (1.3 m). The understory is characterized by the palm *Geonoma schottiana* Mart. and the herbaceous layer is dominated by *Nidularium innocentii* Lem. (Martins *et al.* 2013). The IÇA fragment has the largest forest area and the smallest perimeter/area ratio. Land use in the surrounding areas includes pasture, cultivation of irrigated rice, extraction of clay for pottery, and peat extraction in BAS. The three areas currently have drainage ditches at their forest edges at a depth of approximately 1 m in MDS and BAS and of 1.8 m in IÇA.

Vegetation sampling

In each area, data was collected from 13 plots of 5 m × 20 m with an approximate distance of 100 m between them and 50 m from the forest edge. We sampled all shrubs and trees with a circumference at breast height (CBH) ≥12 cm (equivalent to DBH ≥3.81) and height ≥3 m; this limit was chosen because of the high density of very thin stems in SWRFs. Cover value were calculated by summing the relative density and dominance. Classification into families followed APG III (2009) for Magnoliophyta and Smith *et al.* (2006) for Monilophyta. Scientific names followed the Brazilian Flora Checklist (Forzza 2012). Vouchers were deposited in the ICN Herbarium (Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brazil).

Soil sampling and analysis

Three subsamples of soil (0–15 cm depth) were collected at the same time, pooled to one sample per plot, and the physical and chemical features were analyzed (Santos *et al.* 2005). We evaluated the following chemical parameters (see also Tab. 2): pH in water, exchangeable cations (K^+, Mg^+, Na^+ and Ca^+), extractable aluminum (Al^{3+}), total acidity (H^+ and Al^{3+}), P, B, Mn, Fe, Zn, Cu, S, cation exchange capacity

Table 1. Location of the three areas of Swamp *Restinga* Forest considered in this study and principal geographic, edaphic and climatic characteristics of each forest fragment.

Com	Lat (S) and Long (W)	Area (ha) per. (m)	**Dist. (km)**	**Soil type**	**Soil text.**	**Alt. ± sd**	**AR ± sd**	**AT ± sd** (°C)	**TMC ± sd** (°C)
MDS	29°18'73" 49°55'12"	41 5.578	17	Gleissolo Háplico	Medium	10.6 ± 4.5	1.568 ± 266	19.3 ± 3.4	14.4 ± 1.3
IÇA	28°44'01" 49°13'56"	166 5.454	7.5	Gleissolo Melânico	Medium	15.9 ± 0.9	1.669 ± 399	19.5 ± 3.5	14.6 ± 1.3
BAS	29°02'37" 49°31'67"	31 2.956	4.6	Organossolo Háplico	Medium	7.7 ± 0.7	1.745 ± 608	20.3 ± 1.1	14.0 ± 0.9

Com: community, MDS: Morrinhos do Sul, RS, BAS: Balneário Arroio do Silva, SC, IÇA: Içara, SC; Lat: latitude; Long: longitude; Per: perimeter; Dist: distance to sea; Text.: texture; Alt.: Mean altitude (m.a.s.l.); sd: standard deviation; AR: Mean annual rainfall (mm/y); AT: Mean annual temperature; TMC: Mean temperature of month coldest. Sources for climatic data: National Institute Meteorology, Torres Station (MDS), Urussanga (IÇA) and Araranguá Station (BAS) (INMET 2012). The soil classification system followed EMBRAPA (2006), equivalent to Gleysols and Histosols to FAO soil classification (FAO 2006), see in the text.

(CEC) and total organic carbon (TOC). The analyses were performed at the Laboratory of Soil Analyses at UFRGS, according to the methods presented by Tedesco *et al.* (2004). The percentages of sand, silt and clay were determined using the Pipette method (Gee & Bauder 1986). For an evaluation of density and soil moisture, thirteen undisturbed composite soil samples were collected at sampling dates close together from each plot using volumetric rings of 272 cm^3 and soil sample extractors. To calculate the water content of the soil (wet weight minus dry weight), the samples were weighed on a precision scale before and after being processed in the oven at 105°C for 24 hours. Classification into soil orders was conducted according to EMBRAPA (2006).

Data analysis

We performed a sampling sufficiency analysis using an individual-based rarefaction curve with a confidence interval of 95%, according to Colwell *et al.* (2004). The species were grouped according to their distribution: restricted to Atlantic Rainforest *s.s.*, belonging to the Atlantic Forest formations *s.l.* (Oliveira-Filho & Fontes 2000), or widely distributed (present in two or more biomes *sensu* IBGE 2004). These groups were based on Lorenzi (1992), Jarenkow (1994), Sobral *et al.* (2006), the list of species of the Cerrado seeds network (2013) and the Brazilian Flora Checklist (Forzza 2012). Conservation status of tree species was assessed based on Klein (1990; we used this work because currently no official list exists for SC), IBAMA (1992), Rio Grande do Sul (2003), MMA (2008) and IUCN (2013). The phytosociological parameters of density, frequency, cover value, and dominance (basal area/ha) were calculated for each area. To evaluate the differences in community structure between areas we used the Rényi diversity profile (Tothmeresz 1995) and mean values per plot for height, density and evenness (J'). Soil variables were compared between areas by randomization testing (10,000 iterations) using Euclidean distance as a measure of resemblance.

After analysis of the correlation matrix between the total set of soil variables (chemical, physical and altitude), we conducted a canonical correspondence analysis (CCA) using a matrix containing a subset of variables with correlations below 0.7 (B, Mn, sand, silt, humidity and altitude) and a matrix of species abundances in the plots. The goal was to determine the proportion of variation in soil chemical and physical parameters that could explain the pattern of composition and abundance of species. The inertia scores of locations were calculated to evaluate the statistical significance of the model. Independence of the matrices was determined by a permutation test with 1000 permutations. Due to the high variation in species composition in MDS, we conducted a principal coordinate analysis (PCA) separately for this area, with Rho as the measure of resemblance (Borcard *et al.* 2011).

CCA analyses were performed with the vegan package (Oksanen *et al.* 2013) on the R platform (version 2.25.3; R Development Core Team 2013), randomization tests were performed with Multiv 2.4.2 (Pillar *et al.* 1997), and all other analyses were performed with PAST 2.15 (Hammer *et al.* 2001). We adopted a significance level of 0.05 for all analyses.

Results

Soil characteristics

The soils of the three communities differed significantly for the majority of variables and in most cases they differed significantly between all three areas (Tab. 2). Soils from both MDS and IÇA were classified as Gleysols. Soils with higher organic matter content were classified as Melanic Gleysols (equivalent to Gleissolo Melânico, EMBRAPA 2006) in IÇA, and as Haplic Gleysols (Gleissolo Háplico, EMBRAPA 2006) in MDS. Both areas showed a similar pattern regarding soil variables: medium texture, deficiency in phosphorus and calcium, low base saturation, high aluminum saturation and topographic variation between plots; the latter being more pronounced for MDS (standard deviation ± 4 m) than IÇA (standard deviation ± 1 m). MDS presented medium values for organic matter content, CEC, clay activity and phosphorus. IÇA showed high values for organic matter content, CEC and aluminum, and low clay activity. Plots at higher topographic positions showed both higher Al and silt values, and lower levels of Ca and Mg (Tab. 2).

BAS soils were classified as Haplic Histosols (Organossolos Háplicos, EMBRAPA 2006) and were characterized by medium texture and clay activity, low base saturation and aluminum saturation, but high aluminum concentration. Compared to soils in the other areas, BAS soils had a higher concentration of exchangeable bases (K, Ca and Mg), Zn, Mn and B; higher values of organic carbon (TOC), sand, P, Ca, CEC and sodium; extremely acidic pH; five to six times higher soil water content; and the lowest topographic variation (Tab. 2).

Composition and structure of vegetation

Inspection of the individual-based rarefaction curves showed that the asymptote was reached in BAS and IÇA, whereas the curve for MDS indicated that more species would have been found with increased sampling effort (Fig. 1). Although the density of individuals was similar between all three areas, MDS and IÇA differed significantly from BAS in terms of mean vegetation height, species density (i.e., richness per plot), Shannon diversity and evenness. The number of species, genera and families in MDS was much higher than in the other areas, with IÇA showing intermediate values (Tab. 3, Fig. 2). Observation of the diversity profiles showed that using diversity indices with a relatively higher weight on species richness ($\alpha < 2$) MDS

Table 2. Soil parameters (μ: mean value, sd: standard deviation) in three Swamp *Restinga* Forest communities. MDS: Morrinhos do Sul in Rio Grande do Sul (RS); BAS: Balneário Arroio do Silva; and IÇA: Içara; Both BAS and IÇA are in Santa Catarina (SC). Different letters indicate significant differences between areas, based on randomization testing.

	MDS		IÇA		BAS	
Soil parameters	μ	Sd	μ	Sd	μ	Sd
Sand (g)	381.8 **a**	87.7	419.6 **a**	56.3	512.6 **b**	133.0
Silt (g)	422.8 **a**	60.9	427.8 **a**	62.1	271.3 **b**	127.4
Clay (g)	195.4 **a**	82.8	152.5 **a**	22.8	216.1 **a**	127.8
Density (g/cm^3)	0.9 **a**	0.2	0.6 **b**	0.2	0.12 **c**	0.0
Humidity (g)	89.5 **b**	27.2	71.9 **b**	21.8	435.0 **a**	73.0
pH (H^2O)	4.5 **a**	0.3	4.2 **b**	0.1	3.64 **c**	0.1
SMP	5.4 **a**	0.6	4.37 **b**	0.1	3.60 **c**	0.3
P (mg/dm^3)	5.1 **a**	0.8	13.1 **b**	3.3	20.62 **c**	4.3
K (mg/dm^3)	72.1**a**	38.9	122.8 **b**	43.7	147.3 **b**	32.0
Al $cmolc/dm^3$	1.6 **a**	1.2	5.8 **b**	0.9	0.67 **a**	0.2
Ca $cmolc/dm^3$	1.2 **a**	0.7	1.0 **a**	0.6	7.18 **b**	1.5
Mg $cmolc/dm^3$	0.8 **a**	0.3	0.8 **a**	0.4	3.17 **b**	0.7
Na (mg/dm^3)	15.0 **a**	3.0	31.5 **b**	14.5	120.4 **c**	36.0
Al+H $cmolc/dm^3$	10.6 **a**	6.5	28.7 **b**	4.3	72.81 **c**	21.7
CTC $cmolc/dm^3$	12.8 **a**	6.5	30.8 **b**	4.3	83.45 **c**	21.2
% SAT CTC(Bases)	20.6 **a**	12.1	7.1 **b**	3.5	13.69 **a**	4.4
% SAT CTC (Al)	40.3 **a**	23.3	73.7 **b**	10.8	5.86 **c**	1.5
S (mg/dm^3)	18.8 **a**	8.9	71.3 **b**	62.0	68.0 **b**	22.2
Zn (mg/dm^3)	2.0 **a**	0.7	1.9 **a**	0.8	3.21 **b**	0.8
Cu (mg/dm^3)	1.5 **a**	0.5	0.6 **b**	0.2	0.12 **c**	0.0
B (mg/dm^3)	0.4 **a**	0.2	0.9 **b**	0.1	0.62 **c**	0.1
Mn (mg/dm^3)	31.9 **a**	28.6	8.5 **b**	7.5	34.0 **a**	21.8
Fe (g/dm^3)	2.2 **a**	1.0	0.4 **b**	0.3	0.95 **c**	0.5
TOC (% C)	3.5 **a**	2.2	8.3 **b**	4.3	39.3 **c**	2.8

was the most diverse community, and using diversity indices with more weight on abundance (α ≥ 2) IÇA was the most diverse and (α ≥ 3.5) MDS was the least diverse (Fig. 3).

Considering the three areas together, we found 110 tree or shrub species that met our inclusion criteria, and only 6.3% (7 species) occurred in all three communities. We found that 80% of the species were present in MDS (89 species). BAS presented 21.6% (26 species) and IÇA, 35% (39 species) of total species richness (Fig. 2). Sixty-nine species (62% of total) are widely distributed (present in two or more biomes *sensu* IBGE 2004), 31 species (28%) are limited to Atlantic Forest *s.l.* and 11 species (10%), were restricted to Atlantic Forest *s.s.* (Supplemental material 1). Eighteen of the species are currently considered to be threatened or endangered. Of these, 15 are arboreal, one is a heart of palm (*E. edulis*) and two are arborescent monilophytes: *Alsophila setosa* and *Cyathea corcovadensis*. In our study, *Ocotea elegans* was registered for the first time in Rio Grande do Sul (Supplemental material 1).

Table 3. Structural parameters from quantitative surveys of the tree stratum (height ≥3 m and circumference at breast height ≥12 cm) in Swamp *Restinga* Forest communities located in Morrinhos do Sul (MDS), Balneário Arroio do Silva (BAS) and Içara (IÇA). For each column, different letters indicate significant differences. Com.: Community; Max. height: maximum height (m); Spec. density: species density (richness/plot); Dens. ind.: density of individuals; sd: standard deviation; H': Shannon Diversity Index (nats/ind.); and J': Pielou equability.

Com.	Max. Height*	Spec. density ± sd	Dens. ind./ha	H'	J'
MDS	15.03 ^{a}	19.6 ± 4.9 ^{a}	3.792 ± 1.107 ^{a}	2.459 ^{a}	0.900 ^{a}
IÇA	15.46 ^{a}	15.6 ± 3.6 ^{a}	3.361 ± 1.028 ^{a}	2.492 ^{a}	0.913 ^{a}
BAS	13.38 ^{b}	9.8 ± 2.6 ^{b}	3.938 ± 1.067 ^{a}	1.773 ^{b}	0.843 ^{b}

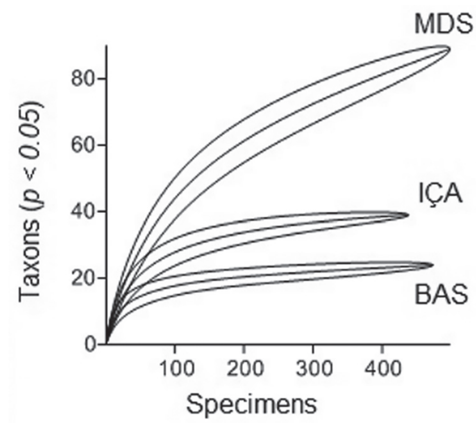

Figure 1. Individual-based rarefaction curves for three Swamp *Restinga* Forest communities in Balneário Arroio do Silva (BAS), Morrinhos do Sul (MDS) and Içara (IÇA). The measured values are from 13 plots per site and have a 95% confidence interval.

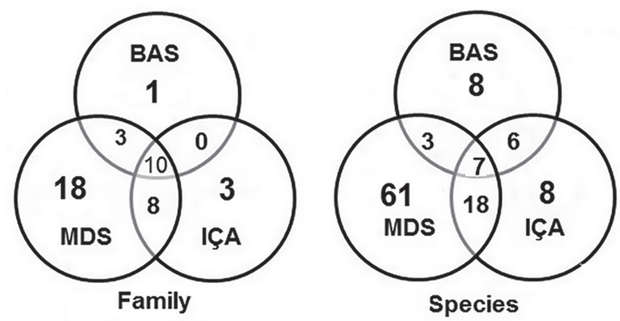

Figure 2. Venn diagram of sampled families and species in Swamp *Restinga* Forest tree communities located in Morrinhos do Sul (MDS), Balneário Arroio do Silva (BAS) and Içara (IÇA).

The tallest trees were recorded in MDS (up to 20 m): *Syagrus romanzoffiana*, *Magnolia ovata* and *Handroanthus umbellatus*. Typical understory species in other studies, *G. schottiana* (BAS), *Mollinedia schottiana* and *C. corcovadensis*

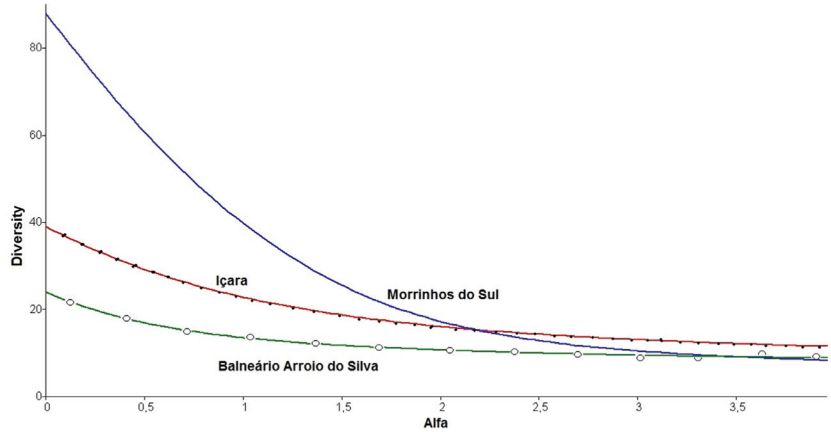

Figure 3. Diversity profile of the tree stratum in Swamp *Restinga* Forest communities located in Morrinhos do Sul (continuous line), Içara (dotted line) and Baln. Arroio do Silva (circles).

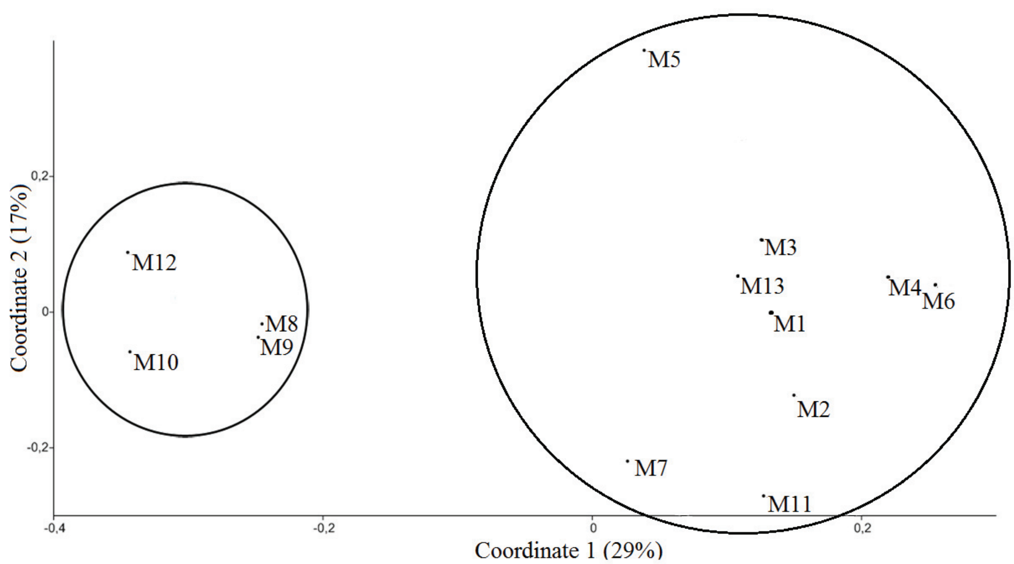

Figure 4. Ordination diagram (principal component analysis) of the tree stratum in the Swamp *Restinga* Forest in Morrinhos do Sul in Rio Grande do Sul. The circles indicate the two groups of plots, with the smaller group on the left side of the graph representing sites with drier conditions due to slightly higher altitude. Species names have been omitted to increase readability.

(MDS) were considered a part of the tree stratum in this study (height ≥3 m), due to the generally low vegetation height. *Ocotea pulchella* and *Ficus cestrifolia* were the tallest species in BAS. In IÇA, *Psidium cattleianum, S. romanzoffiana* and *Casearia silvestris* were the tallest.

In MDS, 21 families (58% of families) were represented by a single species (24% of species). Myrtaceae (23%), Lauraceae (7%), Euphorbiaceae (5%) and Fabaceae (5%) were the richest. In IÇA, Myrtaceae (S = 14) represented 36% of species, five families were represented by two species (5%) each, and 15 families (38%) were represented by only one species (6%). In BAS, four families were represented by two species (18%) and eight were represented by only one species (33%) (Supplemental material 1).

In both MDS and BAS, one single species, *E. edulis* and *O. pulchella,* respectively, had both the highest frequency (100%) and the highest relative cover (16.1% and 24.6%, respectively). In IÇA, *H. umbellatus* was the most frequent (100%) and *Myrcia glabra* had highest relative cover (9.9%). In BAS, two species from Lauraceae totaled 27.2% in cover, exceeding five species from Myrtaceae with 26.9% cover and three species from Arecaceae with 10.7% cover (Supplemental material 1).

In the MDS community, 42% (38 species) were represented by only one individual and a high number of species showed a low density of individuals, with the exception of *E. edulis*. In terms of cover, 12 species were necessary to achieve 50% of the total cover. The five species with the highest relative cover were *E. edulis* (16.1%), *Myrciaria floribunda*, *Actinostemon concolor* (4.5% each), *H. umbellatus* (4.4%) and *Guapira opposita* (3.4%). The PCA calculated only for MDS showed that plots were clearly separated into two groups: four plots on a higher topographic position and thus better drained, and one group consisting of the other seven plots (Fig. 4). Some species were found only in these higher areas and had very low frequency and abundance: *Albizia edwallii*, *Aniba firmula*, *Bathysa australis*, *Brosimum glaziovii*, *Cabralea canjerana*, *C. silvestris*, *Cedrella fissilis*, *Chrysophyllum inornatum*, *Eugenia multicostata*, *Garcinia gardneriana*, *Hirtella hebeclada*, *Myrciaria plinioides*, *Nectranda membranacea*, *Ormosia arborea*, *Protium kleinii*, *Rudgea jasminoides*, *Schefllera calva* and *Trichilia lepidota*. Other species were found in plots where the water table was near the surface over time: *A. concolor*, *F. cestrifolia*, *H. umbellatus*, *Inga sessilis*, *Jacaranda puberula*, *M. ovata*, *Marlierea eugeniopsoides* and *M. excoriata*.

In IÇA, seven species were necessary to achieve 50% of the total cover: *Myrcia brasiliensis* (18.9), *M. glabra* (9.9%), *H. umbellatus* (9.4%), *Faramea montevidensis* (8.6%), *M. multiflora* (6.6%), *Eugenia beaurepaireana* (5.1%) and *S. romanzoffiana* (4.9%). Myrtaceae (44.9%), Rubiaceae (10.5%) and Bignoniaceae (9.5%) together displayed 65% of cover (Supplemental material 1).

In BAS, we found lower species richness, evenness and vegetation height than the other areas (Fig. 2, 3). Five species accounted for nearly 53% of cover: *O. pulchella* (24.6%), *Myrcia pulchra* (11.7%), *M. multiflora* (8.5%), *Byrsonima niedenzuiana* (7.9%) and *Myrsine lorentziana* (6.6%) (Supplemental material 1).

Relationship between soil and vegetation

The CCA calculated for vegetation and soil data for all three areas explained 31.5% of the total variation ($p = 0.005$). The communities were clearly separated along the first two axes of the diagram. Plots of BAS on the right side of the figure were characterized by high values of humidity and sand, whereas on the left side of the figure MDS and IÇA were characterized by high silt content. MDS and IÇA were separated along the second axis. Altitude was not significant (Fig. 5).

Discussion

We compared three communities of SWRF in terms of structure and composition in relation to soil factors. The studied communities showed considerable differences in terms of floristic composition, abundance, and diversity parameters. Floristic similarity between the three areas was very low, with only seven (6.3%) shared species. This is likely a result of specific characteristics of the three communities related to the variation in environmental conditions (such as much more restrictive conditions in BAS) as well as to

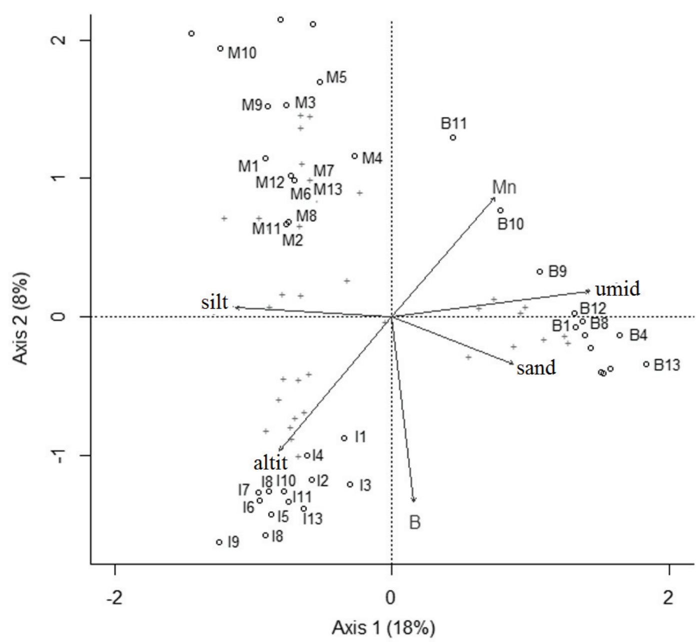

Figure 5. Canonical correspondence analysis of selected soil parameters (manganese, silt, sand, humidity, boron and altitude) and the most abundant tree species (abundances > 10 individuals: 36 spp.) in Morrinhos do Sul (M), Balneário Arroio do Silva (B) and Içara (I). Species names (+) have been omitted to increase readability.

variation in geographic factors (such as the proximity to slope forests in MDS, where the microtopographic variation allows for establishment of trees from these forests). The number of species found in the two areas with Gleysols was high compared to data from other SWRFs in South and Southeast Brazil (Silva *et al.* 2007), and a high percentage of species had very low frequency values on the local scale. At BAS, the area with Histosols, the richness, diversity and evenness were the lowest of all three areas in our study. Jacomine (2000) asserted that swamp forests can occur under varying soil conditions, mostly as a function of the moisture conditions. However, floristic conditions, vary not only as a consequence of the gradient of the water table depth, but as shown by Rodrigues & Nave (2000), in consequence of a number of factors. On the one hand, floristic and structural heterogeneity depends on the spatial heterogeneity of the physical characteristics of the environment. On the other hand, factors such as conservation status of the remnants and the composition of the surrounding vegetation matrix influence the arrival of propagules and thus plant establishment. The environmental heterogeneity and the relationship to other forests both appear to be key factors explaining the differences that were presented in this study (see also Oliveira-Filho *et al.* 1994; Silva *et al.* 2007). Overall, even though we only compared three communities situated relatively closely to each other, our results demonstrated that the SWRF in southern Brazil is a forest formation with high floristic heterogeneity, and is far from uniform.

The community in MDS had the highest number of total species, which was associated with the greater variation in substrate conditions, mainly topographic variation and hence variation in hydromorphic features. Differences in species composition between lower and higher sites were evident from the ordination diagram of this site (Fig. 4). The close relationship between soil properties and microtopographic variation on the one hand, and the association of tree species to very specific soil conditions (even over short gradients or environmental gradients at a small scale) on the other hand, has been widely demonstrated (e.g., Johnston 1992; Clark *et al.* 1999; Poulsen *et al.* 2006), including in *Restinga* areas in southeastern Brazil (Scarano 2002). Curcio (2006) studied soil and vegetation on the Iguaçu river floodplain, and likewise they found higher species richness at localities with greater variation in soil permeability and in greater proximity to slope forests; the same is evident in MDS. Proximity to slope forests of the Atlantic Forest (SAF) is the second factor explaining the higher richness in MDS. Slope forests are likely to be the origin of a large part of the *Restinga* flora and act as a source of diaspores of the more mesophyllic and hydrophilic species in these communities (Araújo & Lacerda 1987; Mantovani 2003). From the 89 species sampled in the MDS community in our study, 57 had been found by Jarenkow (1994) and Molz (2011) in their studies of SAF located relatively close to our study site. Of those species found in the highest plots in our study, only *A. edwallii* and *A. firmula* had not been sampled in the SAF studied by these authors.

In the IÇA community, the deeper drainage ditches likely affected environmental conditions and floristic composition, leading to greater floristic, structural and edaphic similarity with MDS than with BAS. However, despite the fact that soils in IÇA in general were more fertile that in MDS, due to higher organic matter and K content, the total species richness was not as high as in MDS. In a review of wetland forests in the southeastern United States, Lugo *et al.* (1988) concluded that differences in soil fertility did not seem to limit the establishment or the distribution of species in swamp forests, in contrast to humidity, which did impose these limits. According to Lugo *et al.* (1988), these species can grow well both on rich alluvial soils or nutrient-poor sites (e.g., siliceous sands or peatlands). The same seems to be true in our study.

The community in BAS represented a more extreme condition of SWRF, with lower richness and height than the other two communities. This can be attributed to more stressful environmental conditions, such as the high water content in the soil, likely due to longer periods of soil flooding (hypoxia or anoxia), and possibly due to the influence of salinity (higher sodium content). The Histosols present in the BAS community were identified by a histic horizon that predominantly comprised organic material, containing 80g/kg or more of organic carbon, resulting from accumulations of plant litter on the surface. This resulted in high superficial organic matter content and can contribute to the soil CEC and the retention of interchangeable cations, especially in soils with low clay content (White 2009) as shown in Tab. 2. Lugo *et al.* (1988) showed that stress resulting from salinity can reduce the number of tree species, and that low soil aeration can lead to a reduction in the diameter of stems. According to Marques *et al.* (2003) and Oliveira & Joly (2010), conditions of frequent or nearly constant flooding exert a strong selective role, as few tree species can survive under conditions of frequent water saturation, which explains the lower species richness. Some species occurred only in this community: *Boehmeria macrophylla*, *Cecropia pachystachya*, *Clusia criuva*, *G. schottiana*, *Miconia sellowiana*, *Myrcia palustris*, *Myrsine coriacea* and *Vernonanthura puberula*. Of these, however, only *G. schottiana* (48 individuals) and *C. criuva* (7 individuals) were more abundant. *G. schottiana* is an understory palm, very abundant in primary forests and in forests of quaternary coastal plains and semi-swamp situations (Sandwith & Hunt 1974) from Piauí to the south of Rio Grande do Sul (Sobral *et al.* 2006).

The species that can be considered more resistant to water saturation and medium salinity due higher density – even though not restricted to BAS – were *M. pulchra* and *O. pulchella*, which differed in density and cover from the other species. *Myrcia pulchra* occurs in Cerrado forests (Ratter *et al.* 2003), in the *Campos rupestres* (Rosa 2009) and in the Atlantic Forest *s.s.* (Sobral *et al.* 2006). *Ocotea pulchella* is a widely distributed species in riparian forests of the Cerrado and in Atlantic Forest biomes, and is a species without clear preferences regarding soil conditions (Forzza 2012; Unicruz 2013). In the IÇA community, the most important species in terms of density and cover were *M. glabra, M. brasiliensis* and *H. umbellatus*. *Myrcia glabra* is a selective hygrophyte, exclusive to Brazilian SAF, where it has a wide range from São Paulo state to RS (Sobral *et al.* 2006; Forzza 2012). *Myrcia brasiliensis* occurs over a broad altitudinal range in the Atlantic Forest *s.l. Handroanthus umbellatus* is present in lowland broadleaf forests of the Paraná Basin and in the Cerrado biome, and is considered a characteristic species of areas totally or partially soaked (Reitz 1974; Lorenzi 1992; Sobral *et al.* 2006). *Euterpe edulis*, a mesophyllic or slightly hygrophyllic species (Sandwith & Hunt 1974), is widely distributed in the Atlantic Forest, and *A. concolor* is likewise distributed in all Brazilian biomes (Smith *et al.* 1988; Forzza 2012); they both deserve to be highlighted due to their great importance in MDS. Altogether, this brief description of the distribution ranges of the most dominant species in the three communities shows the dominance of species with rather wide distributions among all of the studied forest fragments. Many are species that occur under tropical conditions and find the limit of their distribution in our study region (Rambo 1951, see also Jarenkow 1994). Evidence of this is the occurrence of the Lauraceae *O. elegans* in MDS, which was recorded for the first time in RS in our study.

Our results agree with those of Menezes *et al.* (2010), who stated that no specific tree flora exists for the swamp forests of south and southeast Brazil, as a consequence of the recent geological history of the coastal region. According to these authors, changes in floristic patterns between communities in this region occur as a function of the proximity of propagules as a source of species with high tolerance to waterlogging, as discussed for our study sites above; and additionally, as a result of the phytogeographical limitation of the these species as a consequence of the climatic constraints in these subtropical regions.

The great contribution of Myrtaceae and Lauraceae species to community richness is consistent with several studies of *Restinga* communities (e.g., Scarano 2002; Kindel 2002; Hentschel 2008) and indicates that these families contain many species tolerant to restrictive edaphic conditions. The family Fabaceae, with high species richness and individuals in different neotropical forest formations (Leitão-Filho 1987; Koponen *et al.* 2004; Toledo *et al.* 2011), showed high species richness in our study when we consider the generally lower importance of the family in forests in RS (Santos *et al.* 2012).

In the literature, when it comes to *Restinga* vegetation, often only SARFs are considered; i.e., communities on sandy and nutrient-poor soils with poor water retention that feature a relatively low tree species richness. Comparing the data that Scherer *et al.* (2009) obtained at 15 SARF sites to our study, only 30 species (27% of our total species number) were found to be in common between SARF and SWRF, 26 species occurred only in SARF and 85 only in SWRF. These differences between the two types of *Restinga* are currently not reflected in environmental legislation, for example in CONAMA Resolution 441 (CONAMA 2011). This might lead to insufficient representation of one of the vegetation types in protected areas or insufficient consideration of other conservation issues.

In conclusion, we showed that the structural floristic pattern of the tree stratum in three SWRF areas (lowlands coastal plain) in northern RS and southern SC differed considerably. The differences ranged from forests with extreme waterlogging (BAS) and low species richness to areas that already can be considered to be in a transitional situation to slope forests of the Atlantic Forest with high species richness (MDS). Both hydrological variation and proximity to slope appeared to be important factors defining the species composition of these communities. While the frequency of many species was very low, the generalist species with broad distribution ranges predominantly contributed to the high tree diversity in SWRFs in southern Brazil. This diversity of site conditions and the differences in community composition and structure between sites need to be considered, in addition to the presence of many endangered plant species, when it comes to the preservation of SWRFs in conservation units (Harris & Pimm 2004; Waechter 1985).

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