UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL
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Variações florísticas e estruturais em jaboticabais na floresta estacional no Planalto Sul-Brasileiro

Daniel Grasel

Porto Alegre, março de 2016

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Dissertação apresentada ao Programa de Pós-Graduação em Botânica da Universidade Federal do Rio Grande do Sul como parte dos requisitos para a obtenção do título de Mestre em Botânica.

Orientador: Prof. Dr. João André Jarenkow

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Resumo

Nós investigamos as relações entre a diversidade e a estrutura do componente arbóreo com as variáveis ambientais, em quatro posições microtopográficas (MPs), ao longo de um gradiente formado entre zonas úmidas depressionais florestadas e terras firmes em jaboticabais (FDWs) no Planalto Sul-Brasileiro. A riqueza específica e a diversidade foram similares nas terras firmes e menores nas zonas úmidas, enquanto que os parâmetros estruturais diferiram pouco entre as MPs. Uma análise de espécies indicadoras mostrou que poucas espécies são indicadoras das terras firmes, revelando que a distribuição das espécies foi relativamente uniforme em comparação às zonas úmidas. Os mesmos padrões foram revelados por uma análise de correspondência canônica (CCA), que mostrou que os alagamentos foram os principais determinantes da zonação de espécies arbóreas. Aparentemente, *Plinia peruviana* (Poir.) Govaerts (Myrtaceae) é a única espécie com distribuição praticamente restrita às MPs estudadas, mas os jaboticabais podem ter uma importância desproporcionalmente maior na preservação de espécies que são pouco abundantes em outras florestas na região. A ocorrência exclusiva de solos distróficos nas áreas de estudo, em uma região onde solos eutróficos predominam, indicam que as terras firmes estudadas representam zonas transicionais entre as zonas úmidas e a matriz florestal. Como estudo pioneiro em zonas úmidas depressionais florestadas no Planalto Sul-Brasileiro, nossos resultados sugerem que ao menos toda a área correspondente às depressões topográficas deve ser protegida, até que estudos complementares proponham zonas de amortecimento apropriadas, com base em critérios biológicos. Jaboticabais são ecossistemas únicos cuja restauração, manejo e preservação são cruciais para manter ambientes espacialmente heterogêneos e, consequentemente, a riqueza específica e as funções e serviços ecossistêmicos.

Palavras-chave Floresta Atlântica. Floresta estacional. Zonas úmidas geograficamente isoladas. Jaboticabais. Análise de correspondência canônica. Análise de espécies indicadoras.

Abstract

We investigated the relationships between tree component diversity and structure with environmental variables of four microtopographic positions (MPs) along a wetland-upland gradient in forested depressional wetlands (FDWs) on the South Brazilian Plateau. Species richness and diversity were quite similar in the uplands and lowest in the wetlands, while structural parameters differed little among MPs. An indicator species analysis showed that few species were indicators of the upland sites, suggesting that species distribution was relatively uniform in comparison to the wetlands. The same patterns were revealed by a canonical correspondence analysis (CCA) that showed flooding to be the main factor driving tree species zonation. Apparently, *Plinia peruviana* (Poir.) Govaerts (Myrtaceae) is the only tree species with practically restricted distribution to the studied ecosystems, although FDWs and their surrounding uplands can have a disproportionately higher importance in the preservation of species that are under-represented in other regional forests. The occurrence of exclusively dystrophic soils in the study areas, in a region where eutrophic soils predominate, indicates that the studied uplands represent transitional zones between the FDWs and the forest matrix. As a pioneer study in FDWs on the South Brazilian Plateau, our findings suggest that the whole area of the topographic depressions should be protected at least until complementary studies propose proper buffer zones based on biological criteria. FDWs are unique ecosystems whose restoration, management and preservation are crucial to maintain spatial environmental heterogeneity and consequently species richness and ecosystem functions and services.

Keywords Atlantic forest. Seasonal forest. Geographically isolated wetlands. *Jaboticabais*. Canonical correspondence analysis. Indicator species analysis.

Sumário

Introdução geral

A composição florística e a estrutura das formações vegetacionais no Planalto Sul-Brasileiro são relativamente bem conhecidas, o que se deve à realização de intensivos e extensivos estudos florísticos e fitossociológicos (e.g., Reitz 1965; Vibrans et al. 2012, 2013a, b). Tais estudos abrangem desde ambientes com predomínio de vegetação herbácea, como campos de altitude (Iganci et al. 2011), banhados (Magalhães et al. 2016) e afloramentos rochosos (Rocha et al. 2015), até ambientes florestais, desde florestas ribeirinhas (Giehl e Jarenkow 2008) até florestas próximas aos divisores de água das microbacias hidrográficas (Orihuela et al. 2015). Estes últimos certamente são mais bem conhecidos do que os primeiros, especialmente no que tange ao componente arbóreo. Contudo, banhados ocupados por florestas não foram alvo de qualquer estudo vegetacional no Planalto Sul-Brasileiro, sendo a sua ocorrência pouco mencionada na bibliografia especializada.

Algumas das poucas informações existentes sobre a vegetação dos referidos banhados encontram-se nos planos de zoneamento (Guadagnin 1994) e de manejo do Parque Estadual do Turvo (Derrubadas-RS; SEMA 2005), onde os mesmos são referidos como jaboticabais em função da ocorrência de densas populações da espécie arbórea *Plinia peruviana* (Poir.) Govaerts (Myrtaceae), conhecida popularmente como jaboticabeira. De acordo com Guadagnin (1994), a incomum distribuição agregada e restrita de *Plinia peruviana* nos jaboticabais gerou até mesmo especulações sobre a possibilidade destas populações terem sido implantadas e manejadas por indígenas, a exemplo de algumas espécies amazônicas úteis aos povos florestais nativos. Além disso, a vegetação nos jaboticabais é conhecida também pela abundância da palmeira *Syagrus romanzoffiana* (Cham.) Glassman e pela riqueza de epífitos (Guadagnin 1994; SEMA 2005).

De acordo com a classificação das zonas úmidas brasileiras proposta por Junk et al. (2014), jaboticabais correspondem a depressões topográficas sujeitas a afloramentos polimodais e imprevisíveis do lençol freático em decorrência do acúmulo da água das chuvas ("*rain water fed wetlands in small depressions*"). Na literatura internacional, são conhecidos como zonas úmidas depressionais florestadas (*forested depressional wetlands*; e.g., Casey e Ewel 2006), sendo completamente circundadas por terras firmes (Tiner 2003). Em geral, zonas úmidas depressionais são pequenas (< 1 ha; Iop et al. 2012), representando uma parcela também pequena da área total ocupada pela matriz vegetacional circundante (e.g., 0,12% no Parque Estadual do Turvo; Guadagnin 1994). Além disso, podem apresentar distribuição restrita, como é o caso dos jaboticabais no Planalto Sul-Brasileiro, que ocorrem exclusivamente em áreas planas próximas aos divisores de água das microbacias hidrográficas (SEMA 2005).

Apesar da distribuição restrita e da pequena área total ocupada, as zonas úmidas depressionais abrigam uma parcela desproporcionalmente maior da biodiversidade regional em comparação a outros tipos de zonas úmidas (Williams et al. 2003; Scheffer e van Geest 2006). Tal constatação é extremamente preocupante diante do estado precário de preservação dos jaboticabais no Planalto Sul-Brasileiro. A maior parte desses ecossistemas (fora de unidades de preservação) foi convertida para atividades agropecuárias, e os poucos remanescentes se encontram degradados ou desconectados da matriz florestal, sujeitos a inúmeros fatores de perturbação, que incluem drenagem, aterramento, pastoreio e pisoteio pelo gado, extração seletiva de plantas, caça, invasão de espécies exóticas, obras viárias, construção de reservatórios de água e mudanças climáticas (Brinson e Malvárez 2002; Junk 2013).

Nesse contexto, torna-se evidente a necessidade da realização de pesquisas em ecossistemas de referência com o propósito de criar subsídios para o estabelecimento de estratégias de restauração, manejo e preservação de jaboticabais. Para contribuir com esse objetivo, nós conduzimos um estudo para avaliar as relações entre as variáveis ambientais (relacionadas a características edáficas e topográficas) e a composição e estrutura de comunidades arbóreas ao longo de um gradiente formado entre zonas úmidas depressionais florestadas e terras firmes, em jaboticabais na floresta estacional no Planalto Sul-Brasileiro. Especificamente, nós abordamos as seguintes questões: (1) A estrutura florestal, a composição específica, a riqueza e a diversidade de espécies arbóreas varia ao longo do gradiente formado entre zonas úmidas e terras firmes? (2) Podemos esperar a ocorrência de espécies típicas em posições específicas do perfil microtopográfico?

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Forest Diversity and Structure in Depressional Wetlands on the South Brazilian Plateau[*]

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Forest Diversity and Structure in Depressional Wetlands on the South Brazilian Plateau

Introduction

Depressional wetlands (DWs), also known as "geographically isolated wetlands" (a term still under discussion; see Leibowitz 2015; Mushet et al. 2015), are defined as those completely surrounded by uplands (Tiner 2003). In general, DWs are small (< 1 ha), occur in low densities and can occupy less than 1% of forest landscapes (Guadagnin 1994; SEMA 2005; Iop et al. 2012). Despite these characteristics, DWs fulfill a myriad of ecosystem functions and services (Leibowitz 2003; Cohen et al. 2016), harboring a disproportionately greater share of biodiversity in relation to other wetland ecosystems (Williams et al. 2003; Scheffer and van Geest 2006).

In the Atlantic Forest biome on the South Brazilian Plateau (IBGE 2004), DWs are practically restricted to flat areas close to the water divisors of the river basins (SEMA 2005). According to the classification proposed by Junk et al. (2014), they correspond to "rain water fed wetlands in small depressions", being subject to polymodal and unpredictable water table upwelling. These DWs (when vegetated) show highly variable vegetation physiognomies, varying from predominantly herbaceous to arboreal communities (forested depressional wetlands – FDWs), presenting different levels of woody species encroachment determined by local variations in the hydrological conditions (see also Palik et al. 2007).

On the South Brazilian Plateau, the FDWs and their immediate surroundings (or just the surroundings of the DWs) are known as *jaboticabais* because of the high abundance of the fruit tree *Plinia peruviana* (Poir.) Govaerts (Myrtaceae) (known as *jaboticabeira*; SEMA 2005), which occurs in the FDW-upland interface. In these ecosystems, microtopography determines large micro-spatial heterogeneity from the FDWs to the water divisors of the topographic depressions, in distances that can be as small as 30-40 m. In the FDWs, microrelief is highly irregular due to the occurrence of many well-drained hummocks (ca. 30 cm-high and ca. 1-2 m-wide; see also Teixeira et al. 2008), interspaced by permanently water-saturated hydromorphic soils. From the FDWs toward the more elevated surrounding areas, soil profundity tends to decrease, and rocky outcrops are common on the water divisors of the depressional basins.

At a local scale, microtopography is widely recognized as shaping vegetational patterns through its direct or indirect influence on a myriad of abiotic and biotic variables (e.g., Courtwright and Findlay 2011). From the microtopographically-controlled factors, soil moisture is one of the most important drivers of plant communities and the most affected by the microrelief (Moeslund et al. 2013). Higher sites generally present drier soils than lower sites because of the water runoff, while lower areas tend to be moister because of the water input from higher areas and the proximity of the water table (Rennó et al. 2008). Given the paramount importance of water availability in structuring plant communities, forests are expected to show distinct compositional and structural patterns between areas subject to flooding and drought (Jirka et al. 2007; Balvanera et al. 2011).

Despite being environmentally heterogeneous, a feature directly linked to species richness (Stein et al. 2014) and ecosystem functions and services (Lovett et al. 2005; Turner et al. 2012), the FDWs on the South Brazilian Plateau historically have been neglected. The majority of these ecosystems outside of preservation units are partially degraded or converted, and the few remaining are disconnected from the forest matrix, being subject to several threats (e.g., draining, grounding, grazing and trampling by cattle, harvest of plants and animals, invasion of exotic species, road works, construction of water reservoirs, and climate change; Brinson and Malvárez 2002; Junk 2013). Part of this scenario is due to the lack of studies on the vegetation of *jaboticabais*, which is surprising, given the well-documented and the increasingly recognized ecological importance of DWs (e.g., the special issue of *Wetlands*, Vol. 23, No. 3, September 2003; Cohen et al. 2016). However, FWDs have received less attention, and little is known about the relationships between environmental variables and forest diversity and structure in these ecosystems (Previant and Nagel 2014).

The current environmental status, combined with the state of knowledge about the FDWs on the South Brazilian Plateau, point to the need for intensive research efforts to create subsidies for the restoration, management and preservation of *jaboticabais*. To contribute to this goal, we conducted a fine-scale study to investigate the relationships between environmental variables (related to edaphic and microtopographic features) and the composition and structure of tree communities along a wetlands-upland microtopographic gradient. Specifically, we addressed the following questions: (1) Do forest structure, species composition, richness and diversity vary between microtopographic positions along the wetland-upland gradient? (2) Can we expect the occurrence of typical species in specific microtopographic positions?

Material and methods

Study areas

The study was conducted in two subtropical FDWs embedded in remnants of the semi-deciduous seasonal forest on the South Brazilian Plateau (Oliveira-Filho et al. 2015), both situated on the Uruguay River basin (the reduced number of preserved FDWs and logistic problems prevented the selection of more study areas). The first FDW, with ca. 0.31 ha (forested only in the periphery), is surrounded by a forest remnant with ca. 9.5 ha, located within a private property, in the municipality of São João do Oeste, Santa Catarina State (27°05’39’’S, 53°34’17’’W; 498 m a.s.l.). The second FDW, with ca. 0.94 ha (almost entirely forested), is situated at Turvo State Park (a preservation unit with 17,491 ha; SEMA 2005), in the municipality of Derrubadas, Rio Grande do Sul State (27°12’49’’S, 53°51’14’’W; 433 m a.s.l.) (Fig. 1). Regional landscape shows several forest remnants (60% with no more than 20 ha; Vibrans et al. 2012) embedded in an agricultural and livestock matrix.

According to Köppen’s classification, the climate in the region is subtropical humid without a dry season (Cfa type; Alvares et al. 2014). The annual averages of temperature and rainfall are ca. 20°C (Pandolfo et al. 2002) and ca. 1,900 mm (Pinto 2011), respectively. Soils originate from basaltic rocks, resulting in predominantly eutrophic ones, formed in hilly relief (IBGE 1990).

Vegetation sampling

We performed a tree species survey in 80 plots of 5 × 10 m (with two subplots of 5 × 5 m) distributed along a wetland-upland microtopographic gradient. In each study area, we established, starting from the north, 10 radial transects at fixed distances proportional to the size of the FDWs perimeters. Along all transects, we allocated plots in four microtopographic positions (MPs): inside (wetlands) and immediately outside (lower slopes) the FDWs, and in areas with 60 cm (middle slopes) and 120 cm (upper slopes) of elevation in relation to their limits. The beginning of the FDWs was arbitrarily established by the presence of permanently water-saturated hydromorphic soils (Magalhães et al. 2016). As proposed by Damasceno-Junior and Pott (2011), the major axis of the rectangular plots was aligned to the terrain level curves to better represent specific environmental conditions. Once the FDW of the first study area indicated no trees in the central zone, we established all plots of the wetlands at ca. three meters

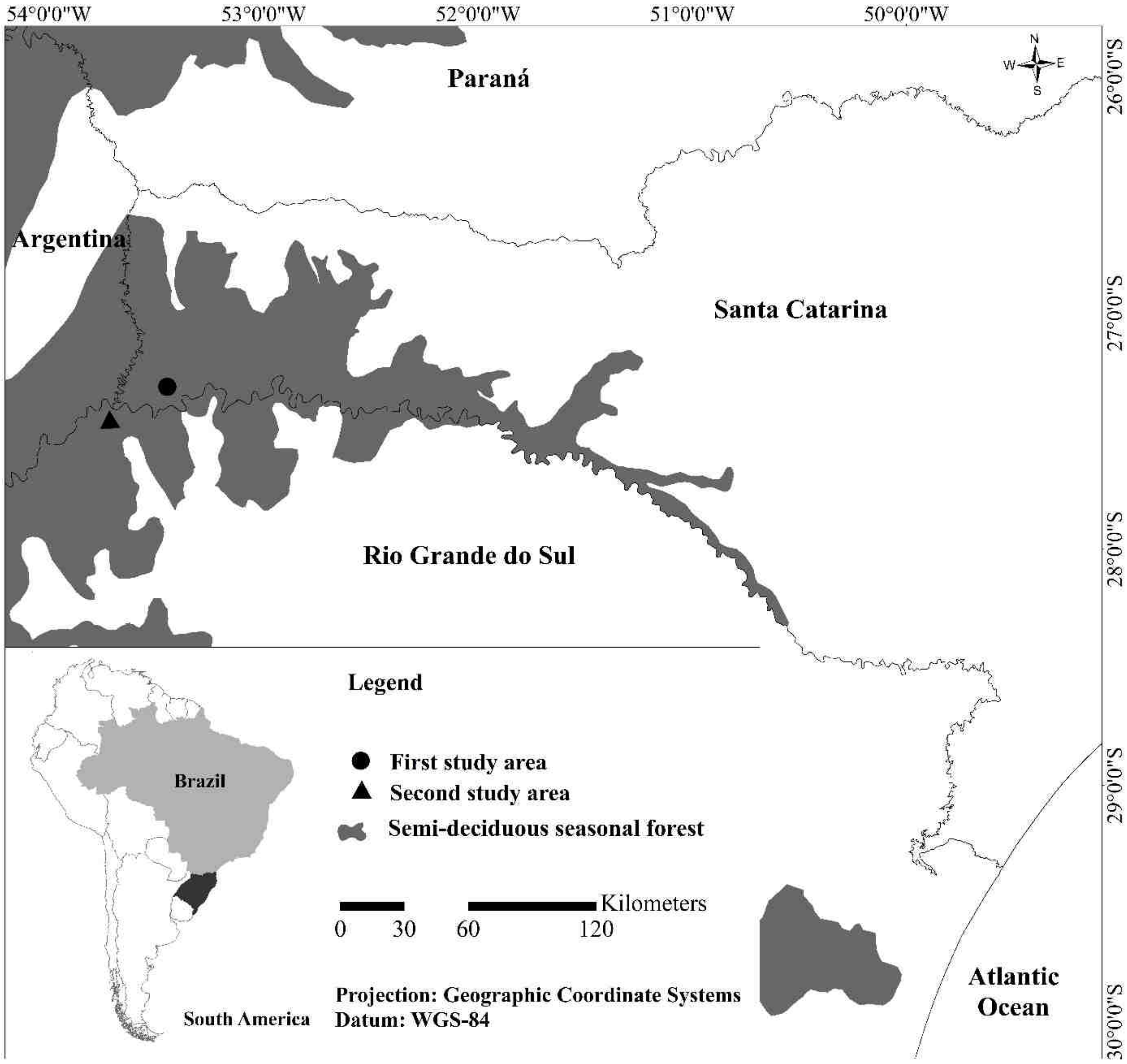

Fig. 1 Map showing location of the study areas in southern Brazil

from their boundaries. We sampled all trees with at least one stem with a perimeter at breast height (pbh) ≥ 15 cm. The species identification was done by consulting a specialized bibliography, the collection of the Herbarium ICN of the Universidade Federal do Rio Grande do Sul (UFRGS) and specialists. The revision and updating of the taxa names was based on Flora do Brasil (2016), and the APG IV (2016) classification system was adopted for families.

Microtopographic survey, soil depth measurement and soil analysis

Two “environmental variables” related to microtopographically driven differences in soil water availability were measured in each plot: (1) average elevation (AE; in cm above or below the FDWs boundaries), which was given by averaging the elevations of the corners of the subplots; and (2) slope, the maximum difference in elevation (in cm) between the corners. To perform these detailed topographic surveys (and establish plots at different elevations in the transects), we used a 20 m long water-filled levelling hose and a tape measure graduated in millimeters, following Cardoso and Schiavini (2002).

We measured soil depth with an iron bar 1.5 m long in the four corners of each plot to obtain the average soil depth (ASD) per plot. A fourth environmental variable, the "average vertical distance to the water table" (AVDWT), was obtained by subtracting the average soil depth from the average elevation. Positive AVDWTs indicated that the tree roots are prevented from accessing the groundwater vertically by coming into contact with the rocks. On the other hand, negative AVDWTs indicated free access to the groundwater.

The soil chemical and textural features were obtained from the analysis of eight composite samples (20 cm depth) collected in the center of the plots of each MP. The soil analyses were performed at the UFRGS Soil Laboratory, based on the EMBRAPA (1997) protocols. The following variables were obtained: percentages/quantities of clay, silt, sand, organic matter (O.M.), phosphorus (P), potassium (K), aluminum (Al), calcium (Ca), magnesium (Mg), sulfur (S), zinc (Zn), copper (Cu), boron (B) and manganese (Mn); pH in water suspension, potential acidity (Al+H), cation exchange capacity (CEC), sum of bases (SB), saturation of bases (V) and saturation of aluminum (m).

Data analysis

We calculated the phytosociological parameters of absolute density (AD) and importance value index (calculated to vary from 0% to 100%) for each species of all MPs (Kent 2012). According to Oliveira-Filho et al. (2001), we prepared tree frequency distributions into classes of diameter and height for the MPs, employing class intervals with exponentially increasing ranges to compensate for the decrease and/or increase in tree density toward larger diameters and heights. Differences in the main structural parameters (abundance, basal area, diameter at breast height and height) among MPs were analyzed using Kruskal-Wallis tests, since the Shapiro-Wilk test indicated that the data were not normally distributed and the Levene's test indicated unequal variances. Significant differences between MPs were compared by means of Dunn's *post hoc* tests. The same tests were used to compare differences in environmental variables between MPs.

We compared the species richness of the MPs using individual-based rarefaction curves with a confidence interval of 95% (Colwell et al. 2004). The species richness was also estimated using Jackknife 1, which is the estimator most correlated with observed richness, according to Walther and Moore (2005). The diversity of the MPs was compared through diversity profiles based on the Rényi series (Tóthmérész 1995), in which alpha = 0 corresponds to richness, alpha = 1 to Shannon's index, and alpha = 2 to Simpson's reciprocal index (Melo 2008).

To identify indicator species of the MPs, we performed an Indicator Species Analysis (ISA) by calculating the Indicator Values (IVs) of the species, an index that is based on the relative density and relative frequency of the species (Dufrêne and Legendre 1997). The significance of the IVs was tested using 999 Monte Carlo permutations.

We used canonical correspondence analysis (CCA) in order to analyze the relationships between species abundance and environmental variables (ter Braak 1987). The appropriate ordination method for direct gradient analysis was chosen by analyzing the gradient lengths using a detrended correspondence analysis (DCA). The resulting gradient lengths (axis 1 = 3.789 s.d.; axis 2 = 4.808 s.d.) indicated that the species showed unimodal responses to underlying environmental variations, justifying the use of CCA (ter Braak 1985). As required by CCA, we organized the data for species and environmental variables in two matrices. The first matrix contained the abundances of species per plot. Species with less than five individuals in the total sample were removed, resulting in a 27 species × 79 plots matrix (one plot was excluded for not having trees with pbh $\geq$ 15 cm). Before the ordination, we log-transformed [log $(x + 1)$] the abundance values to give less weight to dominant species (McCune and Grace 2002). The second matrix initially contained all environmental variables, which were standardized according to standard deviation to make them comparable (McCune and Grace 2002). After a preliminary CCA, we eliminated poorly correlated variables ($r < 0.5$ with the two first axes) and highly redundant ones ($r \geq 0.7$ among variables). The six variables maintained in the final CCA were AE, Cu, Clay, ASD, K and O.M. We tested the null hypothesis that no relationship existed between the matrices of species abundances and environmental data with 999 Monte Carlo permutations (ter Braak 1987). In order to verify the correlations between species and the six environmental variables of the final CCA, we employed Spearman's rank correlation coefficients (Kent 2012).

ISA, DCA and CCA were run in PC-ORD 6.19 (McCune and Mefford 2011), Kruskal-Wallis was performed in BioEstat 5.3 (Ayres et al. 2007), and PAST 3.11 (Hammer et al. 2001) was used for all other analysis.

Results

We sampled 563 individuals belonging to 63 species, 47 genera and 25 families. From the wetlands to the upper slopes, we recorded 165, 137, 129 and 132 individuals; and 27, 37, 37 and 36 species, respectively (Table 1). Total basal area was 13.9 m², while the basal area from the wetlands to the upper slopes was 3.5, 3.3, 3.9 and 3.2 m², respectively.

Table 1 Phytosociological parameters of the tree species (pbh ≥ 15 cm) sampled in four microtopographic positions along a wetland-upland gradient in forested depressional wetlands on the South Brazilian Plateau

Species	Family	Absolute density (ha^{-1})				Importance Value Index			
		WSs	LSs	MSs	USs	WSs	LSs	MSs	USs
1. *Syagrus romanzoffiana* (Cham.) Glassman*	Arecaceae	**540**	**160**	**100**	**180**	**25.6**	**10.7**	**6.6**	**12.4**
2. *Sebastiania brasiliensis* Spreng.*	Euphorbiaceae	**300**	50	40	20	**14.6**	2.9	3.0	1.3
3. *Luehea divaricata* Mart. & Zucc.*	Malvaceae	**110**	**30**	**30**	30	**11.3**	**4.1**	**4.8**	1.6
4. *Ficus luschnathiana* (Miq.) Miq.	Moraceae	**40**	–	10	–	**8.3**	–	2.4	–
5. *Ruprechtia laxiflora* Meisn.*	Polygonaceae	**60**	**10**	–	–	**4.7**	**3.5**	–	–
6. *Guarea macrophylla* Vahl*	Meliaceae	**90**	–	–	–	**4.6**	–	–	–
7. *Gymnanthes klotzschiana* Müll.Arg.	Euphorbiaceae	**60**	20	30	10	**4.4**	2.0	2.4	1.1
8. *Erythrina falcata* Benth.	Fabaceae	**40**	–	–	–	**3.7**	–	–	–
9. *Plinia peruviana* (Poir.) Govaerts**	Myrtaceae	**60**	**120**	**40**	–	**3.3**	**14.2**	**3.6**	–
10. *Actinostemon concolor* (Spreng.) Müll.Arg.	Euphorbiaceae	**40**	**330**	**260**	**120**	**2.3**	**12.5**	**9.7**	**5.7**
11. *Eugenia hiemalis* Cambess.	Myrtaceae	40	–	–	10	2.0	–	–	0.6
12. *Sorocea bonplandii* (Baill.) W.C.Burger, Lanj. & de Boer	Moraceae	40	**60**	40	20	1.9	**3.3**	2.3	1.2
13. *Apuleia leiocarpa* (Vogel) J.F.Macbr.	Fabaceae	20	**70**	**60**	**30**	1.9	**7.9**	**5.9**	**6.1**
14. *Vitex megapotamica* (Spreng.) Moldenke	Lamiaceae	20	10	–	–	1.5	1.3	–	–
15. *Eugenia subterminalis* DC.	Myrtaceae	40	**70**	10	–	1.4	**4.1**	0.7	–
16. *Chrysophyllum marginatum* (Hook. & Arn.) Radlk.	Sapotaceae	30	20	**80**	**110**	1.4	1.9	**5.1**	**8.6**
17. *Ocotea diospyrifolia* (Meisn.) Mez	Lauraceae	20	–	–	–	1.3	–	–	–
18. *Campomanesia xanthocarpa* (Mart.) O.Berg	Myrtaceae	10	10	–	–	0.6	0.6	–	–
19. *Machaerium stipitatum* Vogel	Fabaceae	10	20	30	30	0.6	2.0	2.9	2.5
20. *Diatenopteryx sorbifolia* Radlk.	Sapindaceae	10	**50**	**70**	**80**	0.6	**4.4**	**6.5**	**8.6**
21. *Nectandra lanceolata* Nees	Lauraceae	10	–	–	–	0.6	–	–	–
22. *Nectandra megapotamica* (Spreng.) Mez	Lauraceae	10	–	–	10	0.6	–	–	0.8
23. *Myrocarpus frondosus* Allemão	Fabaceae	10	10	20	40	0.6	1.3	1.5	2.5
24. *Myrsine* sp.	Primulaceae	10	–	–	–	0.6	–	–	–
25. *Trichilia catigua* A.Juss.	Meliaceae	10	–	30	**50**	0.6	–	2.0	**2.8**
26. *Myrsine loefgrenii* (Mez) Imkhan.	Primulaceae	10	–	–	–	0.6	–	–	–
27. *Casearia sylvestris* Sw.	Salicaceae	10	20	10	30	0.6	1.3	0.9	2.1
28. *Annona neosalicifolia* H.Rainer	Annonaceae	–	**40**	20	–	–	**3.0**	1.5	–
29. *Cordia trichotoma* (Vell.) Arráb. ex Steud.	Boraginaceae	–	10	10	–	–	2.2	0.7	–
30. *Chrysophyllum gonocarpum* (Mart. & Eichler ex Miq.) Engl.	Sapotaceae	–	30	**60**	40	–	2.1	**3.9**	2.2
31. *Helietta apiculata* Benth.****	Rutaceae	–	30	30	**110**	–	1.7	3.3	**8.6**
32. *Pisonia ambigua* Heimerl	Nyctaginaceae	–	20	–	–	–	1.7	–	–
33. *Balfourodendron riedelianum* (Engl.) Engl.	Rutaceae	–	20	40	30	–	1.3	3.2	1.9

34. *Allophylus edulis* (A.St.–Hil. A.Juss. & Cambess.) Hieron. ex Niederl.	Sapindaceae	–	20	20	**50**	–	1.2	1.7	**3.8**
35. *Pilocarpus pennatifolius* Lem.	Rutaceae	–	20	20	20	–	0.9	0.9	1.2
36. *Zanthoxylum petiolare* A.St.–Hil. & Tul.	Rutaceae	–	10	10	–	–	0.8	0.9	–
37. *Eugenia involucrata* DC.	Myrtaceae	–	10	–	–	–	0.7	–	–
38. *Machaerium paraguariense* Hassl.	Fabaceae	–	10	–	–	–	0.6	–	–
39. *Jacaranda micrantha* Cham.	Bignoniaceae	–	10	–	–	–	0.6	–	–
40. *Maclura tinctoria* (L.) D.Don ex Steud.	Moraceae	–	10	–	–	–	0.6	–	–
41. *Eugenia burkartiana* (D.Legrand) D.Legrand	Myrtaceae	–	10	–	–	–	0.6	–	–
42. *Strychnos brasiliensis* Mart.	Loganiaceae	–	10	20	10	–	0.6	1.5	0.6
43. *Calliandra foliolosa* Benth.****	Fabaceae	–	10	20	**70**	–	0.6	1.3	**4.0**
44. *Muellera campestris* (Mart. ex Benth.) M.J. Silva & A.M.G. Azevedo	Fabaceae	–	10	–	–	–	0.6	–	–
45. *Solanum sanctae–catharinae* Dunal	Solanaceae	–	10	20	–	–	0.6	1.3	–
46. *Campomanesia guazumifolia* (Cambess.) O.Berg	Myrtaceae	–	10	–	20	–	0.6	–	1.3
47. *Trema micrantha* (L.) Blume	Cannabaceae	–	10	10	–	–	0.6	0.6	–
48. *Cordia americana* (L.) Gottschling & J.S.Mill.	Boraginaceae	–	–	**20**	10	–	–	**5.8**	2.3
49. *Peltophorum dubium* (Spreng.) Taub.	Fabaceae	–	–	**10**	–	–	–	**4.2**	–
50. *Trichilia clausseni* C.DC.	Meliaceae	–	–	30	40	–	–	1.9	2.7
51. *Aspidosperma australe* Müll.Arg.	Apocynaceae	–	–	30	10	–	–	1.9	0.6
52. *Holocalyx balansae* Micheli	Fabaceae	–	–	20	10	–	–	1.7	1.2
53. *Plinia rivularis* (Cambess.) Rotman	Myrtaceae	–	–	10	10	–	–	1.3	0.9
54. *Eugenia pyriformis* Cambess.	Myrtaceae	–	–	10	–	–	–	1.1	–
55. *Urera baccifera* (L.) Gaudich. ex Wedd.	Urticaceae	–	–	10	10	–	–	0.6	0.6
56. *Trichilia elegans* A.Juss.	Meliaceae	–	–	10	–	–	–	0.6	–
57. *Eugenia uniflora* L.	Myrtaceae	–	–	–	**40**	–	–	–	**3.8**
58. *Handroanthus heptaphyllus* (Vell.) Mattos	Bignoniaceae	–	–	–	20	–	–	–	2.8
59. *Bunchosia maritima* (Vell.) J.F.Macbr.	Malpighiaceae	–	–	–	10	–	–	–	0.8
60. *Myrcianthes pungens* (O.Berg) D.Legrand	Myrtaceae	–	–	–	10	–	–	–	0.7
61. *Matayba elaeagnoides* Radlk.	Sapindaceae	–	–	–	10	–	–	–	0.7
62. *Cordia ecalyculata* Vell.	Boraginaceae	–	–	–	10	–	–	–	0.6
63. *Casearia decandra* Jacq.	Salicaceae	–	–	–	10	–	–	–	0.6

WSs wetlands, *LSs* lower slopes, *MSs* middle slopes, *USs* upper slopes. The species are ordered by decreasing Importance Value Index, from the wetlands to the upper slopes. The phytosociological parameters of the ten species with the highest Importance Value Indices of each microtopographic position are shown in bold type. * Indicator species of the wetlands (*n* = 5; 7.9%), ** Indicator species of the lower slopes (*n* = 1; 1.6%), **** Indicator species of the upper slopes (*n* = 2; 3.2%)

The majority of structural parameters did not differ between MPs according to the Kruskal-Wallis tests (Table 2). Significant differences were found only in the second diameter class (10-20 cm) and in the fourth height class (≥ 16 m), but Dunn’s post hoc test did not detect differences in the height class. In general, the major differences among structural parameters occurred between the wetlands and the upland sites, especially in the second (10-20 cm) diameter class (Fig. 2), in the third (8-16 m) and the fourth (≥ 16 m) height class (Fig. 3), and in the maximum height and diameter classes.

Table 2 Structural parameters (mean ± SD) of tree species (pbh ≥ 15 cm) sampled in four microtopographic positions along a wetland-upland gradient in forested depressional wetlands on the South Brazilian Plateau, with a non-parametric (Kruskal-Wallis) analysis of variance

Structural parameters	WSs (n = 20)	LSs (n = 20)	MSs (n = 19)	USs (n = 20)	H	*p*
Abundance (ind. plot^{-1})	8.3 ± 4.2	6.9 ± 3.8	6.8 ± 3.6	6.6 ± 3.5	2.80	0.424
Basal area (m^2 plot^{-1})	0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.2	0.2 ± 0.1	1.58	0.665
Average dbh (cm plot^{-1})	14.3 ± 3.7	15.0 ± 5.7	15.3 ± 4.8	13.8 ± 4.4	1.23	0.747
Maximum dbh (cm ind. plot^{-1})	28.1 ± 15.4	31.7 ± 12.4	35.5 ± 19.7	28.9 ± 14.2	3.09	0.378
Dbh 5-10 cm (ind. plot^{-1})	2.9 ± 2.1	3.8 ± 2.6	3.4 ± 2.7	3.4 ± 2.2	1.42	0.701
Dbh 10-20 cm (ind. plot^{-1})	4.3 ± 2.7^{a}	1.6 ± 1.4^{b}	2.0 ± 1.9^{b}	2.0 ± 1.5^{b}	12.89	**0.005**
Dbh 20-40 cm (ind. plot^{-1})	1.0 ± 1.0	1.2 ± 0.8	1.1 ± 1.0	1.1 ± 1.1	1.29	0.731
Dbh ≥ 40 cm (ind. plot^{-1})	0.1 ± 0.3	0.3 ± 0.6	0.4 ± 0.5	0.3 ± 0.4	2.09	0.554
Average height (m plot^{-1})	9.3 ± 2.2	9.4 ± 2.2	10.3 ± 2.4	9.6 ± 2.2	1.98	0.577
Maximum height (m ind. plot^{-1})	13.3 ± 3.3	14.7 ± 4.1	15.8 ± 3.6	14.9 ± 3.9	6.11	0.106
Height 2-4 m (ind. plot^{-1})	0.4 ± 0.7	0.1 ± 0.2	0.2 ± 0.4	0.1 ± 0.2	1.71	0.635
Height 4-8 m (ind. plot^{-1})	2.2 ± 1.6	3.2 ± 2.7	2.4 ± 2.5	2.7 ± 1.5	2.24	0.524
Height 8-16 m (ind.plot^{-1})	5.6 ± 3.6	3.0 ± 2.1	3.5 ± 2.4	3.4 ± 2.6	6.49	0.090
Height ≥ 16 m (ind. plot^{-1})	0.2 ± 0.5	0.7 ± 0.7	0.8 ± 0.8	0.6 ± 0.7	7.93	**0.048**

WSs wetlands, *LSs* lower slopes, *MSs* middle slopes, *USs* upper slopes. Different superscript letters indicate significant differences ($p < 0.05$) in structural parameters between microtopographic positions using Dunn's *post hoc* tests. Significant *p*-values are shown in bold type

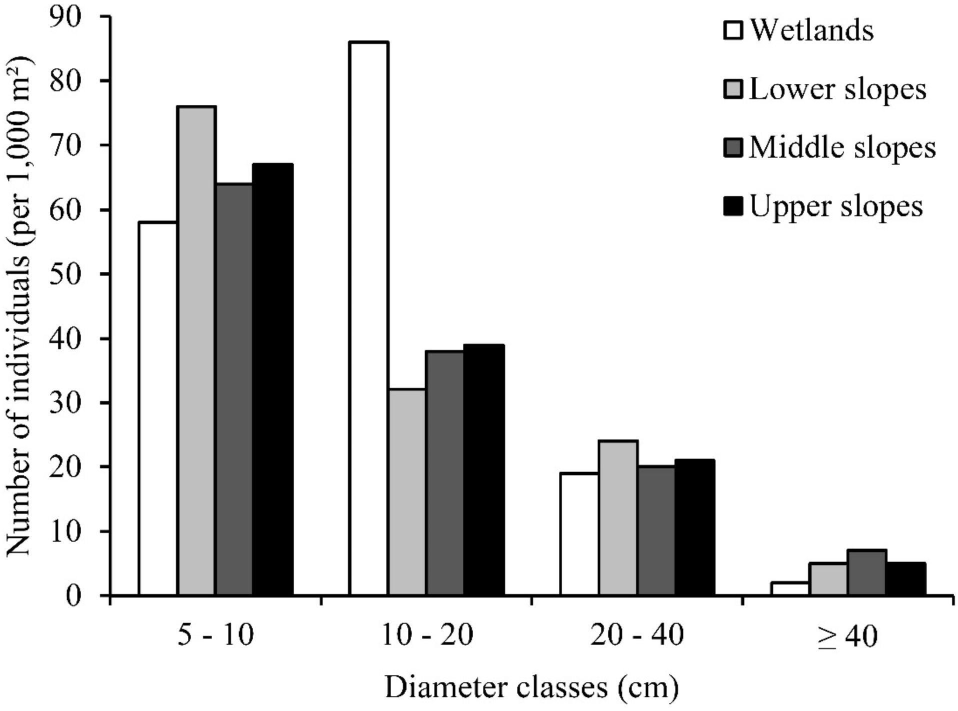

Fig. 2 Diameter classes distribution of the tree species (pbh ≥ 15 cm) sampled in four microtopographic positions (MP) along a wetland-upland gradient in forested depressional wetlands on the South Brazilian Plateau

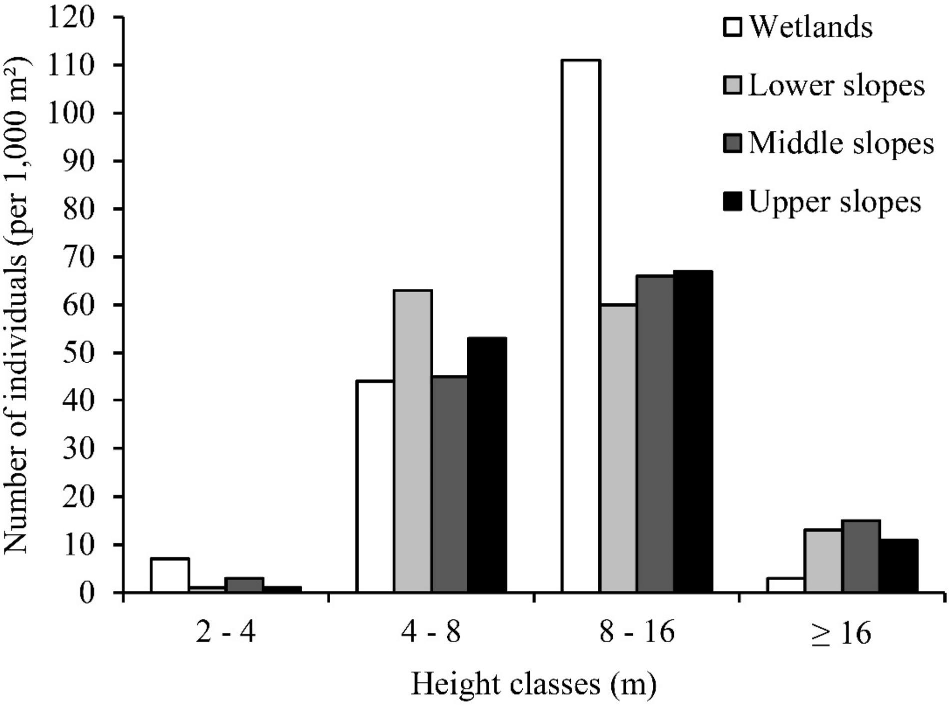

Fig. 3 Height classes distribution of the tree species (pbh ≥ 15 cm) sampled in four microtopographic positions (MP) along a wetland-upland gradient in forested depressional wetlands on the South Brazilian Plateau

The individual-based rarefaction curves revealed significant differences in the expected number of species, with a lower species richness projected for the wetlands (Fig. 4). The wetlands also had the lowest species richness estimated by Jackknife 1 (37.5 ± 4.0), while the other MPs presented closely similar estimates (lower slopes = 54.1 ± 4.1; middle slopes = 48.4 ± 3.2; and upper slopes = 49.3 ± 3.1; global Jackknife 1 was 79.8 ± 4.1). Diversity was similar and successively increased from the wetlands to the upper slopes when major emphasis was given to the dominant species (e.g., alpha = 4, Fig. 5). However, when only the richness was considered (alpha = 0), the upland sites presented closely similar and higher estimates than the wetlands. In the upland sites, the upper slopes presented fewer species than the lower slopes and the middle slopes, causing the crossing of the profiles.

According to the ISA, five species are indicators of the wetlands, one of the lower slopes and two of the upper slopes. For the middle slopes, no indicator species were identified (Table 1).

Kruskal-Wallis tests showed that all considered environmental variables differed significantly among MPs, except the levels of O.M. (Table 3). According to chemical fertility, the soils of all MPs were classified as dystrophic, with base saturation lower than 50% (the

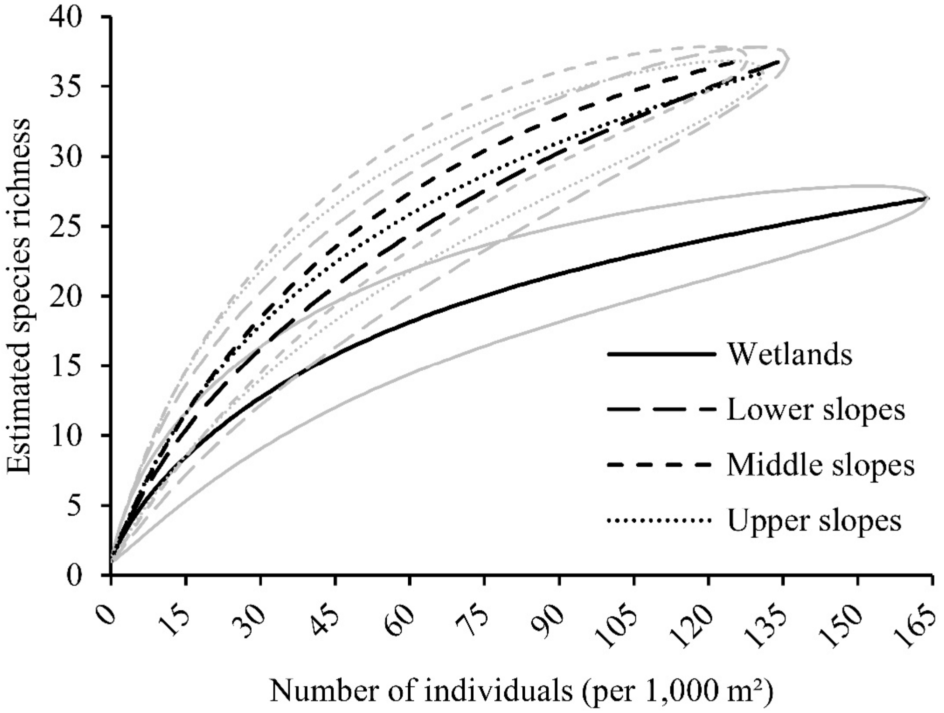

Fig. 4 Individual-based rarefaction curves comparing the estimated richness of the tree species (pbh ≥ 15 cm) sampled in four microtopographic positions (MP) along a wetland-upland gradient in forested depressional wetlands on the South Brazilian Plateau. Lines in gray indicate the 95% confidence interval

composite soil sample of the upper slopes of the second study area presented exactly 50% of base saturation). All soils were found to have high acidity (pH ≤ 5.5; Tedesco et al. 1997).

The results of the CCA are shown in two diagrams in Figs. 6-7, while Table 4 shows the intraset correlations between environmental variables and the first two ordination axes, in addition to weighted correlations between environmental variables. The eigenvalues of the two first axes of the CCA (axis 1 = 0.376; axis 2 = 0.220) indicate a short gradient (< 0.5), meaning that many species occurred in all MPs, varying basically in their abundances (ter Braak 1995). Of the total of 63 species, 12 (19%) occurred in all MPs, 10 (16%) in three MPs, and 18 (29%) in two MPs. From the wetlands to the upper slopes, there were six, seven, three and seven exclusive species respectively, totaling 23 (36%) species exclusive to only one MP.

The first two axes of the CCA ordination explained 11.6% of the species-environment relationships (axis 1 = 7.3%; axis 2 = 4.3%), and the species-environment correlations for these axes were 0.882 and 0.776 (*p* = 0.001), respectively. Axis 1 was highly correlated with AE, Cu, clay and K, while axis 2 was highly correlated with ASD, O.M. and K.

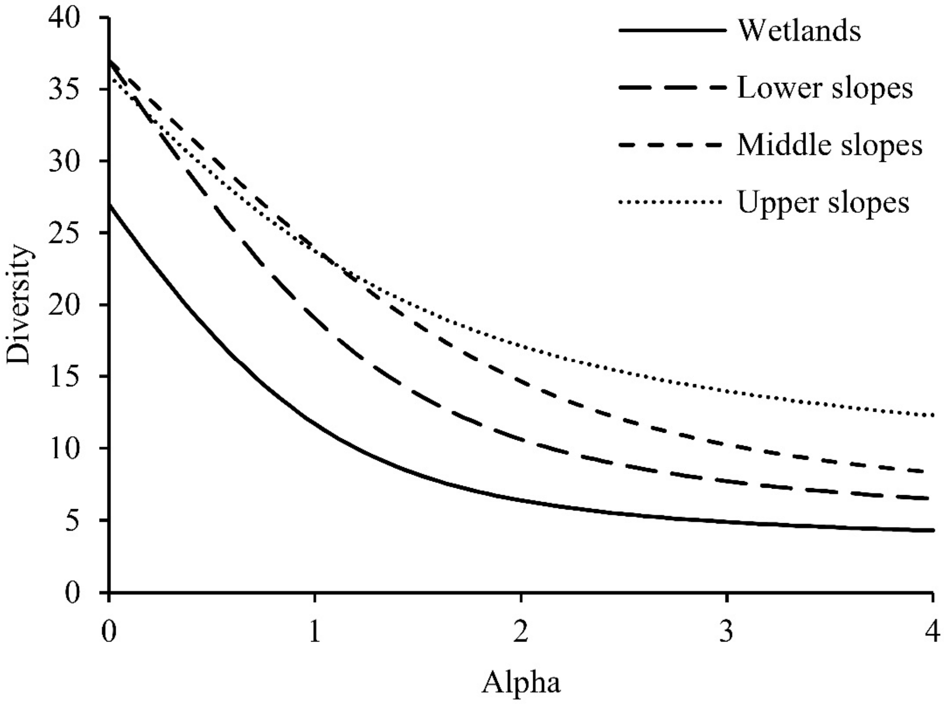

Fig. 5 Diversity profiles (based on the Rényi series) of the tree species (pbh ≥ 15 cm) sampled in four microtopographic positions (MP) along a wetland-upland gradient in forested depressional wetlands on the South Brazilian Plateau

The plots arrangement in the first CCA diagram (Fig. 6) indicates that the strongest gradient (mainly related to Cu and AE) occurs in axis 1, starting at the left side, with a set of plots from the wetlands, and ending at the right side, with the three sets of plots from the uplands. The second axis, in turn (mainly related to ASD and O.M.), contributes more to the segregation of the sets of the upland plots. The plots of the lower slopes occurred at the upper side of the second axis, with a subset of plots (from the first study area; with an average elevation 20% lower than the other subset) close to the set of the wetland plots. On the other hand, the majority of the plots of the upper slopes were found at the lower side of the second axis. Three sets of plots were clearly distinguished (wetlands, lower slopes and upper slopes), and one set (middle slopes) presented a superimposed and intermediate position relative to the lower slopes and the upper slopes.

In the second CCA diagram (Fig. 7), the first axis segregated the species that were predominant in the wetlands from the majority of the species that were predominant in the uplands. The species *Syagrus romanzoffiana* (Cham.) Glassman, *Sebastiania brasiliensis* Spreng., *Luehea divaricata* Mart. & Zucc., *Guarea macrophylla* Vahl and *Ruprechtia laxiflora* Meisn., located on the left side of the first axis, were the most abundant species in the wetlands.

Table 3 Environmental variables (mean ± SD) of four microtopographic positions along a wetland-upland gradient in forested depressional wetlands on the South Brazilian Plateau, with a non-parametric (Kruskal-Wallis) analysis of variance

Environmental variables	WSs (n = 20)	LSs (n = 20)	MSs (n = 20)	USs (n = 20)	H	*p*
Average elevation - AE (cm)	-9.5 ± 11.3^{c}	23.6 ± 8.6^{b}	84.6 ± 15.0^{a}	140.7 ± 28.0^{a}	73.42	< **0.001**
Slope (cm)	18.3 ± 11.2^{b}	45.3 ± 15.4^{a}	64.2 ± 30.1^{a}	74.6 ± 53.6^{a}	35.44	< **0.001**
Average soil depth - ASD (cm)	67.2 ± 11.7^{ab}	73.7 ± 20.0^{a}	61.3 ± 16.7^{ab}	51.7 ± 26.8^{b}	8.23	**0.041**
Average vertical distance to the water table - AVDWT (cm)	-76.0 ± 15.9^{dc}	-49.8 ± 21.7^{c}	23.4 ± 16.3^{b}	89.7 ± 27.8^{a}	69.67	< **0.001**
Clay (%)	45.0 ± 3.1^{a}	42.0 ± 4.1^{ad}	37.5 ± 5.6^{bde}	36.5 ± 1.5^{ce}	32.84	< **0.001**
Silt (%)	49.0 ± 3.1^{a}	45.5 ± 2.6^{a}	38.5 ± 4.6^{b}	37.0 ± 5.1^{b}	59.49	< **0.001**
Sand (%)	6.0 ± 0.0^{c}	12.5 ± 1.5^{b}	24.0 ± 10.3^{a}	26.5 ± 6.7^{a}	64.07	< **0.001**
pH in H_2O	4.6 ± 0.1^{cb}	4.5 ± 0.2^{dc}	4.7 ± 0.2^{b}	4.8 ± 0.0^{a}	43.50	< **0.001**
P (mg/dm^3)	11.6 ± 4.6^{a}	6.2 ± 2.9^{bd}	6.1 ± 0.2^{cb}	7.7 ± 1.3^{da}	34.74	< **0.001**
K (mg/dm^3)	84.0 ± 16.4^{db}	91.5 ± 39.5^{b}	88.0 ± 3.1^{cb}	135.0 ± 36.9^{a}	20.69	< **0.001**
Organic matter - O.M. (%)	5.1 ± 0.5	5.0 ± 0.1	5.9 ± 1.4	6.0 ± 1.2	1.88	0.598
Al (cmol$_c$/dm^3)	2.5 ± 0.9^{ab}	3.4 ± 1.1^{a}	1.8 ± 1.4^{b}	0.4 ± 0.1^{c}	43.26	< **0.001**
Ca (cmol$_c$/dm^3)	4.9 ± 0.3^{ce}	3.5 ± 1.2^{db}	5.8 ± 1.4^{be}	9.1 ± 0.4^{a}	54.73	< **0.001**
Mg (cmol$_c$/dm^3)	1.5 ± 0.1^{b}	1.3 ± 0.5^{b}	1.8 ± 0.9^{b}	2.9 ± 0.6^{a}	35.74	< **0.001**
Al+H (cmol$_c$/dm^3)	24.0 ± 6.9^{b}	36.5 ± 2.2^{a}	23.4 ± 11.3^{b}	17.7 ± 6.9^{b}	45.21	< **0.001**
CEC (cmol$_c$/dm^3)	30.6 ± 6.6^{b}	41.6 ± 0.4^{a}	31.2 ± 9.0^{b}	30.2 ± 8.0^{b}	46.16	< **0.001**
Sum of bases - SB	6.5 ± 0.3^{b}	5.0 ± 1.8^{b}	7.8 ± 2.3^{b}	12.4 ± 1.1^{a}	50.79	< **0.001**
Saturation of bases - V (%)	22.5 ± 5.6^{cb}	12.0 ± 4.1^{d}	29.5 ± 15.9^{b}	42.5 ± 7.7^{a}	47.02	< **0.001**
Al saturation - m (%)	27.1 ± 8.3^{a}	41.7 ± 16.0^{a}	19.8 ± 16.4^{a}	3.1 ± 0.6^{b}	50.79	< **0.001**
S (mg/dm^3)	14.0 ± 1.0^{d}	24.0 ± 0.0^{cb}	24.5 ± 1.5^{b}	27.0 ± 2.1^{a}	59.01	< **0.001**
Zn (mg/dm^3)	6.8 ± 1.2^{b}	9.4 ± 0.7^{a}	9.7 ± 0.1^{a}	12.8 ± 3.3^{a}	49.02	< **0.001**
Cu (mg/dm^3)	7.6 ± 0.5^{a}	4.5 ± 2.0^{b}	3.2 ± 0.7^{b}	3.4 ± 1.1^{b}	49.02	< **0.001**
B (mg/dm^3)	0.3 ± 0.1^{cb}	0.4 ± 0.1^{b}	0.6 ± 0.1^{ad}	0.8 ± 0.3^{a}	53.33	< **0.001**
Mn (mg/dm^3)	14.0 ± 7.2^{d}	27.5 ± 5.6^{cb}	53.0 ± 34.9^{b}	88.0 ± 40.0^{a}	47.02	< **0.001**

WSs wetlands, *LSs* lower slopes, *MSs* middle slopes, *USs* upper slopes. Different superscript letters indicate significant differences ($p < 0.05$) in environmental variables between microtopographic positions using Dunn's *post hoc* tests. Significant *p*-values are shown in bold type

In the uplands, the species distribution was more uniform, but the second canonical axis revealed the association of some species with specific environmental conditions. At the upper side of the second axis occurred species such as *Plinia peruviana* (Poir.) Govaerts, *Apuleia leiocarpa* (Vogel) J.F.Macbr., *Sorocea bonplandii* (Baill.) W.C.Burger, Lanj. & de Boer and *Annona neosalicifolia* H.Rainer, which were most plentiful in sites with deep soils, and consequently with highly negative AVDWTs (lower slopes). In the other hand, at the lower side of the second axis, species such as *Helietta apiculata* Benth., *Chrysophyllum marginatum* (Hook. & Arn.) Radlk., *Calliandra foliolosa* Benth. and *Myrocarpus frondosus* Allemão were

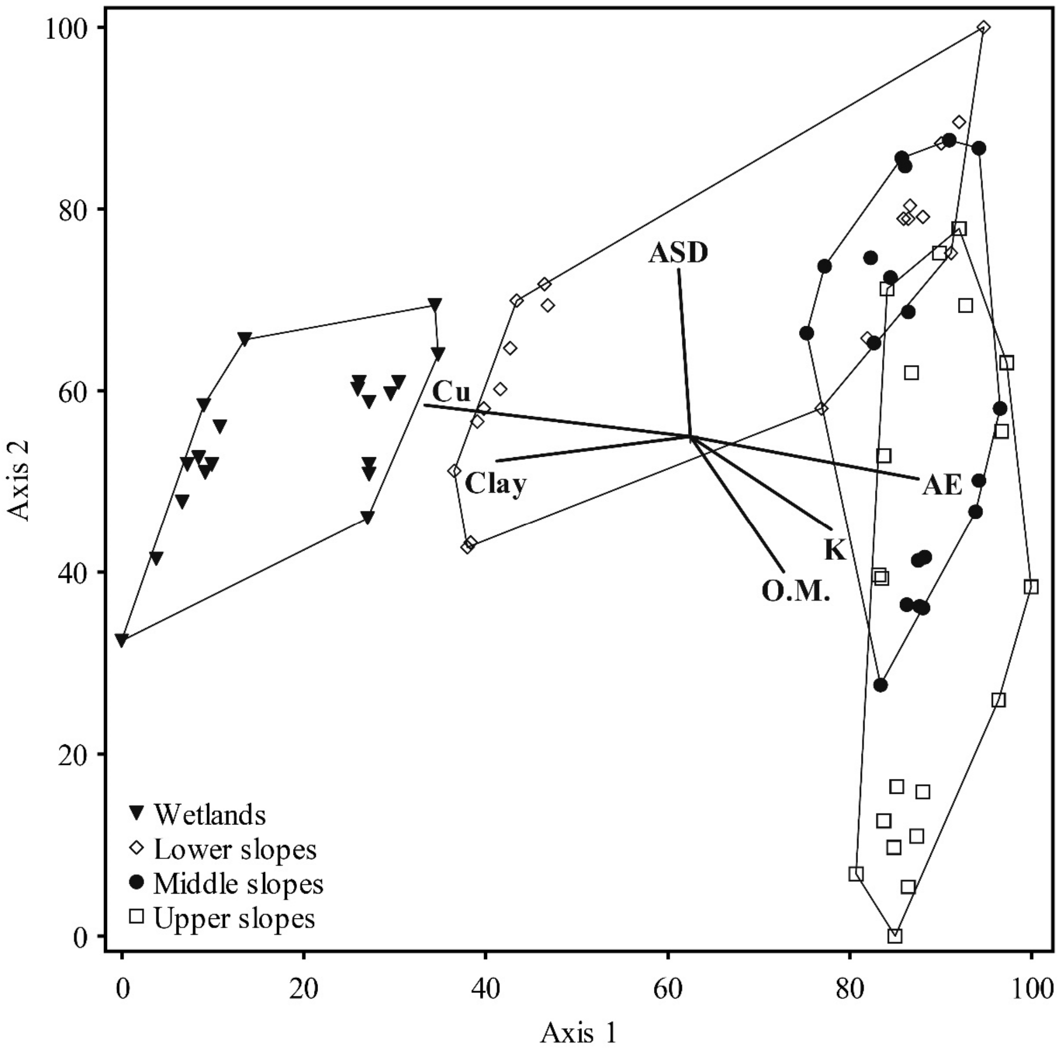

Fig. 6 Biplot diagram of the CCA ordination for plots and environmental variables of four microtopographic positions (MP) along a wetland-upland gradient in forested depressional wetlands on the South Brazilian Plateau

most abundant on sites with shallow soils and highly positive AVDWTs (upper slopes). *Chrysophyllum gonocarpum* (Mart. & Eichler ex Miq.) Engl. and *Balfourodendron riedelianum* (Engl.) Engl. were the unique species of the diagram in that their highest abundances were in the middle slopes. The plots of this MP were allocated at sites with positive AVDWTs, but horizontally close to sites with negative AVDWTs.

The patterns observed in the second CCA diagram are confirmed by the Spearman's rank correlations coefficients between the species abundances and the environmental variables, presented in Table 5. Of the 27 species considered in the CCA, 13 (48.1 %) were correlated with AE, 10 (37.0%) with Cu, eight (29.6%) with clay, seven (25.9%) with ASD, six (22.2%) with K and five (18.5%) with O.M.

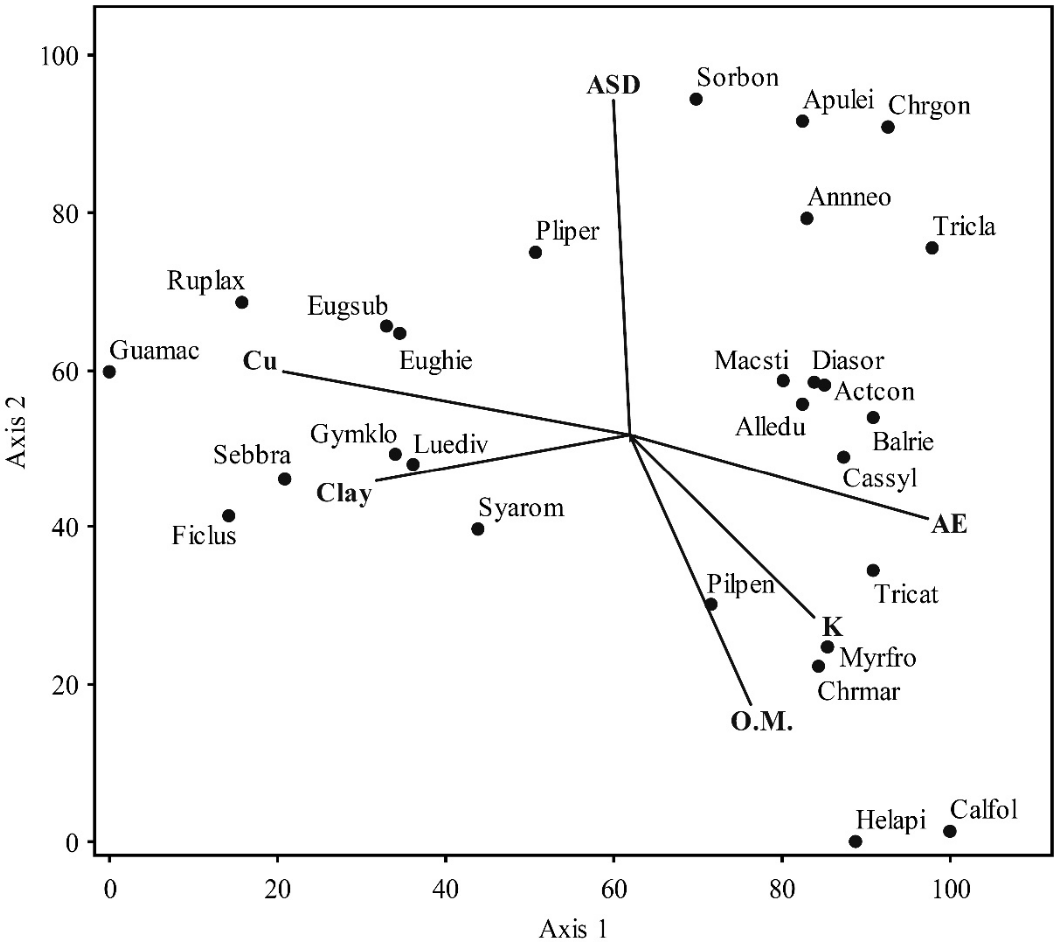

Fig. 7 Biplot diagram of the CCA ordination for the 28 species (with ≥ 5 individuals) and environmental variables of four microtopographic positions along a wetland-upland gradient in forested depressional wetlands on the South Brazilian Plateau. Species are identified by their abbreviated names (full names in Table 1)

Table 4 Canonical correspondence analysis (CCA) of the 27 tree species (pbh ≥ 15 cm) sampled in four microtopographic positions along a wetland-upland gradient in forested depressional wetlands on the South Brazilian Plateau: matrix of *intraset* correlations between environmental variables and the first two ordination axes, and matrix of weighed correlations between environmental variables

Environmental variable	Axis 1	Axis 2	Cu	AE	Clay	K	ASD	O.M.
Cu	-0.932	0.170	1					
AE	0.799	-0.226	-0.615	1				
Clay	-0.681	-0. 123	0.591	-0.682	1			
K	0.496	-0.492	-0.649	0.402	-0.501	1		
ASD	-0.043	0.901	0.227	-0.202	-0.009	-0.354	1	
O.M.	0.325	-0.727	-0.497	0.264	0.022	0.546	-0.543	1

Table 5 Spearman's rank correlation coefficients between the abundance of the 27 species and the six environmental variables used in the canonical correspondence analysis (CCA)

Species	AE	Cu	Clay	ASD	K	O.M.
Sebastiania brasiliensis	**-0.537*****	**0.514*****	**0.330****	-0.109^{ns}	-0.131^{ns}	-0.052^{ns}
Guarea macrophylla	**-0.410*****	**0.418*****	**0.249***	0.162^{ns}	-0.031^{ns}	-0.024^{ns}
Syagrus romanzoffiana	**-0.339****	**0.315****	**0.422*****	**-0.273***	-0.112^{ns}	0.030^{ns}
Ruprechtia laxiflora	**-0.313****	**0.339****	**0.401*****	0.172^{ns}	**-0.281***	-0.200^{ns}
Ficus luschnathiana	**-0.262***	0.191^{ns}	0.154^{ns}	-0.043^{ns}	0.001^{ns}	0.107^{ns}
Plinia peruviana	**-0.236***	0.136^{ns}	0.191^{ns}	0.200^{ns}	**-0.241***	-0.062^{ns}
Luehea divaricata	**-0.226***	**0.323****	**0.254***	0.018^{ns}	-0.217^{ns}	-0.094^{ns}
Gymnanthes klotzschiana	-0.214^{ns}	**0.243***	0.088^{ns}	-0.119^{ns}	-0.168^{ns}	-0.147^{ns}
Eugenia subterminalis	-0.189^{ns}	0.184^{ns}	**0.248***	-0.036^{ns}	**-0.416*****	-0.063^{ns}
Eugenia hiemalis	-0.093^{ns}	0.201^{ns}	0.205^{ns}	0.074^{ns}	-0.177^{ns}	**-0.225***
Annona neosalicifolia	-0.056^{ns}	-0.151^{ns}	-0.050^{ns}	0.053^{ns}	0.041^{ns}	-0.016^{ns}
Sorocea bonplandii	-0.034^{ns}	0.051^{ns}	-0.044^{ns}	**0.350****	-0.153^{ns}	**-0.318****
Apuleia leiocarpa	0.058^{ns}	-0.043^{ns}	-0.134^{ns}	**0.330****	-0.076^{ns}	**-0.250***
Actinostemon concolor	0.072^{ns}	**-0.334****	-0.103^{ns}	0.067^{ns}	**0.336****	0.196^{ns}
Casearia sylvestris	0.105^{ns}	-0.178^{ns}	-0.083^{ns}	0.102^{ns}	**0.260***	0.154^{ns}
Machaerium stipitatum	0.115^{ns}	-0.076^{ns}	-0.076^{ns}	-0.051^{ns}	-0.053^{ns}	-0.088^{ns}
Pilocarpus pennatifolius	0.174^{ns}	-0.051^{ns}	-0.111^{ns}	**-0.228***	-0.031^{ns}	-0.049^{ns}
Balfourodendron riedelianum	0.178^{ns}	-0.145^{ns}	-0.146^{ns}	-0.052^{ns}	-0.010^{ns}	-0.003^{ns}
Chrysophyllum gonocarpum	0.189^{ns}	-0.083^{ns}	**-0.264***	**0.277***	-0.036^{ns}	-0.190^{ns}
Myrocarpus frondosus	0.190^{ns}	-0.105^{ns}	-0.052^{ns}	-0.201^{ns}	0.070^{ns}	0.043^{ns}
Helietta apiculata	0.216^{ns}	**-0.324****	-0.049^{ns}	**-0.366*****	0.210^{ns}	**0.289****
Trichilia catigua	**0.223***	-0.148^{ns}	-0.075^{ns}	-0.127^{ns}	0.054^{ns}	0.058^{ns}
Diatenopteryx sorbifolia	**0.224***	-0.151^{ns}	-0.201^{ns}	0.060^{ns}	-0.029^{ns}	-0.124^{ns}
Chrysophyllum marginatum	**0.241***	**-0.244***	0.002^{ns}	**-0.299****	0.092^{ns}	0.179^{ns}
Allophylus edulis	**0.251***	-0.005^{ns}	-0.194^{ns}	-0.044^{ns}	-0.091^{ns}	-0.142^{ns}
Calliandra foliolosa	**0.294****	**-0.405*****	-0.092^{ns}	-0.221^{ns}	**0.340****	**0.315****
Trichilia clausseni	**0.315****	-0.026^{ns}	**-0.301****	0.148^{ns}	-0.032^{ns}	-0.181^{ns}

The species are ordered by decreasing correlation with average elevation. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, *ns* non-significant. Significant correlations ($p < 0.05$) are shown in bold type

Discussion

Although microtopography has determined contrasting environmental conditions along the wetland-upland gradient, our results show that the constraining soil conditions imposed by flooding are more important determinants for tree species zonation and forest structure than water shortage and soil chemical and textural characteristics (see similar results in Pélissier et al. 2002; Budke et al. 2007; Giehl and Jarenkow 2008). Furthermore, the unpredictability of flooding (characteristic in the studied wetlands), compared to predictable flooding, is particularly limiting for the establishment and development of most species because they have limited adaptations to utilize environments subject to the variable frequency of these events (Junk et al. 1989). In fact, almost all the trees of the wetlands are restricted to hummocks, which are relatively well drained and subject to less frequent and durable flooding than the surrounding areas (see also Teixeira et al. 2008).

The severity with which permanently waterlogged soils subject to unpredictable flooding limit the establishment of tree species demonstrates the importance of hummocks in determining the density of the woody component in FDWs. Indeed, the wetland of the second study area, where we observed the highest number of hummocks, presents also the highest abundance of trees (99, vs. 66 of the other wetland). The relatively high density of hummocks in the two study areas determined a higher total density of trees in the wetlands than in the three slope positions. However, these differences were primarily due to a larger number of smaller-sized trees in the wetlands (especially those of the second diameter class or of the third height class; see Table 2 and Figs. 2-3), which also presented few large-sized trees compared to the three slope positions. These patterns can be attributed to the high mortality rates of big trees in areas with waterlogged soils, culminating in the dominance of species with small basal areas and heights (Ferry et al. 2010). The large quantity of inclined and fallen trees that we observed in the studied wetlands indicate that uprooting may be the most common mode of tree death in FDWs. In these ecosystems, uprooting is probably caused by low anchorage due to limited production of roots in waterlogged soils as well as by the high phosphorous availability (see *P* levels in Table 3) that may reduce the investment in roots (Toledo et al. 2012). In the uplands, the larger-sized trees were recorded on the middle slopes, where they are probably less susceptible to uprooting. The soils of this MP are relatively deep, present low levels of phosphorous, and are not subject to waterlogging.

With regard to the species composition, we revealed patterns that are also common to other forested wetland (e.g., swamp forests in the Atlantic and the Amazon rainforests; respectively, Teixeira et al. 2008; Pitman et al. 2014), such as a high density of palms and a lower species richness, diversity and equability in the wetlands than in the adjacent, well-drained forests. The studied slope position, in turn, shows quite similar richness (observed and estimated) and biodiversity values, as well as a relatively uniform species composition, reflected in the small number of indicator species compared to the wetlands. However, the species densities vary widely between the lower and the upper slopes, probably as a consequence of both variations in the environmental conditions (especially the hydrological conditions, directly related to the AVDWTs) and competitive interactions. Therefore, by influencing the surrounding upland forests diversity and structure (Previant and Nagel 2014; especially those of the lower slopes, which presented the highest estimated richness), FDWs should not be considered as only an impoverished version of these forests.

The contrasting hydrological conditions from the wetlands to the upper slopes are directly reflected in the species composition. In short distances along the wet-dry gradient, we sampled rare and common species characteristics from wetland forests and well-drained/shallow soils of the region (e.g., Ruschel et al. 2007; Silva et al. 2007). In general, the species sampled are not exclusive to *jaboticabais,* but the absolute densities of some species can be several times higher than that observed in other regional forests (e.g., Ruschel et al. 2007; Giehl and Jarenkow 2008), especially those recorded in the wetlands and in the lower slopes (e.g., *Eugenia subterminalis* DC., *Luehea divaricata*, *Plinia peruviana*, *Ruprechtia laxiflora*, *Sebastiania brasiliensis,* *Syagrus romanzoffiana*). Therefore, FDWs/*jaboticabais* can have a disproportionately higher importance in the preservation of species that are under-represented in other forest ecosystems (see also Previant and Nagel 2014).

Of all the species sampled, *Plinia peruviana* is probably the only one with practically restricted distribution to the *jaboticabais*, being rarely sampled in forest inventories. For example, in surveys carried out by Vibrans et al. (2012, 2013) in the plateau of the Santa Catarina state (93.6 ha sampled in 234 sites), the authors found only four individuals with diameter at breast height (dbh) ≥ 10 cm, which results in an estimate of only 0.04 trees/ha. Considering only the individuals with dbh ≥ 10 cm in our study (42.5 trees/ha), the estimated density of the species is 995 times higher. In both studied areas, *Plinia peruviana* is restricted to the wetlands and to the lower and middle slopes, where we recorded the highest values of AVDWT and the most acid and nutrient-poor soils. The narrow environmental tolerances and habitat specialization indicate that *Plinia peruviana* can be threatened with extinction, once the current preservation status of the FDWs on the South Brazilian Plateau is extremely delicate.

The singular species composition (and physiognomy) of the *jaboticabais* can be attributed in part to the occurrence of dystrophic soils (characteristic from areas with sediment deposition; Budke et al. 2007), in a region where eutrophic soils predominate (IBGE 1990). Apparently, the plots of the upper slopes were established at the transition zone between dystrophic and eutrophic soils (near or on the water divisors of the topographic depressions), once base saturation constantly increased from the lower slopes toward the other upland sites, reaching 50% in the upper slopes of the second study area. Therefore, all the upland sites studied probably represent transition zones between the FDWs and the forest matrix. Previant and Nagel (2014), studying vernal pools and the surrounding forests in the Upper Peninsula of Michigan, USA, identified a transition zone 31 m wide between the pools and the forest matrix, a width close to the average length of the transects in the uplands of our study (24.8 ± 6.2 m).

These findings suggest that the whole area of the topographic depressions should be protected at least until complementary studies propose proper buffer zones.

Further studies should consider a wider range of upland soil conditions in order to also contemplate eutrophic soils, allowing a more detailed analysis of species turnover. Similar studies should also be conducted on other plant life forms, enabling the creation of integrated biological criteria to guide policymakers decisions in the establishment of proper strategies of restoration, management and preservation of the studied ecosystems.

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Considerações finais

No presente estudo, nós abordamos pela primeira vez a diversidade e a estrutura do componente arbóreo em jaboticabais, relacionando-as às variáveis ambientais ao longo de um gradiente formado entre zonas úmidas depressionais florestadas e terras firmes circundantes.

De modo geral, as espécies arbóreas amostradas não são exclusivas aos jaboticabais, embora possam ser sub-representadas em outros ecossistemas. No entanto, *Plinia peruviana* apresenta alta abundância e ocorrência praticamente restrita aos ambientes estudados, deixando de ocorrer nas áreas mais elevadas das depressões topográficas, o que torna evidente a importância dos jaboticabais na preservação desta e de outras espécies.

Mostramos também que a composição e a estrutura do componente arbóreo diferem principalmente entre áreas sujeitas a alagamentos e áreas com solos distróficos bem drenados, demonstrando que as características ambientais contrastantes das terras firmes estudadas contribuem pouco para a estruturação das comunidades em relação aos alagamentos. Contudo, nossas considerações são limitadas a solos distróficos, que ocorreram das áreas alagadas até as áreas circundantes próximas ou sobre os divisores de água das depressões topográficas. Uma vez que a saturação por bases das terras firmes aumentou constantemente de acordo com a elevação do terreno, há fortes indícios de que as áreas de estudo são circundadas por solos eutróficos, que predominam na região. Portanto, as terras firmes estudadas provavelmente são zonas transicionais entre as zonas úmidas depressionais e a matriz florestal.

Nossos resultados sugerem que ao menos toda a área das depressões topográficas deve ser protegida até que novos estudos, contemplando também solos eutróficos, sugiram zonas de amortecimento apropriadas para a preservação dos jaboticabais. Contudo, estes estudos devem abranger também outras formas de vida, o que permitirá o estabelecimento de medidas preservacionistas baseadas em critérios biológicos integrados, ao invés de medidas direcionadas apenas para a preservação dos recursos hídricos.

Nossas observações de campo permitem sugerir que o componente arbóreo pode representar uma parcela muito menor da diversidade vegetal nos jaboticabais do que representa em outros ecossistemas florestais na região. Isso se deve principalmente à grande diversidade de epífitos e de outras espécies herbáceas que ocorrem nas zonas úmidas depressionais, que podem ser ambientes muito heterogêneos. Em relação às espécies herbáceas terrícolas, nós observamos distintas composições entre banhados com predomínio do componente herbáceo e do componente lenhoso. Da primeira para a segunda condição, há a diminuição da luminosidade no sub-bosque e o aumento da quantidade de montículos (*hummocks*) na base das árvores, que criam condições ambientais distintas das áreas permanentemente encharcadas do entorno. Essas observações criam perspectivas futuras para testar a hipótese de que zonas úmidas depressionais que apresentam estágios intermediários de sucessão da vegetação lenhosa abrigam uma quantidade maior de espécies herbáceas do que banhados com predomínio dos componentes herbáceo ou lenhoso.