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Diversity and Structure of Natural Regeneration in Swamp Forests in Southeastern Brazil

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Abstract

Many factors can influence the structures and distributions of plant communities. Plant diversity of swamp forests reflect responses to water stress conditions. We evaluated the floristic diversity, structure, and composition of the regenerating shrub-tree species of six swamp forests in *veredas* ecosystems (northern Minas Gerais, Brazil), and the floristic similarities between them. All individuals ≥ 1 cm in diameter at ground level and < 3 cm in diameter at breast height were sampled in one hundred 25 m^2 plots in each area. A total of 5442 individuals were recorded, distributed among 134 species, 85 genera, and 47 botanical families, with a diversity (Shannon) of 3.38 and equability (Pielou) of 0.69. Beta diversity was high, while similarities between the areas were low, with only two species common to all six sites. The forests showed different compositions, diversities, and natural regeneration structures, reflecting their ecotone nature and past anthropic impacts.

Keywords: Flooded Areas, Juveniles, Phytosociology, Succession, *Vereda*.

1. INTRODUCTION

The Brazilian *Cerrado* (neotropical savanna) constitutes a mosaic of several phytophysiognomies (Fernandes et al., 2016). *Veredas* (palm swamps) ecosystems are complex systems associated with *Cerrado* watercourses (Bijos et al., 2017). They are characterized by the presence of the palm tree *Mauritia flexuosa* L.f. (Arecaceae), "*buriti*", which grows in water-saturated sites and are of great importance to biodiversity (Endress et al., 2017). Depending on the ages of those systems, swamp forests will develop in their lower sections and demonstrate successional stage changes (Boaventura, 2006), although few studies have yet been undertaken in areas of swamp forests to examine that phenomenon (Nunes et al., 2015) while focusing on their regenerative strata (Ávila et al., 2016).

Natural regeneration refers to forest growth from the initial stages of establishment and development (Pastório et al., 2018), and describes gradual processes that can restore the structure, function, and composition of an ecosystem to its pre-disturbed state (Chazdon & Guarigata, 2016). That regeneration is shaped by natural socio-ecological processes, but can be sustained, improved, or impaired over time through human interventions (Chazdon et al., 2014). Studies of the regenerative strata allow insights into their potential for regeneration and for the success of environmental restoration efforts (Menino et al., 2012); such studies are also fundamental to establishing economic strategies for forest management and conservation (Santos et al., 2017).

Veredas are important environments to study considering their low resilience, degrees of anthropization, and ecosystem complexity (soil, topography, and composition) (Oliveira et al.,

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2009). Plant diversity tends to be low in those water-stressed environments due to environmental constraints associated with soil saturation (Parolin et al., 2010), although high diversity may occur on a regional scale due to their natural isolation.

The present study sought to examine the floristic compositions of six swamp forests in northern Minas Gerais State, analyze their natural regeneration and vegetation similarities, as well as address the following questions: (i) how does the diversity and composition of those swamp forests vary?; (ii) is there high floristic similarity between the study sites?; and, (ii) is local diversity (α diversity) lower than the diversity between areas (β diversity)?

2. MATERIALS AND METHODS

2.1. Study area

The present study was carried out in the Pandeiros River Environmental Protection Area (EPA) in northern Minas Gerais State, in southeastern Brazil. The EPA covers an area of 393,060 ha and includes the entire Pandeiros River basin, within the municipalities of Januária, Bonito de Minas, and Cônego Marinho (Nunes et al., 2015). The regional climate is tropical humid and dry (type Aw according to the Köppen classification system), with well-defined dry winters and rainy summers (Alvares et al., 2014). Our sampling focused on regenerating arboreal and shrub vegetation in six swamp forest: Água Doce (AD), Almescla(AL), Buriti Grosso (BG), Capivara (CA), Pindaibal (PI), and São Francisco (SF) (Fig. 1; Tab.1).

The vegetation in the study area is represented by *Cerrado* and *Caatinga* transition phytophysiognomies, culminating in a mosaic of riparian and dry forests, savanna, and palm swamps (Menino et al., 2012). The swamp forests associated with the palm swamps, the target of this study, occur mainly in the upper-mid Pandeiros River basin (Nunes et al., 2009; 2015).

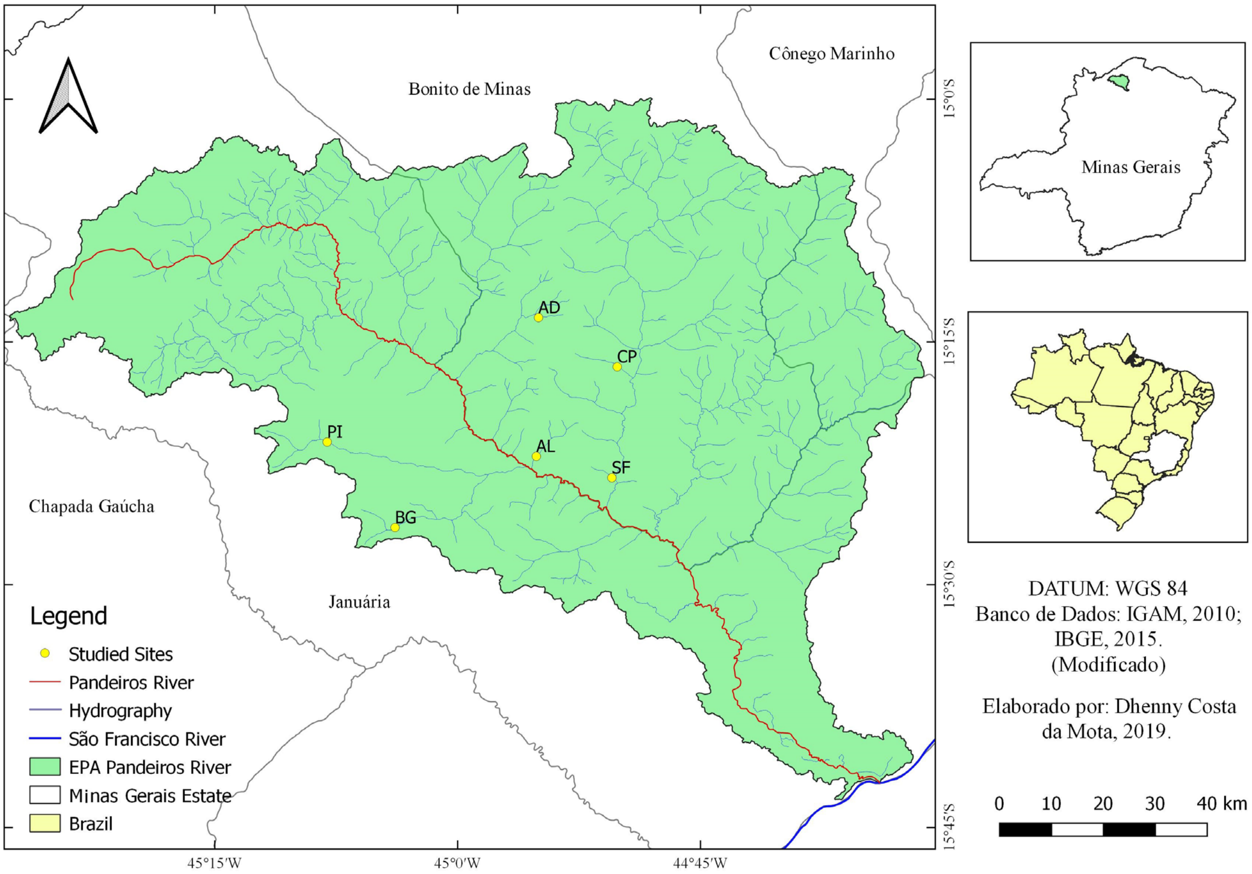

Figure 1. Location of the swamp forests studied (AD, AL, BG, CP, PI and SF) in the Pandeiros River EPA, in northern Minas Gerais State, Brazil.

Table 1. Descriptions of the six swamp forests in the Rio Pandeiros EPA in northern Minas Gerais State, Brazil. Total area in hectares (Neves, 2011); average height of trees in meters; and number of zones (Araujo et al., 2002).

Area	Location	Total area	Water flow	Tree density	Average height of trees	Artificial drainage channel	Natural channel	Fire	Cattle	Zones
AD	15°20’03.1” S 44°51’00.0” W	96	Stable	Dense	25	Absence	Perennial	Absence	Present	Three
AL	15°21’37.2” S 44°54’45.9” W	154	Stable	Dense	30	Present	Perennial	Absence	Present	Three
SF	15°23’4.4” S 44°50’59.6” W	28	Stable	Dense	25	Absence	Perennial	Absence	Absence	Two
BG	15°26’26.6” S 45°3’55” W	350	Irregular	Irregular sparse trees	8	Present	Intermittent	Present	Present	Three
CP	15°16’10.23” S 44°51’13.6” W	82	Absent	Irregular sparse trees	15	Present	Intermittent	Present	Present	Three
PI	15°22’30.2” S 45°2’0,17” W	2,215	Irregular	Irregular sparse trees	15	Present	Intermittent	Present	Present	Three

2.2. Structural survey of the regenerating community

We systematically established one hundred 5×5 m plots (totaling 0.25 ha, distance 15 m between plots, along the water body) where the regenerating arboreal/shrub individuals having ≥ 1 cm DGL (diameter at ground level) and < 3 cm DBH (diameter at breast height – measured 1.30 m above ground level) were sampled. We measured the DGL and total heights of regenerating individuals using a digital caliper and graduated meter respectively, except for regenerating *M. flexuosa* palm seedlings, which did not produce visible stipes capable of measurement. The data were collected during dry season.

We collected a sample of each inventoried plant for identification and deposited prepared specimens in the Montes Claros Herbarium (MCMG), at the Universidade Estadual de Montes Claros. Identifications of the collected botanical material were performed by consulting specialists and the specialized literature. The classification system used for botanical families was the *Angiosperm Phylogeny Group IV* (APG IV, 2016).

2.3. Data analysis

We calculated the phytosociological parameters: absolute and relative density, dominance and frequency, and importance value (Mueller-Dombois & Ellenberg, 1974). The Shannon diversity index (*H’*) and Pielou equability (*J’*) were calculated on a natural logarithmic basis (Brower et al., 1997; Magurran, 2011). The Hutcheson *t-test* was performed to compare diversities between areas using the *H’* diversity index and PAST program software (Hammer et al., 2001).

We determined the floristic similarities between the sampled areas by comparing their species in a presence/absence matrix using the Single Linkage method and Euclidean metric distances with Statistica 10 software (Statsoft, 2011). Additive diversity partitioning was examined in 100 permanent plots established in the six areas at different scales. The total species diversity (γ) was divided into additive components that represented diversity within the community (α, richness of each plot) and diversity between communities (richness between plots, β_1, and between areas, β_2). We used the Vegan package for the partitioning of α and β diversities in R (Oksanen et al., 2015; R Development Core Team, 2018). We used a null model with 1000 randomizations to evaluate the statistical significance of the observed values in relation to expected values.

3. RESULTS

A total of 5442 regenerating individuals belonging to 134 species, 85 genera, and 47 families were encountered in the six sampled areas (supplementary material). The most important families were Fabaceae, with 21 species, followed by Myrtaceae (11 species), Melastomataceae (10), Clusiaceae (7), and Rubiaceae (5). The genera with the highest number of individuals (57.49% of the total) were: *Xylopia* (827 individuals), *Miconia* (665), *Calyptranthes* (520), *Vernonanthura* (454), *Zygia* (347), and *Trembleya* (318). The total diversity (H ‘) was 3.38 and the equability (J’) 0.69. The Hutcheson *t-test* demonstrated significant differences in diversity between areas, except for AL and BG ($t = 0.842$; $df = 1924.5$; $p > 0.05$) and BG and CP ($t = 23.786$; $df = 1479.2$; $p > 0.01$) (Tab. 2).

Table 2. General data of the six swamp forests (AD, AL, BG, CP, PI, and SF) in the Rio Pandeiros EPA (Minas Gerais State, Brazil); Total area in hectares (Neves 2011); NI = number of individuals sampled; S = richness; *H'*= Shannon diversity index; *J'* = Pielou equitability index; AB = basal area ($cm^2.ha^{-1}$). Different letters indicate significant differences for the diversity test ($P \leq 0.05$).

Site	Total area (ha)*	NI	S	*H'*	*J'*	AB
AD	96	1404	46	1.82^{e}	0.48	66.89
AL	154	1210	44	2.28^{c}	0.60	58.43
BG	350	860	29	2.23^{cd}	0.66	38.01
CP	82	724	30	2.07^{d}	0.61	43.04
PI	2215	619	44	2.93^{b}	0.77	33.91
SF	28	625	59	3.18^{a}	0.77	34.98

Analyses of each area individually showed that the most abundant species in AD were *Xylopia emarginata* Mart. (533 individuals) and *Calyptranthes brasiliensis* Spreng. (514), which showed the highest VI and dominance values, as well as *Calophyllum brasiliense* Cambess. (83) and *Blepharocalyx salicifolius* (Kunth) O.Berg (54); 10 species were represented by only a single individual; 82 individuals of *M. flexuosa* were sampled in that area.

The most abundant species in AL were *Zygia latifolia* (L.) Fawc. & Rendle (346) and *X. emarginata* (258), which showed the highest VIs and basal areas, as well as *Miconia* sp. (200) and *Ladenbergia cujabensis* Klotzsch (92). Twelve species were represented by only a single individual; 51 individuals of *M. flexuosa* were encountered in that sampling area.

Trembleya sp. (281), *Miconia* sp. (193), *Byrsonima pachyphylla* A.Juss. (86), and *Aegiphila lhotskyana* Cham. (54) were the most abundant species in BG; seven species were represented by only a single individual. Two species of the family Melastomataceae (*Trembleya* sp. and *Miconia* sp.) were the most dominant and had the greatest VIs because of their abundances. No regenerating individuals of *M. flexuosa* were found.

In CP area, the most abundant species were: *Vernonanthura phosphorica* (Vell.) H.Rob. (317), *Tibouchina sellowiana* (Cham.) Cogn. (101), and *B. pachyphylla* (82). Nine species were represented only by a single individual; only five individuals of *M. flexuos*a were encountered in that sampling area. The most abundant species with the highest VI were *V. phosphorica* followed by *B. pachyphylla*, due to their large basal areas.

The most abundant species in PI were: *V. phosphorica* (122), *L. cujabensis* (71), and *Ludwigia elegans* (Cambess. ex A.St.-Hil.) H.Hara (66); seven species were represented by only a single individual; five individuals of *M. flexuos*a were encountered. As in CP, the most abundant species, and with the highest VI in PI, was *V. phosphorica*, due to its frequency.

Piper gaudichaudianum Kunth (84), *L. elegans* (66), *Richeria grandis* Vahl (63), and *Myrsine umbellata* Mart. (54) were the most abundant species in SF. The species *P. gaudichaudianum* and *M. umbellata* had the highest VI, because of the frequency of the former and the basal area of the latter. Twenty-one species were represented by only a single individual; 50 regenerating individuals of *M. flexuosa* were found in SF.

Only two species were common to all six areas: *Tapirira guianensis* Aubl. and *Miconia* sp., while 10 species were exclusive to AD, 11 to AL, 22 to SF, 11 to BG, seven to CP, and 11 to PI (a total of 72 exclusive species). Floristic similarity showed the formation of a group composed of the BG, CP and PI forests, and another group formed by areas AD and AL (Fig. 2). Area SF was separated from the others.

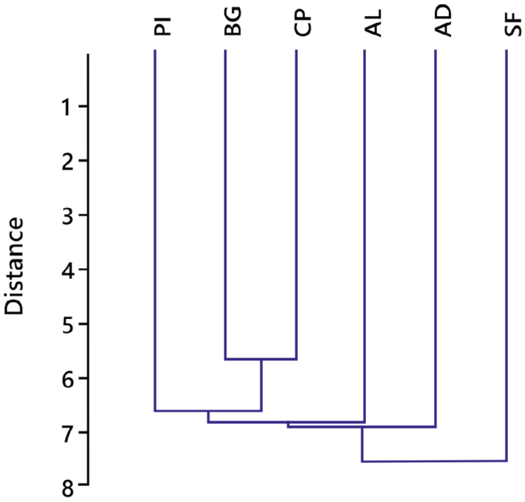

Figure 2. Dendrogram of the floristic similarities of regenerating species in six swamp forests (AD, AL, BG, CP, PI, and SF) in the Pandeiros River EPA, in northern Minas Gerais State, Brazil.

Additive diversity partitioning showed that local species (α) are responsible for 4.29% of the total richness. The exchange of species between plots in each path (β1) represented 36.43%, and the exchange of species between paths (β2) represented 49.28% of the total species richness (γ diversity). The diversity of those components was different from that expected by the null model (p = 0.001; Fig. 3).

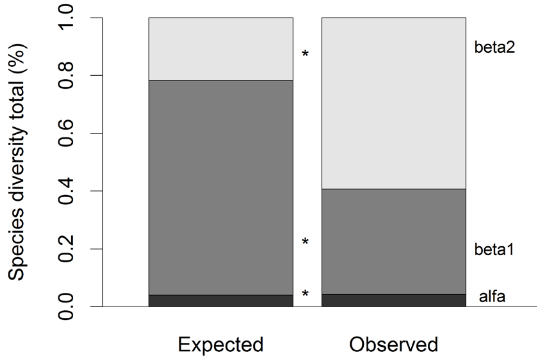

Figure 3. Additive partitioning of γ-diversity into α and β components in 600 plots in six swamp forests in northern Minas Gerais State, Brazil. Observed values were statistically compared with expected values (*$p < 0.001$).

4. DISCUSSION

The swamp forests studied here showed varied structures and compositions, with low similarity between them. Diversity is determined by the numbers of species and their abundances within a community (alpha diversity) and by differences in species compositions and their abundances between areas within the same community (beta diversity) (Magurran, 2011). Beta diversity was thus the component that most explained the total diversity of the swamp forests studied and indicated that each area had a particular flora. The low numbers of species common to those different areas also reinforced that result, because more than half of the species sampled were unique to a single site. Different environmental characteristics, conservation conditions, and land use in each forest can determine those variations, as the areas studied had experienced different anthropic impacts (Neves, 2011) and, consequently, were responding to different degrees of disturbance. The forests in this study experienced external impacts from local inhabitants who use the palm swamps as sources of water, food, and wood, as well as for agriculture purposes (personal observations).

The reduced numbers of species common to all of the forests studied, especially in the same geographic area and watershed, suggest great floristic heterogeneity (Menino et al., 2012). Differences in topography, flooding intensity, and soil conditions at any site will affect the spatial distributions of species and promote phytosociological variations (Teixeira & Assis, 2011).

Plant diversity in each of the six study areas (*H'* varied from 1.82 to 3.18) was relatively low in relation to the high diversity commonly observed in tropical forests, as swamp forest formations are flooded for most of the year and show low diversity because of those anoxic conditions (Kurtz et al., 2013). Additionally, flooding durations and depths will influence swamp forest compositions (Parolin et al., 2010), as water stress selects for tolerant species that can form large populations, with low resulting diversity (Kurtz et al, 2015).

The Brazilian *Cerrado* includes forest, savanna, and grassland formations, so that both forest and savanna communities experience the same climate regime (Ribeiro & Walter, 2008). Soil moisture and fertility levels, as well as geographic proximity, are also important factors contributing to species distributions in those environments (Silva Júnior et al., 2001). Swamp forests, as well as palm swamps, are humid formations within the *Cerrado* biome, with different surrounding plant communities that will influence their species compositions (Teixeira & Assis, 2011). The existence of differing *Cerrado* vegetation types results in numerous species co-occurring throughout the biome, increasing the diversity of any given region. Menino et al. (2012), for example, reported high species diversity between naturally regenerating riparian vegetations in the Pandeiros River study area that was influenced by the occurrence of diverse neighboring vegetation types. In addition to ecological conditions, geographical proximity can also be determinant for floristic composition (Kurtz et al., 2013). The conditions necessary for the establishment of different species in humid forests support the hypothesis that the surrounding vegetation contributes to their varied compositions (Teixeira & Assis, 2011), resulting in a vegetation mosaic. Although some studies have indicated a group of species characteristic of swamp forests, the contributions of the surrounding vegetation were determinant to the diverse of each study area (Kurtz et al., 2014).

The species sampled were organized into two groups: those found more frequently in poorly drained and flooded sites, such as *X. emarginata*, *Z. latifolia* and *R. grandis* (Maas et al., 2015; Garcia et al., 2015; Secco et al., 2015); and those typical of *cerrado* and forest edges, such as *Trembleya* sp., *T. sellowiana,* and *B. pachyphylla* (Mendonça et al., 2008). Flood regime durations and water depths will influence plant ecophysiology, and will require special adaptations to the periodicity of local anoxic conditions (Kurtz et al., 2013). Thus, species tolerant of waterlogging will define the plant typology, and will be both abundant and frequent. In this study, species such as *X. emarginata*, *C. brasiliensis*, *Z. latifolia*, *Miconia* sp., and *Trembleya* sp. were apparently tolerant of soil water saturation, as they were generally very abundant in the regenerative strata of the forests studied. There are groups of species in swamp forests that demonstrate dominance and high densities in saturated soils, composing a group of flooding specialists (Kurtz et al., 2014). Those species significantly contributed to increasing richness in well-drained soils, but less so in terms of their phytosociological parameters. Teixeira & Assis (2011) indicated that swamp forests generally show low plant diversity and are populated by species with high local densities, and identified *C. brasiliense* and *T. guianensis* as indicator species.

The high densities of species typical of humid areas in the swamp forests studied here contributed more to the similarities between the six areas that did their floristics (the presence of species represented by just a few or even a single individual) (Kurtz et al, 2015). Our study areas showed expressive numbers of exclusive species, with SF having the largest number (22 species). The SF area is flooded in the center (where the water table surfaces), but dryer along the edges, with the absence of any grassy zone. It therefore shows no typical separation of the swamp forest and *cerrado* vegetations, with no middle zone (composed mainly of grasses) of palm swamp (Araújo et al., 2002) – which probably allowed the establishment of numerous unique species with varied ecological requirements. The proximity of surrounding vegetation formations, characterized here as the forest-savanna ecotone, explains the co-occurrence of species on soils with different degrees of drainage (Kurtz et al., 2013; 2014; 2015). The varied environmental conditions in swamp forests, particularly in relation to their flooding regimes and topographic variations, allow the establishment of species with different ecological requirements, including generalist species from neighboring areas (Teixeira & Assis, 2011; Kurtz et al., 2013).

The species *X. emarginata* (in AD and AL), *B. salicifolius* and *C. brasiliense* (in AD); *Z. latifolia* and *Miconia* sp. (in AL), and *P. gaudichaudianum*, *M. umbellata*, and *L. elegans* (in SF), were the most important taxa in terms of vegetation structure regeneration in the present study. Those species occur in humid environments, especially in riparian, gallery, and flooded forests, as well as palm swamp forests or wetlands (Ribeiro & Walter, 2008; Teixeira & Assis, 2011). The importance of the species *B. pachyphylla*, *V. phosphorica*, *T. sellowiana*, and *Landerbergia cujabensis* in areas BG, CP and PI, demonstrated the influence of the adjacent vegetations, different soil conditions, and anthropic disturbances in those areas.

In general, the connections between swamp forest in palm swamps and adjacent *Cerrado* formations favored floristic diversity because they allowed colonization by species with different ecological requirements, thus increasing diversity. Anthropic interferences in the areas (being most intense in areas CP, BG, and PI), however, also appeared to be a determining factor of diversity.

The present work indicates that the regeneration potentials of the six areas studied are different (as seen in their respective diversities and compositions), so that conservation, management, or restoration strategies for those environments will be complex, and must be associated with a detailed knowledge of the important species in each area.

5. CONCLUSION

Floristic compositions varied among the forests studied here, with many species being unique to each site, and their presence was determined mainly by environmental characteristics, the influences of the adjacent vegetation, and anthropic impacts – all leading to low floristic similarity between them. Diversity, however, was generally low, due to ecological conditions linked to water stress. The different areas showed high variations in terms of their species contents (β2 diversity) and represent a major contribution to the total diversity of swamp forests within palm swamps in northern Minas Gerais State, Brazil.

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