

http://periodicos.uem.br/ojs/acta ISSN on-line: 1807-863X

Doi: 10.4025/actascibiolsci.v45i1.65557



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The plant community of a stretch of riparian vegetation in the upper Paraná River after 20 years of secondary succession (Batayporã, Mato Grosso do Sul, Brazil)

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ABSTRACT. The study of temporal changes in riparian vegetation is essential for understanding the paths taken by the ecosystem during ecological succession. In order to evaluate the changes in floristic composition, structure, and dynamics of the arboreal vegetation in an area of Semideciduous Seasonal Alluvial Forest, we aim to understand the secondary succession that occurs in the Paraná River floodplain. Based on a study conducted 20 years ago, in the municipality of Batayporã, Mato Grosso do Sul, a resampling was carried out in the same area, using the same methodology. Phytosociological and ecological parameters between the two temporal samplings were collected and compared using Student's 't' test, where it was possible to find statistically significant variations (p<0.05) in the vegetation structure. A total of 603 individuals were sampled, distributed among 51 species and grouped in 46 genera and 31 families. The analysis of the distribution of abundance and importance values (IV) of species visualized in the histogram indicated an expected pattern in forest communities, which is the substitution of early successional species for late successional species. For the successional categories, the comparison of IVs revealed higher values for secondary species in both surveys and changes in the positions of climax and pioneer species, directly influencing the IVs values of these categories for the zones. When compared to the result obtained in the previous study, a replacement of the IV values of pioneer species with climax and dead species is noted. The comparisons showed that this phytocoenosis is evolving to a mature successional stage, a result of the decrease in the main anthropic impacts in the area. The results obtained highlight the importance of temporal monitoring of forest areas to expand the understanding of the pathways of ecological succession in this type of environment and provide information to assist in biodiversity conservation.

Keywords: semideciduous seasonal alluvial forest; riparian forest; phytosociology.

Received on October 26, 2022. Accepted on July 13, 2023.

Introduction

Paraná River is one of the longest rivers in Brazil, and the main river of the Río de la Plata basin. In its upper course, it presents an extensive floodplain on its right bank, known as the Upper Paraná River Floodplain (PIAP). This area has great ecological importance due to the set of heterogeneous environments that includes, for example, permanent floodplains, periodically flooded areas, river islands, fragments of Semideciduous Seasonal Alluvial Forest, and non-forest areas. This complex of heterogeneous habitats performs essential ecosystem services for the rich heritage of aquatic and terrestrial biodiversity (Campos & Souza, 1997).

Over the last 50 years, this region has undergone several anthropic interventions, mainly from the 1970s to the mid-2000s. One of the main impacts during this period was the agricultural occupation, which led to deforestation, with fires and selective logging of timber species, resulting in the fragmentation of native vegetation and restricting it to the banks of water bodies (Campos & Souza, 1997; Cruz & Campos, 2015). There was also the construction of the Porto Primavera Dam (HPP Eng. Sérgio Motta), starting in 1991, which

¹ From the Portuguese: Planície de inundação do alto rio Paraná (PIAP).

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altered the flood-pulse dynamics, interfering in the water level dynamics (Souza Filho, 2016). In order to mitigate the impacts and conserve the remaining biodiversity of the region, in 1997, the Environmental Protection Area of the Islands and Floodplains of the Paraná River (EPA-IFPR Decree s/n, 10/01/1997) was created, which restricted and regulated the use of the areas belonging to this EPA, allowing only the sustainable use of its resources (Brasil, 1997). However, some anthropic impacts, such as drainage of the floodplain and fires, for example, persist to this day (Fragal, Alves, & Souza Filho, 2013), in addition to the presence of cattle and the activities of the upstream hydroelectric plants.

Since the implementation of the EPA-IFPR, the use of the fragmented forest cover was abandoned by agricultural activity, maintaining the same order of magnitude since 1984 (Souza Filho & Fragal, 2013). And since then, these areas in the PIAP are in a process of succession through natural regeneration, and currently consist of secondary forests (Brown & Lugo, 1990).

Succession is a dynamic process that causes changes in the composition, structure, and forest dynamics of a community, increasing the structural complexity of the vegetation (Ellenberg & Mueller-Dombois, 1974; Magnago, Rocha, Meyer, Martins, & Meira-Neto, 2015; Matsuo, Martínez-Ramos, Bongers, van der Sande, & Poorter, 2021). This natural process allows fragmented and fragile ecosystems to recover from disturbances, natural or anthropogenic, and unaffected areas to continue evolving until a relatively stable/mature point is reached (Brancalion, Gandolfi, & Rodrigues, 2015; Magnago et al., 2015). These modifications occur over time and do not develop in a defined time, but can occur very quickly, very slowly, or even inexpressibly (Godóy, Marabesi, Mortari, Aidar, & Buckeridge, 2009).

According to the work done by da Cruz and Campos (2013, 2015) and Cruz, Campos, and Torezan (2018), we observed that the areas of PIAP subjected to major anthropic impacts have undergone secondary succession processes in a rapid manner, and the older forest fragments are under different stages of development, indicating that a secondary forest succession has occurred in the vegetation of this floodplain.

The study of changes in species composition and dynamics is fundamental to the understanding of the successional process, considering the importance of structural and floristic variations for the understanding of forest regeneration (Ribeiro et al., 2013). Campos, Romagnolo, and Souza (2000) analyzed the structure, distribution patterns, and dynamics of tree species and their relationship with soil and topographic profile, in the remaining parts of the Semideciduous Seasonal Alluvial Forest in PIAP. The authors concluded that hydrodynamic processes of sedimentation were the most important factors in the establishment and succession of the vegetation, contributing to the establishment of species and concomitantly with the alteration and evolution of the substrate.

The creation of the EPA-IFPR and the reduction of flood pulses by the Porto Primavera Hydroelectric Power Plant activity provided a change in the riparian forest structure on the right bank of the Paraná River, with an advance in successional stage, and an increase of pioneer species to climactic species and expansion of the forest over the floodplain area.

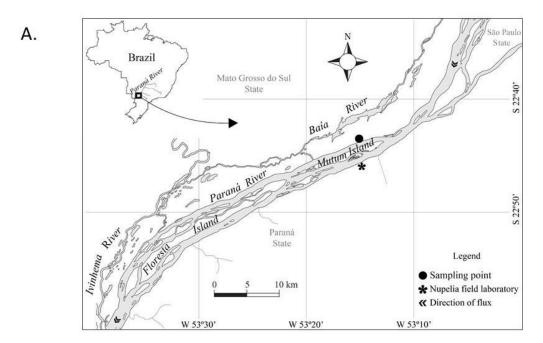
In this sense, the aim of this study was to evaluate the changes in floristic composition, structure and dynamics of the arboreal vegetation in an area of Semideciduous Seasonal Alluvial Forest, 20 years after the first study by Campos et al. (2000), seeking to understand the secondary succession.

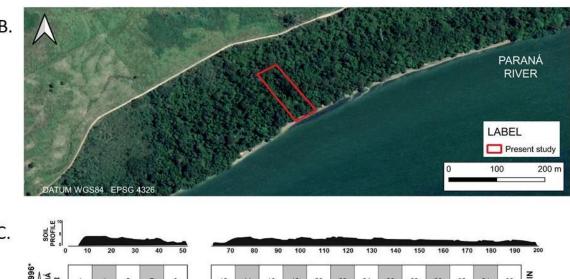
Material and methods

Study area

The evaluated section is located on the right bank of the Paraná River, municipality of Batayporã, Mato Grosso do Sul (22°44'15.04"S, 53°16'11.04"W). This represents one of the least impacted forest fragments within the upper Paraná River floodplain (PIAP) region (Figure 1). This section was previously studied, analyzed, and had its results published by Campos et al. (2000).

The climate of the region is Cfa or humid subtropical according to the Köppen system, with hot summers and rainfall distributed throughout the months of the year, with greater volume between the months of September to December (Romagnolo & Souza, 2000). The topographic profile of the region is flat, with an average slope of 3% from the margin to the interior, and the soil is of the non-hydromorphic alluvial type derived from unconsolidated alluvial sediments (Romagnolo & Souza, 2000).





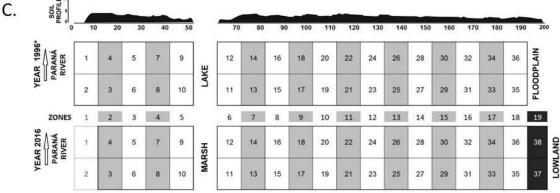


Figure 1. Schematic of the study area and its respective plots. A. Location of the study area, in the municipality of Batayporã, Mato Grosso do Sul (MS), Brazil. B. Area where the plots were installed by *Campos et al. 2000 and in the present study (2016). C. Distribution of plots and zones along the transect. The dotted line shows the plots eroded by the Paraná River and the plots in black have been added to the current survey.

The vegetation cover of the study area is in the Atlantic Forest Biome, under the domain of the Semideciduous Seasonal Alluvial Forest (SSF), in addition to the floodplain areas that extend to the banks of the Baía River (Campos & Souza, 1997).

Due to the anthropization of the region for land use by local inhabitants, exploitation of the areas for tourism (Galvão, Stevaux, & Saad, 2014), water action in flood periods, and farming practices, the forests on the banks of the Paraná River are in different degrees of succession (Romagnolo & Souza, 2000).

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For purposes of comparison with the previous study (1996), the evaluation of the spatial distribution by zones was considered, which includes two plots perpendicular to the water bodies (river, lake and floodplain). Zones 1 and 2 refer to a higher environment, constituting a high dike where flooding does not occur. From these zones, the relief presents a slope (zones 3 to 5), reaching a swamp strip of approximately 10 meters (currently), but which was reported by Campos et al. (2000) as a perennial lake in 1996. Passing the marsh area, there is a four-meter slope in zones 6 and 7. From zones 8 to zone 19, there is again a gentle slope until reaching a low area, but without a swamp. In this area, the herbaceous vegetation is greater (Figure 1C).

Field procedure and data analysis

Using the same methodology employed by Campos et al. (2000), a resampling of the area was carried out, in which no anthropic activities were recorded in the period between the two surveys. Two contiguous and perpendicular transects were demarcated to the Paraná River bed, with 18 plots of 15x10m ($150 m^2$), totaling $5,400 m^2$, 15m parallel to the river bed and 10m perpendicular (Figure 1C). After returning to the survey area, it was found that plots 1 and 2 of the dike were eroded over the years by the Paraná River and no longer exist, as well as the lake, which became a marsh over time (Figure 1C). Based on this fact, the survey was initiated in plots 3 and 4, and two plots were included at the end (37 and 38). These were selected due to the transformation of the floodplain area into a forested region, making them suitable for inclusion in the research. These plots (37 and 38) were also included for us to work with the same total area surveyed by Campos et al. (2000). For the study, all tree individuals with PBH (perimeter at breast height - 1.30m from ground level) $\geq 15cm$ were analyzed. Standing dead individuals were sampled and included in an artificial category named Dead for dynamics assessment. The height of individuals was estimated using a 2-meter-high aluminum stick, and the perimeter was measured with a tape measure.

Most individuals were identified *in situ*. When it was not possible to determine them, reproductive and/or vegetative material was collected for herborization, following the usual techniques for vascular plants and subsequent consultation with specialists. Materials in the reproductive stage were stored in the Nupélia Herbarium (HNUP).

A histogram was created based on the abundance and importance values of the species, ranked according to the present study. The purpose was to visualize the abundance distributions and importance values for different study periods, considering only species with a sample size of 10 or more individuals. In this graph, the number of individuals of each species is ranked in descending order from the present study.

The data recorded in the field were processed and then the usual phytosociological parameters such as density, basal area, volume, importance value index (IVI) and Shannon-Wiener diversity index (H') (Ellenberg & Mueller-Dombois, 1974) were calculated. Calculations were performed employing the FITOPAC program® version 2.1 (Shepherd, 2010). As for the successional category, the species were classified into: Pioneer (P), Secondary (S) and Climax (C), *sensu* Budowski (1965), according to field observations and literature consultation, and Undetermined (U) for the dead ones.

The results regarding the phytosociological parameters (abundance, density, dominance, relative frequency and Importance Value - IV) obtained in this research were compared with those of Campos et al. (2000) to verify whether the temporal change in vegetation presents significant statistical variations through Student's 't' test in the R 4.3.0 software (R Core Team, 2023).

The evaluation of the spatial distribution by zones were used for diversity analysis Shannon-Wiener, successional categories, wealth and abundance.

Results

A total of 603 individuals were sampled. Out of these, 44 (7.29%) belonged to the Dead category, and the others were distributed in 55 species, gathered in 46 genera and 28 families. The families with the highest species richness were Fabaceae (eight spp.) and Lauraceae (six spp.). Annonaceae, Elaeocarpaceae, Euphorbiaceae, Melastomataceae, Myrtaceae, Polygonaceae, Rubiaceae, Sapindaceae, and Sapotaceae were represented by two species each.

The results obtained show variation in relation to floristics and vegetation structure, such as an increase in the number of species, families, dead individual and Shannon-Wiener diversity as well as basal area and volume, and a decrease in the number of individuals and density (Table 1).

Table 1. Data on diversity and structure of tree vegetation in the present study (2016) and *Campos et al. (2000). Upper Paraná River floodplain, Batayporā, Mato Grosso do Sul. NI - number of individuals; NS - number of species; NF - number of families; DI - dead individuals; DI - density of individuals; BA - basal area; TBA - total basal area; V - volume; TV - total volume; H' - Shannon-Wiener diversity.

Parameters	NI	NS	NF	NF DI D (ind ha ⁻¹)		BA (m^2) TBA $(m^2 ha^{-1})$		V (m ³)	TV (m ³ ha ⁻¹)	H'
2016	603	51	31	44	1.118	14.91	27.61	237.38	439.59	3.30
1996*	795	47	28	32	1.472	14.51	26.88	175.79	324.07	3.20

The analysis of species abundance distribution using the Rank abundance distribution plot indicates a pattern expected in plant communities with few species exerting dominance over many others (Figure 2). That is, few species have a high number of individuals, while many species have few individuals sampled, and this pattern becomes more evident as sampling increases. In the present study, the highest abundance values were reached by *Unonopsis guatterioides, Sloanea guianensis, Protium heptaphyllum, Triplaris americana, Zygia cataractae, Pouteria torta* and *Piper tuberculatum*. In the survey by Campos et al. (2000), the highest values were achieved by *Cecropia pachystachya, Guazuma ulmifolia, Inga vera* and *Peltophorum dubium* (Table 2), with *C. pachystachya*, a pioneer species, representing 17% of the total abundance.

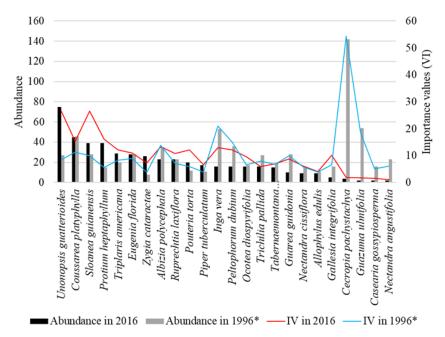


Figure 2. A histogram was used to visualize the abundance distributions and IV (Importance Value) of species with a sample size exceeding 10 individuals in the present study (2016), and in the survey by *Campos et al. (2000). Upper Paraná River floodplain, Batayporã, Mato Grosso do Sul.

Comparing the Importance Values (IV) of the species sampled in the two surveys, we observed that there was a change in the positions occupied by the species. In the present study, *S. guianensis* occupies the first position in IV (26.60), followed by *U. guatterioides* (26.53). *P. heptaphyllum* and *C. platyphylla* (Figure 2). In the survey by Campos et al (2000), *C. pachystachya* occupied the first position in IV (54.35), with more than double the value of the second place *Inga vera* (21.09). In contrast, in the current survey, *C. pachystachya* was represented by only four individuals and with IV of 1.94 (Table 2).

The inter-zone comparisons of Shannon-Wiener diversity index are represented in Figure 3. The diversity values did not very much, as most were between 2.15 and 2.7. Zone 4 showed a higher value of 2.94. This zone contains 35 individuals of 22 different species, in which only the species *Z. cataractae* and the Dead category comprised four individuals, the species *T. americana* included three individuals, while the rest comprised five species with two individuals or one individual per species. Zones 5 and 6 are also exceptions for presenting lower diversity values, 1.64 and 1.55, respectively (Figure 3). In the collections, both contained seven species, among them the Dead category, with zone 5 presenting 10 individuals of the species *Z. cataractae* and eight individuals of the species *T. americana*, respectively, while Zone 6 encompassed 10 individuals of the species *Z. cataractae*.

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Table 2. Tree community structure parameters obtained by *Campos et al. (2000) and the current study (2016). Upper Paraná River floodplain, Batayporã, Mato Grosso do Sul (SC - Successional Class: C - Climax, P - Pioneer, S - Secondary, U - Unclassified; N - Number of individuals; IV - Importance Value; R - 'rank' based on IV).

Charias	S.C.	2	2016		1996*		מוזואנן
Species	SC	N	IV	N	IV	R	HNUP
Sloanea guianensis (Aubl.) Benth.	S	39	26.6	28	9.99	8	13643
Unonopsis guatterioides (ADC) R.E.Fr.	C	75	26.53	27	8.45	11	11178
Individuals killed	U	44	18.83	32	14.75	5	-
Protium heptaphyllum (Aubl.) Marchand	S	39	16.23	15	5.56	21	14185
Coussarea platyphylla Müll.Arg.	C	45	15.31	46	11.23	7	15055
Albizia polycephala (Benth.) Killip ex Record	S	23	13.27	35	13.74	6	3557
Inga vera Willd.	S	16	12.97	53	21.09	2	15038
Triplaris americana L.	S	29	12.22	20	8.29	12	3206
Peltophorum dubium (Spreng.) Taub.	S	16	12.21	36	14.96	4	15642
Pouteria torta (Mart.) Radlk.	S	20	12.21	12	5.9	19	3995
Eugenia florida DC.	S	28	10.9	28	8.94	10	11167
Ruprechtia laxiflora Meisn.	S	23	10.72	23	7.18	14	3984
Gallesia integrifolia (Spreng.) Harms	S	5	10.05	16	6.67	16	3576
Ocotea diospyrifolia (Meisn.) Mez	S	16	9.61	17	6.59	17	14981
Guarea guidonia (L.) Sleumer	S	10	8.76	28	9.96	9	16159
Zygia cataractae (Kunth) L.Rico	S	26	7.25	8	3.74	29	15056
Tabernaemontana catharinensis A. DC.	S	15	6.98	19	6.81	15	3554
Piper tuberculatum Jacq.	C	17	6.63	11	3.9	25	16122
Nectandra cissiflora Ness LC	S	9	6.06	15	5.82	20	12994
Trichilia pallida Sw.	S	16	5.9	27	7.94	13	16153
Spondias mombin L.	S	6	5.02	5	3.81	28	427
Allophylus edulis (A.StHil., Cambess & A. Juss.)	S	9	4.16	11	3.98	24	12204
Sapindus saponaria L.	S	7	4.07	6	4.98	23	3553
Parapiptadenia rigida (Benth.) Brenan	S	5	3.39	3	1.98	30	3574
Eugenia paracatuana O. Berg	С	9	3.2	-	-	-	11948
Cordia sellowiana Cham.	S	4	2.64	2	1.2	35	3537
Annona emarginata (Schltdl.) H.Rainer	S	7	2.52	3	1.27	34	14979
Garcinia brasiliensis Mart.	C	7	2.48	-	-	-	9685
Leptobalanus apetalus (E.Mey.) Sothers & Prance	S	4	2.1	2	0.83	39	8940
Copaifera langsdorffii Desf.	S	1	1.99	1	1.08	36	15082
Cecropia pachystachya Trécul	P	4	1.97	142	54.35	1	3569
Guazuma ulmifolia Lam.	S	2	1.82	54	18.49	3	11160
Sloanea hirsuta (Schott) Planch. ex Benth.	S	2	1.78	5	3.88	26	3997
Salacia elliptica (Mart.) G. Don	C	3	1.62	-	-	-	13893
Casearia gossypiosperma Briq.	S	2	1.52	16	5.16	22	13878
Nectandra grandiflora Ness	S	2	1.22	-	-	-	842
Nectandra angustifolia (Schrad.) Ness & Mart.	S	2	1.08	23	6.19	18	12630
Celtis iguanaea (Jacq.) Sarg.	S	2	1.01	4	1.6	31	3965
Pouteria glomerata (Miq.) Radlk	S	2	0.99	2	0.82	40	3563
Pterocarpus rohrii Vahl.	S	2	0.96	-	-	-	-
Calophyllum brasiliense Cambess.	S	1	0.64	3	1.45	32	3570
Styrax pohlli A.DC.	S	1	0.61	-	-	-	17980
Croton urucurana Baill.	P	1	0.56	1	0.43	42	13582
Nectandra hihua (Ruiz & Pav.) Rohwer	S	1	0.52	3	3.88	27	13295
Citrus aurantium L.	С	1	0.5	1	0.42	44	3971
Machaonia brasiliensis (Hoffmanns. ex Humb)	S	1	0.5	1	0.42	45	3549
Chamb & Schltdl.				•	0.12	10	
Miconia pusilliflora (DC.) Naudin	С	1	0.48	-	-	-	14187
Erythroxylum anguifugum Mart.	P	1	0.47	-	-	-	14983
Nectandra megapotamica (Spreng.) Mez	S	1	0.47	-	-	-	2995
Apuleia leiocarpa (Vogel) J.F.Macbr.	S	1	0.47	2	0.98	37	3555
Eugenia handroi (Mattos) Mattos	S	-	-	3	1.34	33	3969
Psidium guajava L.	S	-	-	2	0.84	38	11168
Chusquea selowii Rupr.	S	-	-	1	0.54	41	3700
Solanum granulosoleprosum Dunal	P	-	-	1	0.43	43	3582
Citrus limon (L.) Osbeck	S	-	-	1	0.42	46	3527
Aegiphilla candelabrum Briq.	S	-	-	1	0.41	47	4696

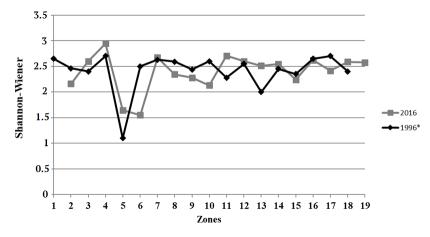


Figure 3. Shannon-Wiener diversity for the respective zones, Batayporā, Mato Grosso do Sul (MS), Brazil.

Analyzing the IV of species by successional category, we observed that secondary species presented the highest values in both surveys (Table 3), followed by climactic species, which inverted the position with pioneers, and, in this study, this category was the one that contained the smallest sample. The Dead category presented a higher IV in the current study when compared to the study by Campos et al. (2000), which, even with the inclusion of the undetermined category, still presented a higher IV.

Table 3. Table containing the values found for the different successional categories, and the representativeness in percentage with respect to the Importance Value (IV). NS - number of species; NI - number of individuals; IV - importance value; dead/undetermined. *Campos et al. (2000).

Donomotore	2016				1996*			
Parameters	NS	NI	IV	IV (%)	NS	NI	IV	IV (%)
pioneer	3	6	3	1	3	144	54.78	18.27
secondary	38	395	221.42	73.8	39	534	207.77	69.26
climax	8	158	56.75	18.91	4	85	21.87	7.29
dead/undet	-	44	18.83	6.28	-	32	15.58	5.18

The results obtained, when compared over a 20-year difference, show a change in the positions of the climax and pioneer species, as supposed by Campos et al. (2000). The pioneer species now present only 3.47% of the number of individuals that they presented 20 years before, and the climax species represent, in this new survey, 185.88% of the number of individuals from before, while the secondary species now present 74.15%.

Analyzing the IV of species by successional category along the zones, it is possible to see a predominance of secondary species, with the exception of Zone 10, where climax species had a higher IV (161.52) when compared to secondary species (119.57). Zones 2 and 14 showed the highest IV of secondary species, 258 and 254.15, respectively. Pioneer species had the lowest IV in all zones when comparing the living and identified individuals. The presence of these species was cataloged in Zones 4, 10, 11 and 12, with IV of 7.84, 18.91, 6.64 and 12.77, respectively (Figure 4). When compared with the result obtained by Campos et al. (2000), we noticed the substitution of IV values of pioneer species for Climax and Dead species on account of natural succession.

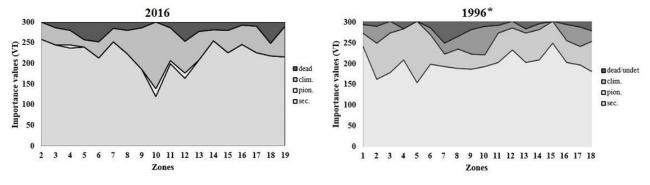


Figure 4. Distribution of IV of species according to successional group along the zones. A. Current study (2016). B. Adapted from *Campos et al. (2000). Pion. - pioneer species; clim. - climax species; sec. - secondary species; dead/undet - dead and undetermined species.

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The Dead category was well distributed in almost all zones, being absent only in Zones 2 and 10 and having the highest IV recorded for Zones 6, 12 and 18 (Figure 4A). In the survey by Campos et al. (2000), zones 5 and 6 (near the lagoon) did not show any dead individuals, but a high IV for pioneer species, indicating that these are undergoing a process of vegetation succession.

Taking into account the work done by Campos et al. (2000) (Figure 4B), we can consider that these environments increased the IV for the undetermined due to the almost total absence of the *C. pachystachya* species, when compared to the 20-year difference between the surveys, where in the first one it had 142 individuals quantified and in this one only four.

Compared to the previous study from 20 years ago, a great change can be observed in the number of individuals at closer distances to the river, due to the death of pioneer and secondary species (Figure 5).

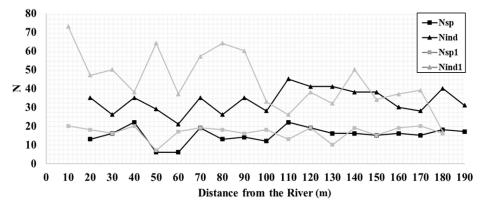


Figure 5. Number of species and individuals in relation to the distance gradient from the river. Nsp - number of species; Nind - number of individuals for the current study (2016) sampling; Nsp1 - number of species; Nind1 - number of individuals for the study sampling of Campos et al. (2000).

However, there are no major changes from intermediate distances. Regarding the number of species, the two periods show the same pattern, indicating the absence of influence of the distance gradient from the river on the richness of tree species. The values found in Student's "t" test showed a statistically significant variation for the phytosociological parameters that we have access to in the study by Campos et al. (2000), such as abundance, importance value, density, dominance and relative frequency where in all analyzes it was possible to find p value less than 0.05 (p<0.05).

Discussion

The families found in the study area are highlighted as the most representative in several areas of the Semideciduous Seasonal Alluvial Forest of PIAP (Campos et al., 2000; Souza & Monteiro, 2005), in the states of Mato Grosso do Sul (Battilani, Scremin-Dias, & Souza, 2005), Minas Gerais (Souza, Araujo, Mello, Scolforo, & Castro Silva, 2007) and São Paulo (Silva & Soares, 2003). As well as in riparian forest areas of extra-Amazonian Brazil (Rodrigues & Nave, 2000).

The vegetation structure, when compared to the survey of Campos et al. (2000), showed an advance of the successional stage, decreasing the density of individuals and increasing the basal area and community volume, while for the floristic structure, it is possible to notice an increase in the number of species, and family and a decrease in the number of individuals (Table 1). According to Nunes, Mendonça, Botezelli, Machado, and Oliveira-Filho (2003) and Matsuo et al. (2021), this result evidences the maturation of the vegetation, in which there is a reduction of smaller individuals, especially of pioneer species, favoring the development of trees with larger basal areas. Compared to what was described by Campos et al. (2000), the occurrence of species categorized by successional stage shows an inverse pattern, with a higher presence of pioneer and climax species. Conversely, secondary species indicate transitional sites, suggesting a replacement of these species by secondary and climax species, indicating that the area is undergoing a process of maturation.

The species *E. paracatuana*, *G. brasiliensis*, *S. elliptica*, *N. grandiflora*, *P. rohrii*, *S. pohlli*, *M. pusilliflora*, *E. anguifugum*, and *N. megapotamica*, were sampled only in this survey, while the species *E. handroi*, *P. guajava*, *C. selowii*, *S. granulosoleprosu*, *C. lemon*, and *A. candelabrum* were sampled only in the study by Campos et al.

(2000). With these results, it is possible to notice a maturation of the site, considering that four climax species were sampled compared to the first collection.

The Shannon-Wiener diversity index of the present study survey was higher than that of other surveys conducted at PIAP (Souza, Cislinski, & Romagnolo, 1997; Fernandes, Leli, Stevaux, Kawakita, & Romagnolo, 2023) and in other riparian vegetation areas (Rodrigues, Monteiro, Junior, Beltrame, & Moscogliato, 2011; Lucheta et al., 2018).

The pattern of species abundance distribution recorded is typical of tropical forests, where a small number of species show high density, and a large number of species show low density (Magnago et al., 2015). However, the set of low abundant species may be of ecological importance and also be responsible for several functions in the ecosystem, such as increasing community resilience against invaders and nutrient retention (Lyons, Brigham, Traut, & Schwartz, 2005).

When compared to the study of the Campos et al. (2000), the sum of the occurrence of species by successional category is inverse when compared to pioneer and climax species, while the secondary species represent transition sites. When we analyze the IV, we notice that the species recorded with the highest values by Campos et al. (2000) belonged to the pioneer and secondary categories, and were replaced by other species belonging to the secondary and climax categories. *C. pachystachya* was the species that presented the most relevant changes. This may be related to the fact that it is a pioneer species and is found mainly in sites with upwelling of the water table and not within dense primary forests (Lorenzi, 2008). *G. ulmifolia*, a secondary species that needs light and hydromorphic soil, is rarely found in primary forests (Carvalho, 2003) (Figure 2).

The significant reductions in the importance values of common species in the wetlands of the PIAP, such as *Calophyllum brasiliense*, *C. pachystachya*, *Croton urucurana*, *I. vera*, *Nectandra angustifolia*, *Nectandra hihua*, *P. tuberculatum*, *P. heptaphyllum* and *Sapindus saponaria*, among others, may also constitute a response to the decrease in the amplitude of floods caused by the upstream hydroelectric power plants, especially the Porto Primavera Hydroelectric Power Plant, which represents the greatest anthropic impact in the region.

Forests in more advanced stages of succession present low floristic representation of pioneer species, and their high mortality rate can be observed, while high recruitment rates and higher density of secondary and climax species are observed (Paula, Silva, Marco Júnior, Santos, & Souza, 2004).

The large number of dead individuals indicates a great dynamic occurring in this ecosystem. This can be explained by the anthropic impact of fragmentation that causes changes in successional stage due to the entry of pioneer species, generating stress on individuals of species more susceptible to factors such as microclimatic changes and wind, but can also explain a natural dynamic of the area, since the area is extremely humid and subject to periodic flooding (Couto, Souza Filho, & Hayakawa, 2011; Souza Filho & Fragal, 2013).

Plant species classified as pioneer species have a rapid growth and a short life span (Liu et al., 2016), but are extremely important for forest dynamics, because the overlay of the area by these species provides ideal conditions for species of later successional groups to develop below the canopy of pioneer species (Magnago et al., 2015). Over the years and with the structural development of the forest, an increase in the mortality rate of these pioneer species is observed due to their short life cycle, a process that allows young individuals of late species to develop, occupying the place of pioneer species (Duarte et al., 2018).

The fluvial dynamics develop complex habitats in the plain affecting aspects such as diversity, distribution and function of plant species that compose the riparian forest (Stevaux, Corradini, & Aquino, 2013). Distance from the river did not reveal any clear pattern on structural and compositional parameters in the sampled zones, unlike the study of Campos et al. (2000), which found higher density values in the zones closer to the river (Figure 6). In the present study, density values of individuals were slightly lower at closer distances to the river, with a small increase at intermediate distances. The number of species does not show a clear pattern in the gradient investigated, but the influence of the lagoon (40-50m distance) is clear, causing a reduction in the number of tree species.

An example of the importance of these analyses can be seen in the study by García-Quintana et al. (2020), in which the structural parameters and floristic composition were fundamental to the knowledge of the characteristics of the evergreen forest in the upper Puyo River watershed, where there were no previous studies. The parameters indicated that the forest presents different stages of vegetation succession, which can be explained by anthropic action in the region, and also made it possible to suggest actions for the restoration of these areas. Another example can be verified in the study by Duarte et al. (2018), where floristic and structural parameter differences served as indicators of the complexity of the

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succession process and were useful in the elaboration of phylogenetic trees of the species found in early and advanced successional stage sites in different forest areas in São Joaquim National Park, in the Planalto Catarinense.

Although there is no species gradient with respect to large individuals, it may exist in the understory where the response to environmental influences tends to be more pronounced and plants more susceptible to stress conditions. Another important factor is that the lower strata naturally have higher species richness, a fact that may help to understand these patterns.

Conclusion

Compared to the 1996 survey, the vegetation structure analyzed in 2016 presents characteristics that distinguish itself in terms of the density of individuals of different successional classes. In addition, it shows greater abundance of individuals of secondary species, low density of pioneer species and also an increase in the density of individuals of climax species. Another relevant aspect is associated with the values measured for basal area. In 2016, a value similar to that of 1996 was recorded, but with a lower density of individuals, indicating that these have larger diameters.

Based on these parameters, we considered that this phytocoenosis is evolving to a more mature successional stage, provided by the reduction of major anthropic impacts in the region. These structural and floristic results highlight the importance of monitoring forest areas for biodiversity conservation.

Acknowledgements

We thank the *Conselho Nacional de Desenvolvimento Científico e Tecnológico* (CNPq) and the Long-Term Ecological Research Program (PELD), which made this study possible; the Center for Research in Limnology, Ichthyology, and Aquaculture (NUPELIA)-UEM, for the logistical support in the fieldwork; Carlos Eduardo Bento Fernandes for his help with the organization of botanical material, and the Academic Writing Center of the *Universidade Estadual de Maringá* for assistance with English language translation and developmental editing.

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