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Zonation of aquatic plant communities along the flooding gradient in subtropical wetlands

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Abstract Aquatic plants play a crucial role in wetlands, and understanding distribution patterns and species composition can be valuable for several purposes. Here, we assessed aquatic plant distribution along a flooding gradient in the transition region between terrestrial and aquatic environments within a wetland complex. We investigated the presence of distinct zones in terms of species richness, composition (beta diversity), and life forms. We established transects along the shoreline, and defined three zones along each transect: floodable zone (zone 1), water-land interface zone (zone 2), and water body zone (zone 3). Clear zonation patterns were identified, due to occurrences restricted to portions of the gradient and significant variations in the coverage of species and life forms. The gradient displayed high beta diversity, with zones 1 and 3 differing significantly in species composition. Turnover explained the observed variation, associated with environmental filtering and interspecific interactions. There was no significant decrease in richness with increasing water depth. Amphibious plants dominated along the gradient. Our study highlights that the life forms inhabiting wetlands represent an adaptive continuum, ranging from plants that tolerate transitory submergence to those entirely limited to the aquatic environment. Understanding species distribution patterns is crucial for delineating wetland boundaries and gaining valuable insights into wetland conservation and restoration, particularly in light of escalating threats and the impacts of climate change.

Keywords: amphibious · community assembly · environmental gradient · hydrophytes · lagoon shoreline zone.

Introduction

Aquatic plants, also known as hydrophytes or aquatic macrophytes, are an important component of the particular biota of wetlands (Junk et al., 2014; Mitsch & Gosselink, 2015). They exhibit typical morpho-physiological adaptations, such as aerenchyma, reduction of supporting tissues and heterophylly, which allow them to survive under periodic or constant flooding conditions (Pompêo and Moschini-Carlos 2003; Thomaz & Esteves, 2011). However, the tolerance to flooding and water saturation of the soil shows different degrees, making aquatic plants a highly heterogeneous group (Cronk and Fennessy 2001). At one end, there are plants whose organization is so intimately related to aquatic life that they have lost the ability to survive in dry environments. At the other end, are typically terrestrial species that can withstand occasional submersion (Arber 1920; Thomaz and Esteves 2011). Along this continuum, we observe species that are more or less adapted to abundant water and a wide variety of life forms (Arber 1920; Scremin-Dias et al. 1999).

In an attempt to improve categories in terms of moisture requirements, Irgang et al. (1984) and Irgang and Gastal Jr. (1996) classify aquatic plants into the life forms of floating, submerged, emergent, amphibious, epiphytic and climbing. Often, these life forms are distributed perpendicular to the shore in a relatively distinct manner, forming a spatial pattern known as zonation (Thomaz and Esteves 2011). In deeper zones, submerged plants occur, while shallow environments host emergent plants and the shore areas with greater water level fluctuations, amphibians tolerant to drought (Irgang and Gastal Jr. 1996). Other plant types (floating, epiphytic and climbing) are distributed between the extremes of the gradient (Thomaz and Esteves 2011). Ramos and Novelo (1993) recognize similar life forms, and also employ a broader eco-physiological classification based on the degree of plant adaptation to flooding. They define three categories of aquatic plants: strictly aquatic plants complete almost their entire life cycle submerged, emerged, or floating; subaquatic plants live a significant part of their life cycle in water, without surviving for extended periods in completely dry soils; and tolerant plants, wich in the event of a water level rise, they can tolerate high moisture in the sediment for a short period (Ramos and Novelo 1993).

The flooding gradient acts as a crucial environmental filter, selecting species based on their ecological tolerances and life forms (Cronk and Fennessy 2001; Catian et al. 2018). While depth and water level fluctuations form the evident basis for zonation occurrences, indirect consequences such as light and nutrient availability, temperature, and water conductivity are related to the community structure along the flooding gradient (Rolon et al. 2008; Roznere and Titus 2017; Lewerentz et al. 2021). Even on a small scale, within a few meters, significant environmental heterogeneity can be observed, contributing to different resource distribution patterns, generating distinct micro-habitats, and consequently, influencing the occurrence of plant species in space (Deák et al. 2017). Additionally, competitive interactions among species play a significant role in their distributions (Keddy 2010; Roznere and Titus 2017). The assembly of plant communities along flooding gradients may be driven, therefore, by niche differentiation in response to both abiotic factors (e.g., physical and chemical habitat characteristics) and biotic factors (e.g., competition) (Vellend 2016).

Investigating distribution and species composition patterns, even on a short scale, can contribute to understanding the underlying processes of plant community assembly (Noleto et al. 2019). This is crucial to make predictions about the effects of environmental changes on the structure and dynamics of wetland vegetation, which can be valuable for the conservation and restoration of these highly complex ecosystems threatened by human activities (Cavalli et al. 2014; Lewerentz et al. 2021). Changes in species composition along environmental gradients (beta diversity; Whittaker 1972) can be attributed to species turnover or nestedness (Baselga 2010). In the case of turnover, species exchange occurs from one point on the gradient to another one, while in nestedness, there is a loss of species, and the less rich site represents a subset of the richer site (Baselga 2010). Understanding the contribution of both factors can aid in comprehending the observed compositional changes and the mechanisms shaping biodiversity at various spatial scales (Fu et al. 2019).

The present study aims to investigate how aquatic plants distribute along the transition region between terrestrial and aquatic environments in a wetland complex. We assess whether it is possible to observe zonation patterns in terms of species richness, composition, and life forms. Regarding species composition, we also determine which component (turnover or nestedness) better explains the observed beta diversity. We hypothesize that species richness will decrease with increasing water depth, as these areas require a higher degree of specialization from aquatic plants. Further, we hypothesize that species and life forms distribute preferentially along the flooding gradient, according to their adaptation to water levels, forming spatial zonation patterns. Additionally, we expect beta diversity to exhibit high values along the gradient due to species turnover, with the extremes showing greater dissimilarity between them, reflecting higher environmental heterogeneity.

Material and methods

Study site

Lagoa do Peixe National Park (LPNP) is situated in the coastal plain of Rio Grande do Sul, Brazil (Fig. 1). The climate in the region is classified as humid subtropical, with an average annual temperature of 17.5 ºC and precipitation ranging from 1300 to 1600 mm, evenly distributed throughout the year (Alvares et al. 2013). The LPNP consists of diverse ecosystems, including various types of wetlands such as lagoons, swamps, marshes, salt marshes, and wet lowlands, which harbor a high diversity of aquatic plants and hold significant importance, especially for migratory birds (Hazin 2008; Rolon et al. 2011; Silveira et al. 2022). We selected three palustrine wetland areas (without tidal influence, see Maltchik et al. 2004) located in the north of the LPNP. Two areas encompassed the shores of Lagoa Pai João, which has a northern portion (31°03'20"S 50º48’26”W) and a southern portion (31°03'2"S 50°48'18"W), connected by a narrow channel. The third sampled area corresponded to a marsh near the Mostardas balneary road (31°06'44"S 50°50'29"W). These water bodies, when filled, flood neighboring areas, and when this happens frequently or for extended periods, it leads to changes in the species composition of these areas (Silveira et al. 2022).

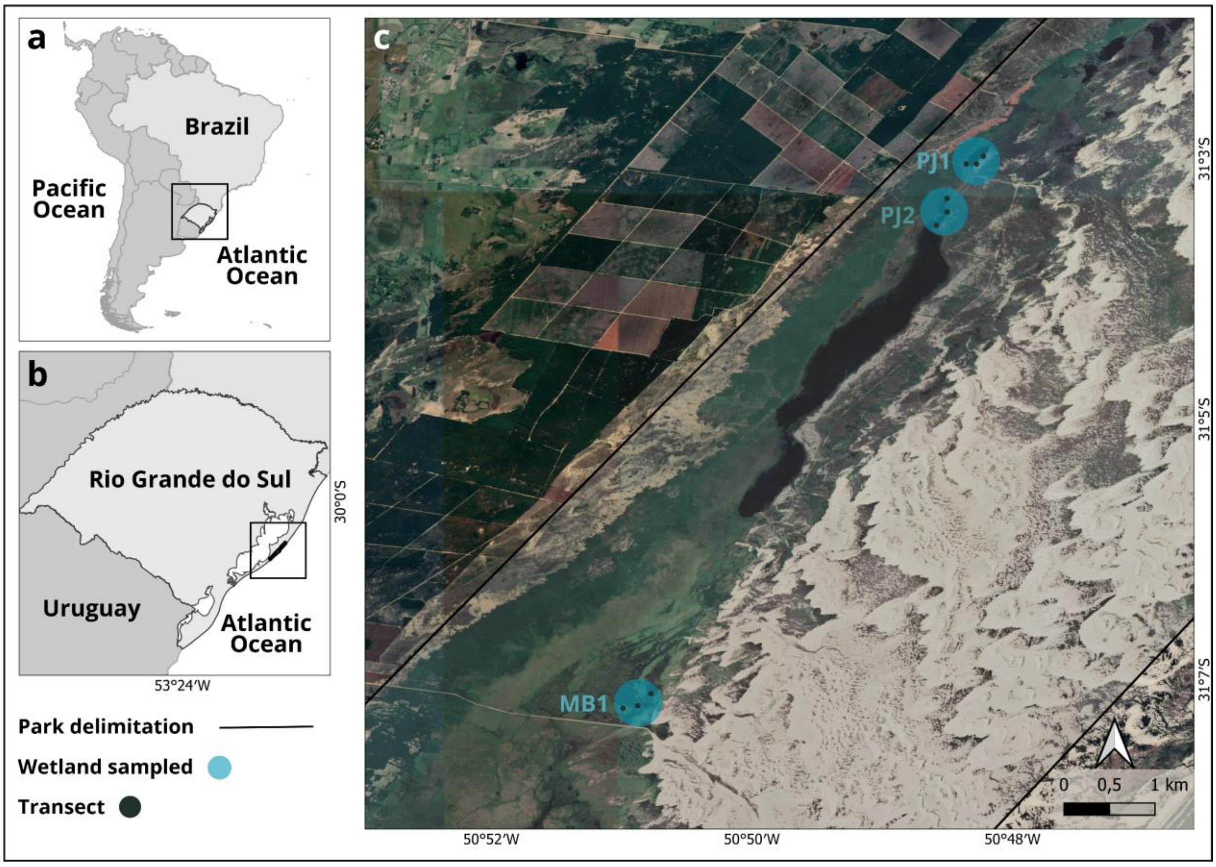

Fig. 1 Study area in Lagoa do Peixe National Park (LPNP). (**a**) South America, with the state of Rio Grande do Sul, Brazil, highlighted in the square; (**b**) LPNP in Rio Grande do Sul state; (**c**) LPNP aerial view with sampled wetlands: two adjacent to Lagoa Pai João (PJ1, PJ2) and one near the Mostardas balneary road (MB1).

Data collection and sampling design

Data collection was conducted in November 2022, during southern hemisphere spring, when most species are in the reproductive stage. Three transects were systematically established perpendicular to the edge of each wetland (Fig. S1 in the Electronic Supplementary Material), with a minimum distance of 200 m between them. Starting from the water-land interface, a distance of 3 m was marked towards the interior of the water body and 3 m towards the upland, totaling a length of 6 m. Each transect covered areas with shallow water and adjacent terrestrial habitat. Contiguous plots of 50 x 50 cm² were allocated along the 6 m length. Each transect consisted of 12 plots, resulting in 36 plots per wetland and 108 in total. Three zones were delimited along the transects. The first four plots of each transect corresponded to the floodable zone (zone 1), characterized by the temporary absence of water but subject to flooding during rainy periods when water levels can raise. The next four intermediate plots corresponded to the water-land interface zone (zone 2), encompassing wet soils to soils covered by water up to 45 cm in height. The remaining plots represented the water body zone (zone 3), with a water depth of up to one meter. In each plot, we estimated the mean water depth, mean vegetation height, vegetation cover, litter cover, percentage of bare soil, and the water surface cover (without emerging vegetation) using the Londo decimal scale (1976). Species names were verified on Flora e Funga do Brasil (2022) website.

Term, definition and classification of aquatic plants

For the current study, we chose the term 'aquatic plants', to be less restrictive concerning the plant species attributed to wetlands (Pivari et al. 2018). We followed the definition provided by Arber (1920), which establishes that aquatic plants constitute a biological group that evolved from terrestrial plants, consisting of organisms adapted to live in aquatic environments to varying degrees. This definition includes typically terrestrial species that can withstand occasional submersion and those exclusively adapted to aquatic life, and plants that live in the varying intermediate situations. The delimitation and classification of life forms (see Table 1) used here were based on Irgang et al. (1984) and Irgang and Gastal Jr. (1996). Life forms were assigned, to each species, based on field observations and literature review. We referred to specialized literature (e.g. Irgang and Gastal Jr. 1996) to confirm the amphibious category, as the sampling period did not allow us to observe how species respond to water level fluctuations. Amphibious species form a very heterogeneous group in these classifications, as they show different degrees of adaptation to fluctuating conditions between flooding and drought. We thus divided this group into three categories by help of the eco-physiological classification used by Ramos and Novelo (1993), including the additional category 'accidental'. Thus, amphibious plants were classified as subaquatic, tolerant, and accidental. Climbers followed the same classification, as they can also exhibit varying degrees of adaptation to the high substrate moisture. Other life forms, unable to survive dry conditions, are designated as strictly aquatic (see Table 1). For classification of individual species, we consulted aquatic plant checklists for Brazil (e.g. Moura Júnior et al. 2013; Moura-Júnior et al. 2015; Oliveira et al. 2019) and examined taxonomic reviews providing ecological descriptions for species (e.g. Lüdtke et al. 2013; Silva-Filho et al. 2013; Affonso et al. 2015; Sosa et al. 2021), books on aquatic flora, and regional flora collections (e.g. Reitz, 1988; Irgang and Gastal Jr. 1996; Pott and Pott, 2000; Wanderley et al. 2007; Amaral et al. 2008). Additionally, we verified the habitats of occurrence for each species on Flora e Funga do Brasil (2023) and Species Link (2023) websites.

Table 1 Classification of life forms assigned to aquatic plants sampled in Lagoa do Peixe National Park, based on Ramos & Novello (1993) - in italics -, Irgang et al. (1984) and Irgang and Gastal Jr. (1996). Strictly aquatic plants are subdivided into five life forms (emergent, rooted submerged, free submerged, rooted floating, and free floating). Subaquatic, tolerant and accidental plants are subdivided into two life forms (amphibious and climbing).

Category	**Description**
Strictly aquatic	*Plant that completes practically its entire life cycle within water, being either submerged, emergent, or floating*
Emergent	Rooted in the substrate, inhabits shallow water, living partially emergent and partially submerged, not enduring periods out of water
Rooted submerged	Rooted in the substrate, lives most of its time submerged in the water column, with flowers typically extending above the water surface
Free submerged	Not rooted in the substrate, lives submerged freely in the water column, with flowers typically extending above the water surface
Rooted floating	Rooted in the substrate at some point, lives floating in the water column
Free floating	Not rooted in the substrate, lives freely floating in the water column, easily carried by the wind
Subaquatic	*Plant that performs a significant part of its life cycle in water and cannot survive for an extended period in completely dry soil. It shows water dependency at some stage of the life cycle and its occurrence is restricted to environments with periodic or constant flooding*

Category	**Description**
Tolerant	*Plant that completes a significant part of its life cycle in completely dry soil, tolerating, for a short period flooded or highly humid soil conditions. It is common in these environments but not exclusive to them*
Accidental	*Plant that completes practically its entire life cycle in completely dry soil, tolerating, for a short period, flooded or highly humid soil conditions. Presence in highly humid environments is rare*
Amphibious	Rooted in the substrate, inhabits wetland margins, enduring periods out of water. When in the water body, it may be emergent, floating, or submerged
Climber	Rooted in the substrate, inhabits wetland margins, grows and develops over other emergent and floating plants

Data analyses

Initially, we assessed the occurrence of distinct water depths among the three zones using the Kruskal-Wallis test, followed by the Dunn test for group comparisons (Kruskal and Wallis, 1952; Dunn 1964). These tests were conducted after confirming the non-normality of the data using the Shapiro-Wilk tests (Shapiro and Wilk 1965) and Bartlett's test for homogeneity of variance (Barrett et al. 1993). A Venn diagram and indicator species analysis (Dufrêne and Legendre 1997) were employed to assess the occurrence of species and their association with zones. The indicator species analysis determines indication values for species in individual groups (zones) and combined groups (De Cáceres et al. 2010). Indicative values (IV) range from 0 (no indication) to 100 (perfect indication). The statistical significance of IV for each species was tested via permutation test with 9999 permutations (De Cáceres et al. 2023). Simple linear regression was utilized to evaluate whether species richness is negatively correlated with water depth.

We employed a multivariate dispersion homogeneity test (PERMDISP; Anderson 2006) to assess differences in beta diversity among zones. This method defines beta diversity as the variability in species composition between groups in a given area, which can be measured as the average dissimilarity between sample units and the centroid (or spatial median) of their group in multivariate space, using an appropriate dissimilarity measure (Anderson et al. 2006). In summary, the PERMDISP method uses Principal Coordinate Analysis (PCoA) to ordinate the dissimilarity matrix. It then calculates distances between group members and the group centroid based on PCoA axes (rather than the original distances). We utilized the Jaccard dissimilarity measure (with presence/absence data) for conducting PERMDISP. Subsequently, we computed the overall statistical significance of the results (ANOVA model; 9999 permutations) and employed Tukey's Honest Significant Differences for paired comparisons between zones.

We applied multiple-site beta diversity partitioning, as proposed and described by Baselga (2010, 2012), to assess the contributions of species nestedness and turnover in determining the total beta diversity in the studied aquatic system. Three dissimilarity measures (based on Jaccard distance for presence/absence data) were used, representing total beta diversity, turnover, and nestedness. Importantly, the nestedness measure is not an absolute measure of nestedness but a dissimilarity measure due to the effect of nestedness patterns (Baselga 2010). The beta diversity component values presented here are mean values generated through 9999 permutations of raw data. We obtained relative values for each beta diversity component by dividing turnover and nestedness values by the Jaccard dissimilarity value (total beta diversity).

Redundancy Analysis (RDA) was employed to examine how the structural variables (mean water depth, mean vegetation height, vegetation cover, litter cover, percentage of bare soil, and the water surface cover) relate to indicator species for each zone of the gradient. Prior to this, we tested linear correlations between pairs of variables. The variable "vegetation cover" was removed due to its highest variance inflation factor (VIF), causing the remaining variables to have VIF < 10. The significance of non-collinear variables was assessed through stepwise selection (ordistep) (Oksanen et al. 2022). To assess the distribution of life forms along the gradient, we created boxplots showing the relative coverage of life forms per water depth zone. Using mean values of relative coverage, we generated a bar chart illustrating species coverage in each zone of the gradient. The analyses were performed using R software (R Development Core Team 2023) with packages *rstatix* (Kassambara 2023), *VennDiagram* (Chen 2022), *ggplot2* (Wickham et al. 2023), *vegan* (Oksanen et al. 2022), *betapart* (Baselga et al. 2023), and *indicspecies* (De Cáceres et al. 2023).

Results

A total of 55 species belonging to 29 botanical families were recorded in the study (Table S1). The families with the highest number of species were Poaceae (eight species, 14.5%), Asteraceae (six species, 10.9%), and Cyperaceae (four species, 7.3%). The predominant life form was amphibious, accounting for 39 species (70.91%), followed by emergent and rooted submerged, each with four species (7.27%). Free submerged had three species (5.45%), while climbers and free floating each accounted for two species (3.64%). Only one species was classified as rooted floating (1.82%). Among amphibious species, 64% (25 species) were classified as tolerant, 28% (11 species) as subaquatic, and 8% (three species) as accidental. The most abundant species were *Ischaemum minus*, with high cover across all three zones, averaging 29.4%, *Luziola peruviana*, with more pronounced cover in zones 2 and 3 (average cover: 17%), and *Panicum aquaticum*, predominant in zones 1 and 2 (average cover: 13.9%), all from the Poaceae (Fig S2).

The water depth varied significantly among the three zones ($p < 0.01$). Zone 1 had no water surface. In zone 2, the average depth was 5.3 cm, while in zone 3, it reached 33.5 cm (Fig. S3). Regarding richness along the gradient, zone 1 exhibited 37 species, followed by 33 in zone 2, and 29 in zone 3 (Fig. 2). However, the increase in water depth along the gradient did not result in a significant decrease in richness ($R^2 = 0.0097$) (Fig. S4).

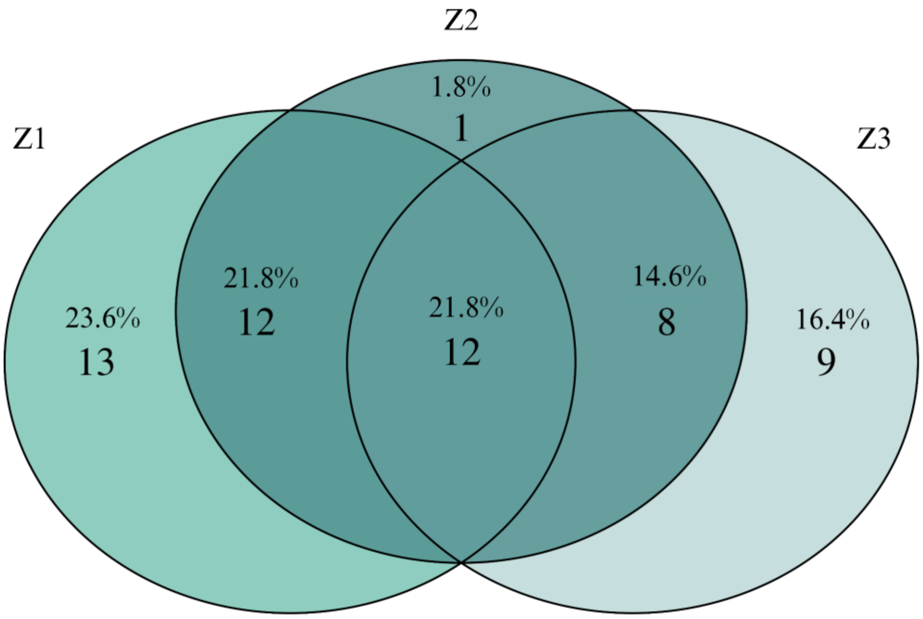

Fig. 2 Venn diagram illustrating the richness and percentage of species restricted to and shared among water depth zones. Z1 - floodable zone; Z2 - water-land interface zone; Z3 - water body zone

We observed a significant sharing of species among zones (Table S2). Only one species, the climber *Vigna longifolia* was recorded as exclusive to zone 2. Twelve species from zone 2 were shared with zone 1 (21.8%), and eight with zone 3 (14.6%). Zones 1 and 2 simultaneously harbor tolerant amphibious species such as *Axonopus parodii*, *Paspalum pumilum*, *Cyperus reflexus*, *Oldenlandia salzmannii*, *Centella asiatica*, and *Gamochaeta americana*. Shared between zone 2 and 3 are the amphibious *Alternanthera philoxeroides* (tolerant) and *Enydra anagallis* (subaquatic), as well as strictly aquatic species *Utricularia* spp., *Schoenoplectus californicus*, *Cabomba caroliniana*, and *Echinodorus grandiflorus*. In the first case (zones 1 and 2), we observed a decrease in species cover towards higher moisture. In the second case (zones 2 and 3), except for *A. philoxeroides*, *C. caroliniana*, and *E. anagallis*, which remained similar in cover, the increase in water depth had a positive effect on the abundance of the others.

Twelve species occurred in all zones. Among them were amphibious subaquatic and tolerant species such as *Bacopa monnieri*, *Ischaemum minus*, *Ludwigia grandiflora*, *Panicum aquaticum*, *Nymphoides humboldtiana*, and *Luziola peruviana*, as well as strictly aquatic species like *Mayaca sellowiana* (emergent) and *Myriophyllum aquaticum* (rooted submerged). Differences in species coverage were observed between zones. *Bacopa monnieri* showed more significant coverage in zone 2, decreasing towards the extremes (zones 1 and 3). The species was identified as an exclusive indicator for zone 2 (Table 2). *Panicum aquaticum* was recorded as an indicator for zones 1 and 2, and *L. peruviana* for zones 2 and 3, due to their more significant coverage in these gradient fragments. *Ludwigia grandiflora* and *N. humboldtiana*, in turn, were more significantly present in zone 3, serving as indicators for it. The strictly aquatic *M. aquaticum* and *M. sellowiana* had higher coverage in zone 3, but they were also recorded, with low coverage (approx. 1%) in zone 1. *Ischaemum minus* showed high relative coverage in all three zones.

Concerning species restricted to the extremes, we recorded 13 in zone 1 (23.6%) and nine in zone 3 (16.4%). Among the species restricted to zone 1, we highlight *Desmodium adscendens* and *Stylosanthes leiocarpa*, both tolerant, which were also indicated for zone 1. *Baccharis dracunculifolia*, *Senecio madagascariensis*, and *Solanum* sp., classified as accidental amphibious species, occurred exclusively in the first portion of the gradient. Species restricted to zone 3 included the strictly aquatic *Pontederia cordata* (indicator), *Egeria densa*, *Egeria najas*, and *Eicchornia azurea*, as well as amphibious subaquatic species, indicators for the zone, *Leersia hexandra* and *Polygonum acuminatum*.

The analysis of indicator species (Table 2) identified seven species for zone 1, a single species for zone 2, and nine species for zone 3. In zones 1 and 2, three species were identified as indicators, and the same was observed for the other extreme of the gradient: three species for zones 2 and 3 (Fig. 3).

Table 2 List of indicator species for water depth zone. IV - indicative values; Z1 - floodable zone; Z2 - water-land interface zone; Z3 - water body zone; significance level - *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$

Species	**IV**	**Z1**	**Z2**	**Z3**
Axonopus parodii	0.626	***		
Gamochaeta americana	0.523	***		
Desmodium adscendens	0.461	***		
Oldenlandia salzmannii	0.451	**		
Centella asiatica	0.402	**		
Bryophyta sp.	0.333	*		
Stylosanthes leiocarpa	0.333	*		
Panicum aquaticum	0.921	***	***	
Cyperus reflexus	0.842	***	***	
Eleocharis maculosa	0.486	**	**	
Bacopa monnieri	0.485		**	
Luziola peruviana	0.862		***	***
Mayaca sellowiana	0.496		*	*
Utricularia gibba	0.441		*	*
Ludwigia grandiflora	0.607			***
Myriophyllum aquaticum	0.585			***
Utricularia breviscapa	0.520			***
Nymphoides humboldtiana	0.502			*
Schoenoplectus californicus	0.497			**
Pontederia cordata	0.441			***
Utricularia foliosa	0.379			*
Leersia hexandra	0.333			*
Polygonum acuminatum	0.333			*

Fig. 3 Photographs of indicator species for zone 1 (a, b, c), zone 2 (d), zone 2 and 3 (e, f), and zone 3 (g, h, i). **a** - *Gamochaeta americana*, **b** - *Axonopus parodii*, **c** - *Oldenlandia salzmannii*, **d** - *Bacopa monnieri*, **e** - *Panicum aquaticum*, **f** - *Cyperus reflexus*, **g** - *Pontederia cordata*, **h** - *Utricularia foliosa*, **i** - *Leersia hexandra*. Photos: a, b, d, f, h - Filipe F. da Silveira; c, e, g - Francieli P. da Silveira; i - Willian S. Piovesani

Regarding beta diversity, PERMDISP showed that zones 1 and 3 of the gradient exhibited significantly distinct species composition (p = 0.003), while zone 2 did not differ significantly from either (Fig. 4). Zone 1 showed the lowest variation in species composition between plots, whereas zone 3 exhibited the highest variation.

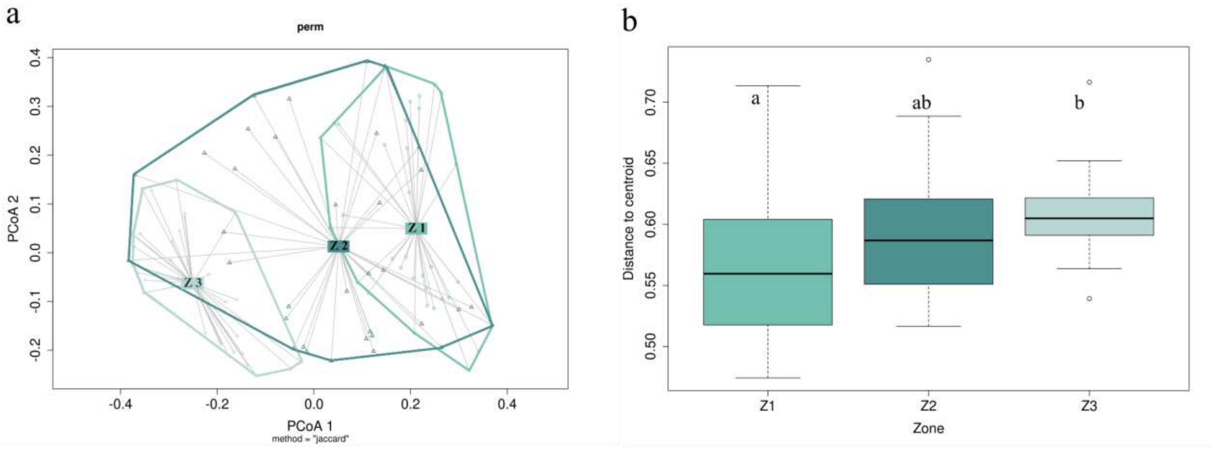

Fig. 4 PERMDISP (**a**) and centroid distance boxplot (**b**) illustrating the variation in beta diversity among water depth zones. Z1 - floodable zone; Z2 - water-land interface zone; Z3 - water body zone. Identical letters indicate zones with similar species compositions, while different letters indicate zones with distinct species compositions

Observing the partitioned beta diversity (Table 3), we note that the variation in species composition along the gradient is explained almost exclusively by species turnover (99.6%). The same pattern is observed among zones and within each zone. When comparing zone to zone, the highest dissimilarity is recorded between zone 1 and 3.

Table 3 Results of beta diversity partitioning along the gradient, among zones, and within each water depth zone. Z1 - floodable zone; Z2 - water-land interface zone; Z3 - water body zone.

Zone	Turnover	Nestedness	Dissimilarity
Z1 + Z2 + Z3	0.996	0004	0.988
Z1 + Z2	0.991	0009	0.979
Z2 + Z3	0.980	0.020	0.957
Z1 + Z3	0.995	0.005	0.983
Z1	0.980	0.020	0.956
Z2	0.983	0.017	0.961
Z3	0.986	0.014	0.963

The RDA (Fig. 5) demonstrated that the structural variables explained 22% of the species distribution, with the mean water depth alone explaining 11% ($R^2adj = 0.11219$, $F = 14.5211$, $p = 0.002$). Zone 3 is associated with the highest mean water depth and the presence of water surface. Aquatic strictly and subaquatic amphibious species, which show a higher degree of specialization to the aquatic environment, are associated with these axes. At the other end of the gradient, we find *A. parodii* and *G. americana* occurring in drained areas, where instead of water surface, the presence of exposed soil is observed.

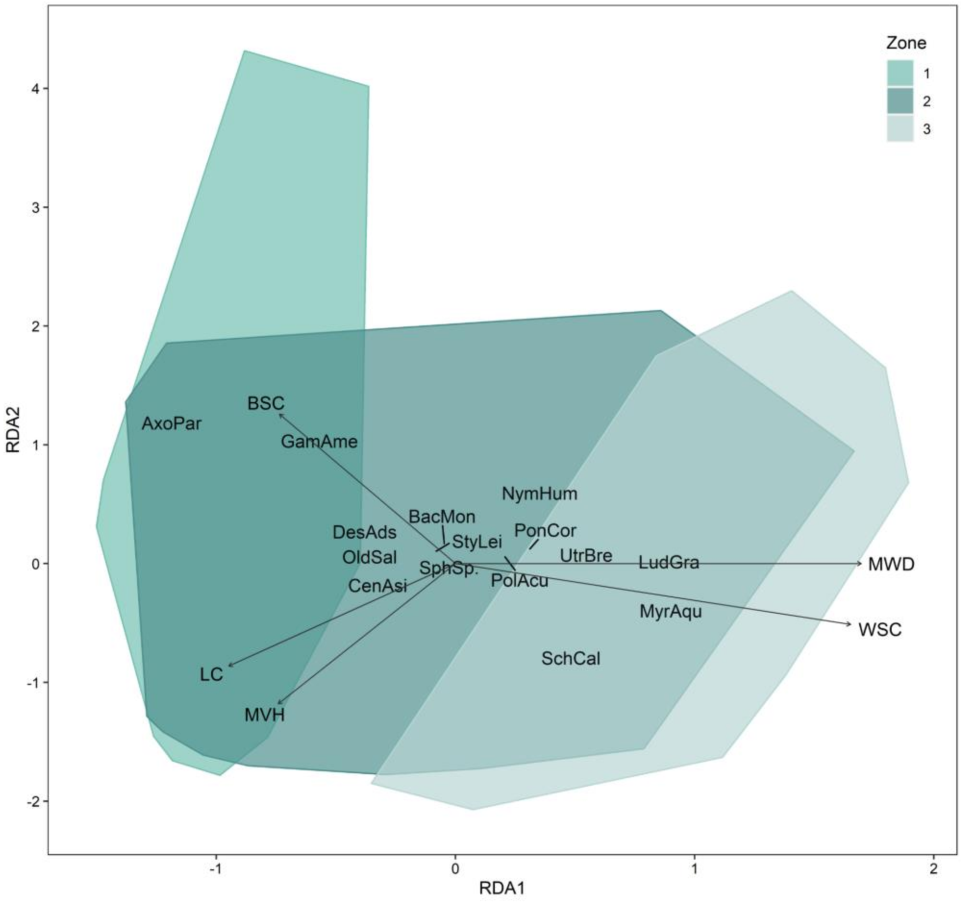

Fig. 5 Redundancy Analysis (RDA) demonstrating the relationship of indicator species with structural variables. Species: AxoPar - *Axonopus parodii*; BacMon - *Bacopa monnieri*; CenAsi - *Centella asiatica*; DesAds - *Desmodium adscendens*; GamAme - *Gamochaeta americana*; LudGra - *Ludwigia grandiflora*; MyrAqu - *Myriophyllum aquaticum*; NymHum - *Nymphoides humboldtiana*; OldSal - *Oldenlandia salzmannii*; PolAcu - *Polygonum acuminatum*; PonCor - *Pontederia cordata*; SchCal - *Schoenoplectus californicus*; SphSp. - *Sphagnum* sp.; StyLei - *Stylosanthes leiocarpa*; UtrBre - *Utricularia breviscapa*. Structural variables: MWD - mean water depth; MVH - mean vegetation height; LC - litter cover; WSC - water surface cover; BSC - bare soil cover

Regarding the distribution of life forms, the amphibious and climbing categories had a wide distribution, being present throughout the entire gradient (Fig. 6). Climbing plants showed low coverage. Amphibious plants, on the other hand, were the most abundant in all three zones. In zone 1, their coverage was close to 100%. As the depth increased, a slight decrease was observed. Emergent and submerged forms were recorded with negligible coverage in zone 1, increasing towards zone 3. In zone 3, we observed the occurrence of all life forms inventoried in this study.

The amphibious plants present in zone 1 are mostly tolerant species. We observed lower coverage of subaquatic amphibious plants and the presence of accidental amphibious plants exclusively for this zone. Tolerant amphibious plants showed higher relative coverage compared to subaquatic ones in zone 2, with the opposite observed in zone 3.

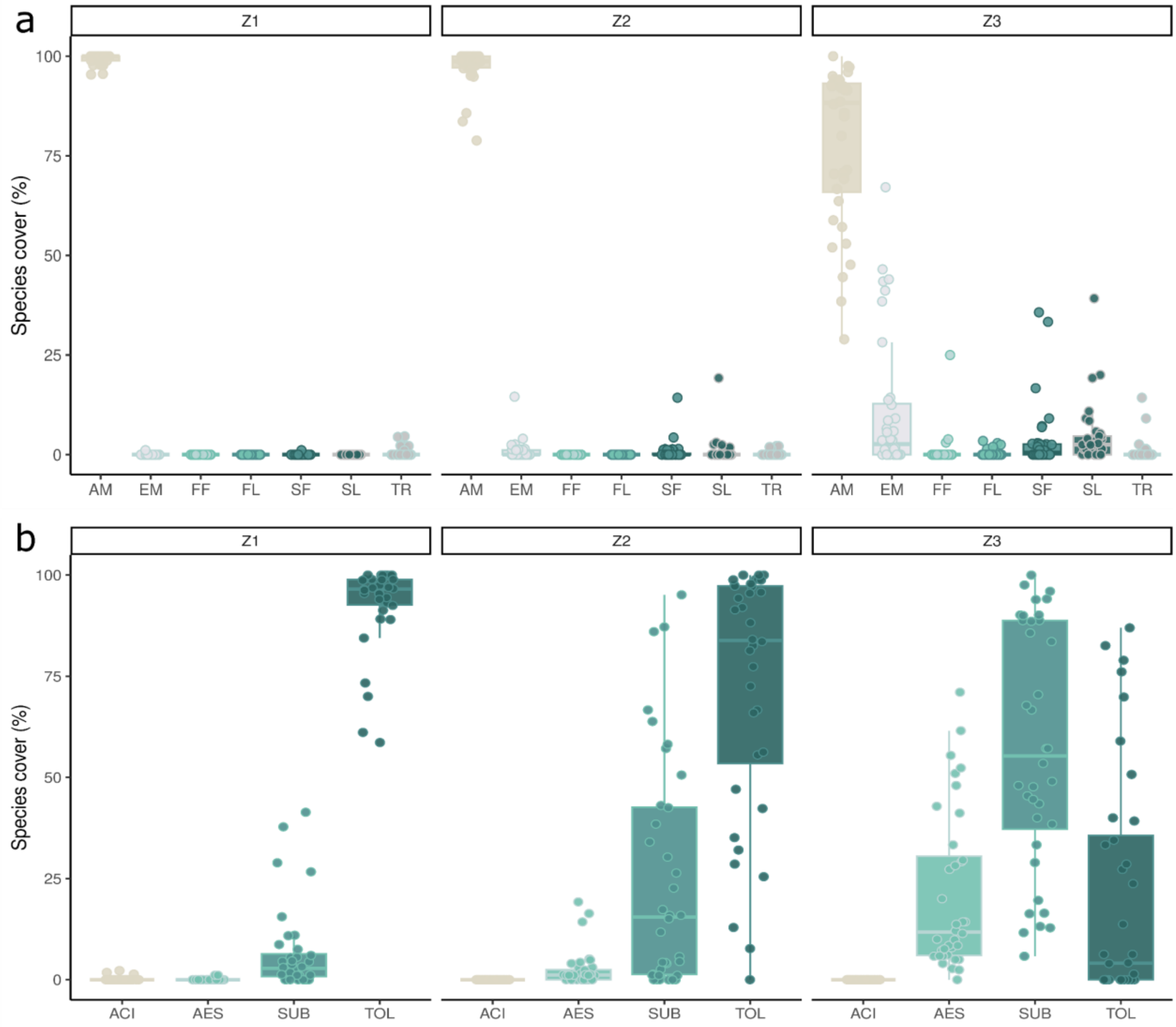

Fig. 6 Boxplots of the relative coverage of species by life forms (**a**) and eco-physiological classification (**b**) in each water depth zone. Z1 - floodable zone; Z2 - water-land interface zone; Z3 - water body zone; A - AM-amphibious; CL - climber; EM - emergent; FF - free floating; FS - free submerged; RF - rooted floating; RS - rooted submerged; B - ACC - accidental, SAQ - strictly aquatic, SUB - subaquatic, TOL - tolerant

Discussion

Our study clearly indicates that species and life forms are preferentially distributed along the depth gradient. We identified clear zonation patterns along the evaluated water depth gradient, characterized by species occurrences restricted to specific portions of the gradient, and variations in species cover along it. The extremes of the gradient (zones 1 and 3) differed considerably from each other in terms of species composition, supporting our initial hypothesis. Given the notable discrepancies in environmental conditions, we expected to find species exclusive to each area, as observed by Noleto et al. (2019), where zones further along the water depth gradient exhibited heterogeneous compositions, with the intermediate region resembling the deeper end. In our study, the intermediate zone (zone 2) appeared similar to the neighboring zones (zones 1 and 3). Only the climber *Vigna longifolia* was recorded as exclusive to zone 2. Occurring rarely, in terms of eco-physiological adaptation, it was classified as tolerant. Although infrequent in the study area, the species is common to coastal environments, especially near watercourses (Snak et al. 2011) and is listed in checklists of aquatic plants for southern Brazil (Oliveira et al. 2019). It also occurs in other environments, such as rupestrian grasslands (Silveira and Miotto 2013) and thus is not a species restricted to waterlogged areas.

The species present in zone 2, in general, showed higher cover in zones 1 and 3 and are mostly amphibious. *Bacopa monnieri* was the only species with greater cover in zone 2, indicating a preference for the water-land interface zone. Irgang and Gastal Jr. (1996) highlight its presence in the coastal region of southern Brazil, with frequent occurrences as an amphibious plant in lagoons or waterlogged areas. In general, variations in cover indicate the existence of preferential zones in the gradient, which is related to the species degree of adaptation to flooding and reflects the ecological niche characteristics of each taxon (Alves et al. 2011; Roznere and Titus 2017; Noleto et al. 2019). However, zonation is not only a physiological but also an ecological and highly complex phenomenon, as species interactions may play a crucial role in the observed distribution (Keddy 2010). Thus, by relating the depth gradient to the distribution and species composition along the flooding gradient, we can observe differences in the effective niche width of each species in the community (Ferreira et al. 2010).

The partitioning of beta diversity revealed that species turnover was responsible for the largest part of the observed variation in species composition along the flooding gradient, both between zones and within each zone. Values were similar across the entire gradient, with the highest turnover value (dissimilarity) for the entire gradient. Within zones, the contribution of nestedness was slightly higher. Overall, higher environmental heterogeneity thus corresponded to higher turnover values. As evidenced by Boschilia et al. (2016), environmental gradients tend to segregate species based on physiological tolerance, and beta diversity can be influenced by environmental factors acting on niche differentiation, combined with the temporal and spatial structures of the landscape. Fu et al. (2021) emphasize that, at a small scale, local environmental conditions have a greater impact on species turnover, exerting a strong filtering pressure on species, while at larger scales, spatial processes, such as dispersal limitation, become more important in determining composition, potentially contributing to a greater relative importance of nestedness as opposed to species turnover.

Variation in the mean water depth explained only 11% of plant community composition along the flooding gradient. However, associated to this gradient, several physicochemical factors that we did not measure, such as light, nutrient availability, and substrate particle size, show significant variation over short distances (Keddy 1983; Lewerentz et al. 2021). Evaluating these abiotic variables in conjunction with water depth can enhance the understanding of the underlying processes of species distribution, as demonstrated by other studies (Ferreira 2005; Rolon et al. 2008; Gillard et al. 2020; Lewerentz et al. 2021), as well as biotic variables, such as competition (Murillo 2018). In future studies in the wetlands in our region it seems interesting to include these factors to contribute to a better understanding of the underlying mechanisms of community assembly.

Concerning life forms, we observe a prevalence of amphibious plants, a pattern commonly found in studies that do not restrict sampling to strictly aquatic plants (Matias et al. 2003; Paz and Bove 2007; Alves et al. 2011; Kafer et al. 2011; Rolon et al., 2011; Sabino et al. 2015). According to Schneider et al. (2018), amphibious plants, along with emergents, exhibit advantages in resource acquisition compared to other life forms because, as they are emerged and rooted in the soil, they are able to capture light and nutrients more easily. We recorded amphibious plants along the entire gradient, indicating their ability to thrive both in flooded areas and outside of water (Pott and Pott 2000). Within this category, we observed significant variation in moisture and water requirements and tolerances, ranging from terrestrial plants that usually occur in non-flooded environments to those that cannot survive extended periods outside of water. The coexistence of species with varying degrees of adaptation to water stress is favored in environments where water levels frequently fluctuate (Preston and Croft 1997; Maltchik et al. 2007). This results in the registration, in the transition region between terrestrial and aquatic environments, of plants that grow to varying degrees in both wet and non-wet areas (Tiner 1991).

Tolerant amphibious and subaquatic plants were present across the entire gradient, with tolerant species predominating in zones 1 and 2, while subaquatic species had higher cover in zone 3. Tolerant plants may exhibit varying preferences for moist environments. For instance, *Centella asiatica* is frequently found in wetlands (Rolon et al. 2011) and also in other habitats such as grasslands, urban lawns, vacant lots, and forest edges (Lorenzi 2008; Souza and Lorenzi 2019, Schenckel et al. 2023). On the other hand, *Panicum aquaticum* predominantly occurs in moist areas and occasionally in drier and higher areas, as well as in disturbed locations like road edges and vacant lots in coastal regions (Flora e Funga do Brasil 2023). Subaquatic amphibious plants are more specialized to the aquatic environment, as is the case with *Nymphoides humboldtiana*, an aquatic herb that can tolerate short periods in water-saturated soils but does not thrive in completely drained soils (Irgang and Gastal Jr. 1996; Amaral et al. 2008).

Accidental amphibians - *Baccharis dracunculifolia*, *Senecio madagascariensis*, and *Solanum* sp. - were found exclusively in zone 1. *Baccharis dracunculifolia* and *S. madagascariensis* are considered ruderals (*S. madagascariensis* also invasive), with a high capacity for dispersion and environmental adaptation (Matzenbacher and Schneider 2008; Plá 2013). Both are also common in native or degraded grasslands without any periods of flooding. These species exhibited extremely low cover, with rare individuals in a poorly developed vegetative stage, indicating that the environmental conditions, with high humidity, are not favorable. *Solanum* was not identified at the species level; however, we did not find adult individuals nearby, which we consider indicative of the species accidental presence in the environment. In general, Ferreira et al. (2017) refer to normally terrestrial plants present on the margins of wetlands as 'occasional amphibians,' while Paz and Bove (2007) use the term 'tolerant.' Both authors emphasize that the presence of these plants in wetlands is determined by the time the water level is low, triggered by an occasional advance of vegetation during dry periods. The presence of such species does not indicate dependence but rather tolerance to flooding for a short period (Paz and Bove 2007). The susceptibility of zone 1 to water level fluctuations was also demonstrated by the presence of some individuals of *Myriophyllum aquaticum* and *Mayaca sellowiana*. These species are strictly aquatic, and their presence in zone 1 is likely due to recurrent hydrological fluctuations in water level.

With the increase in water depth, we observed the emergence of other life forms and a slight decrease in the relative coverage of amphibious plants. In zone 3, we recorded the occurrence of all inventoried life forms and an increase in the coverage of submerged plants. Regarding submerged plants, they are considered the most sensitive to aquatic environmental conditions, requiring high water transparency and low nutrient concentrations (Moura and Henry-Silva 2018; Schneider et al. 2018). The redundancy analysis concordantly associated the fixed submerged species *M. aquaticum* with the presence of water surface. In general, the distribution of life forms demonstrated the typical margin-center zonation pattern, as previously described by other authors, with amphibious and emergent plants at the margin, submerged plants in deeper areas, and other types such as floaters distributed between the extremes (Scremin-Dias et al. 1999; Thomaz and Esteves 2011).

Contrary to our initial hypothesis that species richness should decrease with increasing water level, we did not observe a significant decrease along the gradient. This result differs from other studies reporting species loss with increasing water depth (Matias et al. 2003; Bando et al. 2015; Noleto et al. 2019; Roznere and Titus 2017). Aquatic plants typically predominate in shallow coastal habitats (Vestergaard and Sand-Jensen 2000), which are more heterogeneous compared to deeper zones (Alves et al. 2011). This is often associated with higher diversity, as greater niche diversity tends to result in higher species diversity (Ricklefs, 2010; Alves et al. 2011). Additionally, the water-land interface is a less selective environment, allowing for the occurrence of plants less specialized for aquatic life (Thomaz and Esteves 2011). A reason for our result is that we investigated a rather short gradient (6 m distance), unlike the studies mentioned above (e.g. 25 m in Noleto et al. 2019), and focused on the transition zone between terrestrial and aquatic environments, i.e., we did not explore deeper areas (maximum depth of 89.6 cm). Therefore, the range covered may have been insufficient to detect a reduction in richness along the gradient.

Our study demonstrated that the transition region between terrestrial and aquatic environments in wetlands supports a high number of species and life forms, and their spatial distribution is not random, but forms notable zonation patterns along the flooding gradient The amphibian life form showed a greater number of species, and higher relative cover than other life forms, as well as a broad distribution across the flood gradient. This is indicative of their broad ecological amplitude: they are adapted to tolerate both drought and periodic flooding. Our study highlights that plants inhabiting high-humidity environments represent an adaptive continuum, and even though categories are established, they are not discrete. Considering that wetlands are conservation priorities, and understanding species distribution patterns can assist in establishing the boundaries of these ecosystems and provide support for the development of conservation and restoration strategies. Future studies should focus on the dynamics along the flooding gradient over time. This is especially relevant in the context of global changes, with an increase of extreme events, including both dry and wet periods, which will affect biotic and abiotic characteristics in wetlands and require attention in conservation.

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Captions of Electronic supplementary material

Fig. S1 Schematic illustration of the allocation of sample units in a wetland. Z1 - floodable zone; Z2 - water-land interface zone; Z3 - water body zone

Fig. S2 Bar chart of the average relative cover of species per water depth zone. Legend: Z1 - floodable zone; Z2 - water-land interface zone; Z3 - water body zone

Fig. S3 Boxplot of the mean water depth (MWD) in different zones. Legend: Z1 - floodable zone; Z2 - water-land interface zone; Z3 - water body zone

Fig. S4 Simple linear regression of species richness in relation to the mean water depth (MWD). $R^2 = 0.0097$, p-value = 0.3101

Table S1 List of species occurring in wetland sampled at Lagoa do Peixe National Park with their respective life forms (LF) and eco-physiological classification (EPC). Life Forms: A - AM- amphibious; CL - climber; EM - emergent; FF - free floating; FS - free submerged; RF - rooted floating; RS - rooted submerged; eco-physiological classification (EPC): ACC - accidental, SAQ - strictly aquatic, SUB - subaquatic, TOL - tolerant

Table S2 List of species restricted and shared among zones with their respective life forms (LF) and eco-physiological classification (EPC). Life Forms: AM- amphibious; CL - climber; EM - emergent; FF - free floating; FS - free submerged; RF - rooted floating; RS - rooted submerged; eco-physiological classification (EPC): ACC - accidental, SAQ - strictly aquatic, SUB - subaquatic, TOL - tolerant

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