SOIL SEED BANK IN PANTANAL RIPARIAN FOREST: PERSISTENCE, ABUNDANCE, FUNCTIONAL DIVERSITY AND COMPOSITION

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Abstract: The soil seed bank is a regeneration strategy for most plant species in wetlands such as the Pantanal. Soil depth is an indicator of seed bank persistence. Therefore, our objective was to assess the species composition potentially persistent in the soil seed bank, and verify the effect of depth on seed bank abundance, diversity and functional composition. We collected 40 samples (10 x 10 x 5 cm) at four depths: 0-5, 5-10, 10-15 and 15-20 cm, in ten areas along the Paraguay River (N = 10/depth). We placed the samples in trays in the greenhouse, and recorded the seedlings emergence for three months. We found 44 species from 16 families. Most species are perennial, autochoric and hydrochoric, graminoid and herbaceous, with vegetative propagation via basal regrowth. The abundance, species and functional richness decreased with increased depth. We did not find differences in species and functional composition between depths. The species share traits both related to regeneration and persistence niches in different soil layers, which indicates similarity in the functions executed by the community over a 0-20 cm depth soil profile. Species with potentially persistent seed bank also have several functional traits that allow the long-term persistence of individuals in the community, such as vegetative propagation, which confers a high potential for plant community resilience.

Keywords: flood; functional richness; regeneration niche; seed ecology; wetland.

INTRODUCTION

Floodplains such as the Pantanal are dynamic environments, whereby vegetation types are structured mainly by seasonal flood (Damasceno-Junior *et al.* 2005, Catian *et al.* 2018) and fire (Arruda *et al.* 2016). To overcome such environmental filters, plants have different strategies related to persistence (Bond & Midgley 2001) and regeneration niches (Grubb 1977). Strategies linked to the regeneration niche, such as the persistent soil seed bank, represents a characteristic of several species in areas under seasonal flooding and have the potential to regenerate the community in ecosystems under strong seasonality or after unpredictable disturbances (Brock 2011, Bao *et al.* 2014, Souza *et al.* 2016).

The soil depth can indicate the degree of seed longevity in the seed bank (Bekker *et al.* 1998). The burial prevents the incidence of luminosity, which can keep the seeds in a quiescent or dormant state, preventing germination (Baskin & Baskin 1983). Sediment deposition may bury seeds just dispersed and soil erosion may bring up seeds stored for long periods in the soil. This dynamic can influence the patterns of the species composition, diversity and

abundance in different soil depths. These vertical distributions in the concave river banks and convex river bars may be highly variable, however, in floodplains, they have a pattern of reduction in richness and diversity with increasing depth (O'Donnell *et al.* 2014). Such vertical distribution of the soil seed bank can affect the reestablishment of the vegetation (Goodson *et al.* 2001).

Little attention has been given to the stratification of the soil seed bank in Pantanal (Oliveira *et al.* 2015). Besides, we found no previous studies on stratification of the soil seed bank in the Pantanal riparian forests. Some studies have approached mainly effects of floods on the composition and diversity and spatial distribution (Oliveira *et al.* 2015, Bao *et al.* 2018). Understanding the diversity and abundance of seed banks in deeper soil layers can give a better estimate of the regenerative potential of the soil seed bank in riparian forests, since deeper layers with potential high seed diversity can be overlooked sampling just the soil surface (O'Donnell *et al.* 2014, Oliveira *et al.* 2015). Seeds deeply buried might have an important role to play in the determination of the resilience of the community (Goodson *et al.* 2001).

Seeds must remain viable and not germinate for a sufficient period of time until they are buried to reach the deeper layers (Leck 1989). The duration that seeds can stay in the deeper layers depends on their longevity. The upper soil layers tend to have higher abundance and diversity than deeper layers due to the constant input of seeds into riparian areas (O'Donnell *et al.* 2014). Likewise, due to the smaller number of species, functional diversity also tends to decrease with depth (Petchey & Gaston 2002). Species composition, as well as functional composition, should vary between soil layers due to seed physiological differences among species, which determine the persistence capacity and thus, the residence time of each species in the soil (Long *et al.* 2015).

Considering that soil depth is an indicator of persistence of the seed bank, our objective was to verify the composition of species potentially persistent in the soil seed bank and verify the effect of depth on composition, diversity and abundance of the seed bank. Therefore, we tested the following hypotheses: i) abundance, functional diversity and species diversity decrease with soil depth: ii) the functional and the species composition vary between soil depths, with higher abundance of functional traits linked to persistence niche in the shallower layers.

MATERIAL AND METHODS

Study area

The Pantanal is a large wetland situated in the center of South America, influenced by coalescence of the Paraguay River and its affluents. Sampling was carried out in ten sites along a stretch of 80 km of the Paraguay River between the coordinates 19°31'23.97" S 57°6'1.9" W and 19°41'38" S 56°59'56.4" W, in the municipality of Corumbá, state of Mato Grosso do Sul, Brazil. The minimum and maximum distance between two adjacent sites were 4.2 and 12.1 km, respectively. This floodplain has sandy-loamy to clayey Gleysol, eutrophic or dystrophic and aluminic (Fernandes *et al.* 2007). The climate of Corumbá is Awa, *i.e.*, tropical megathermic, with a mean annual rainfall of 1100 mm, and an average annual temperature of 21-31°C (Soriano 1997). The Paraguay River riparian forest is composed primarily of alluvial seasonal semi-deciduous forest (Damasceno-Junior *et al.* 2005, Arruda *et al.* 2016).

Data collection

We standardized our collections in riparian forest environments, which occurred at the convex banks of the meanders (deposition zones) subject to similar flood regimes, so sediment deposition is expected to be similar. In each site, we collected one sample 10 cm (length) x 5 cm (width) x 5 cm (depth) for each depth (0-5; 5-10; 10-15 and 15-20 cm), at 20 m from the river margin, totaling 10 samples for each depth. The surface layer included the litter. We stored the samples in plastic bags. The species composition and abundance of the seed bank were estimated through of seedling emergence (Thompson *et al.* 1997). Two days after the collecting, we spread the soil samples into 30 x 20 x 6 cm plastic trays, perforated at the bottom, over a 3 cm layer of sterile sand for better drainage. We placed the trays in the greenhouse with ambient temperature, screened to 30% shade and irrigated twice a day. We recorded the seedling emergence for three months until there was no emergence of seedlings in the subsequent days. Unidentified seedlings were transplanted for later identification and added to the counts.

Functional traits

We chose five functional traits representing the capacity of establishment, persistence and regeneration (habit, life cycle, dispersal syndrome, vegetative propagation and life form). We determined the attributes of functional traits utilizing field observation and information from the literature (Pott & Pott 1994, Kissmann 1997, Kissmann & Groth 1999, 2000, Pott & Pott 2000, Lorenzi 2008). When the same species presented more than one attribute within the same trait, prevailed the most evident. In a few species, it was not possible to select just a single attribute, so we adopted two.

Analyses of data

We calculated the functional diversity utilizing the function dbFD of the package FD (Laliberté & Legendre 2010). We used the metrics of functional richness (FRic), functional dispersion (FDis) and functional evenness (FEve). Due to the variables here analyzed being categorical, the FRic was measured as the number of unique trait combinations, not as the minimum volume of the convex hull (Laliberté & Legendre 2010). For the functional composition analysis, we utilized the community-weighted trait means (CWM) of the functional traits, also implemented in the function dbFD (Laliberté & Legendre 2010). The measure of the CWM represents the mean values of each trait of all species present in the community pondered by their relative abundances (Ricotta & Moretti 2011).

We tested the variation of species composition and functional composition between depths applying an analysis of similarity (ANOSIM) with 1000 permutations, utilizing the dissimilarity index of Jaccard on the matrix of presence and absence of species. For better visualization of the species distribution in the depths, we constructed a histogram of the distribution of species abundance between depths. We tested the variation in abundance, FRic and value of each functional trait between depths with a generalized linear model (GLM) and Poisson distribution using the glm function. For the other metrics of functional diversity (FDis and FEve), we utilized Gaussian distribution with the log link function. For the multiple comparisons (Pairwise) between depths, we made post-test of least-square means (LSM) with Bonferroni adjustment, employing the lsmeans function of the package emmeans (Lenth 2016).

To analyze the species diversity we utilized the method of Hill numbers (Chao *et al.* 2014), whereby rarefaction curves combine interpolation (rarefaction) and extrapolation (prediction). This allows simulating larger samples, increasing the degree of comparability, where the overlap of the confidence intervals at 95% can be interpreted as a lack of significant differences (Chao *et al.* 2014). Hill numbers integrate species richness and conversion of the indices of Shannon (H) and Simpson (D). They are represented by different orders of q, of which: $q = 0$ represents the species richness (S) and ignores the abundance, $q = 1$ represents the exponential of the Shannon index [exp(H)], gives more weight to the rare species, and $q = 2$ the inverse of the concentration index of Simpson [$1/(1-D)$], which gives less weight to rare species (Jost 2006). These analyses were performed with the package iNEXT and the function iNEXT (Hsieh *et al.* 2016). We run all analyses in the R statistical programming environment (R Core Team 2018).

RESULTS

Species and functional composition

Fifteen species occurred exclusively in the 0-5 cm layer, other 11 species occurred exclusively at 5-10 cm and another two at 10-15 cm. In the deepest layer (15-20 cm), eight species occurred. Nevertheless, they all also occurred in the other depths (Figure 1). There was no significant variation in the species composition (ANOSIM: $R = 0.01$; $p = 0.4$) and functional composition (ANOSIM: $R = -0.15$; $p = 0.9$) between depths.

Regarding functional traits, only basal resprouting varied between depths ($F_{3,28} = 4.4$; $p = 0.01$), being higher at the depth of 0-5 than in 15-20 cm (LSM: z-ratio = 3.62; $p = 0.002$). The traits with higher expressivity were perennial life cycle, autochorous and hydrochorous dispersal, vegetative propagation via basal resprouting and graminoid and herbaceous habits. The distribution of the values of the most functional traits among depths was approximately homogeneous (Figure 2).
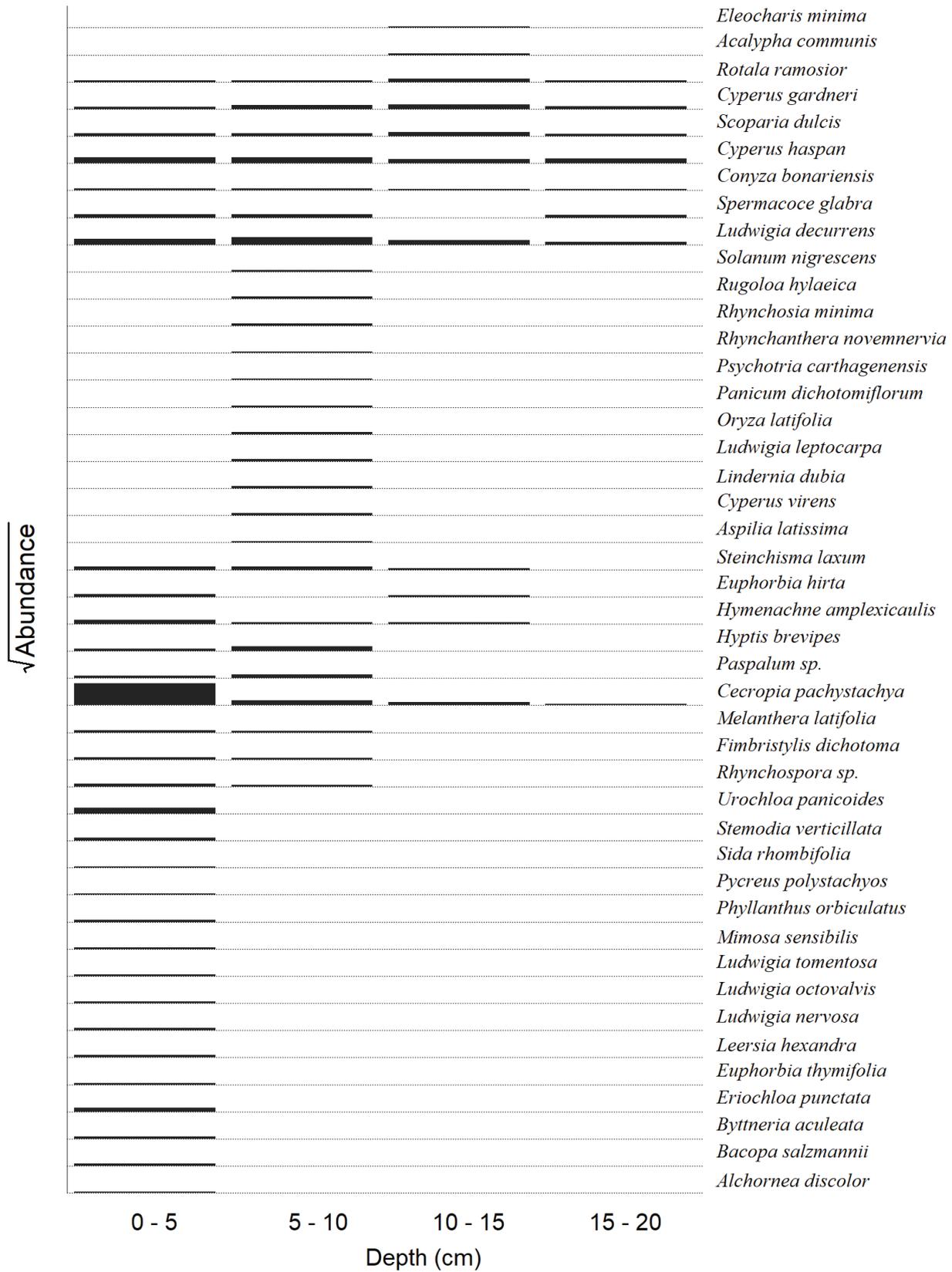
Figure 1. Distribution of the seed bank abundance in the soil depth gradient in a riparian forest of the Pantanal Neotropical floodplain, Brazil. The bar heights are proportional to the square root of abundance.

Abundance

The abundance decreases with increased depth ($F = 8.15_{3,36}$; $p < 0.001$), with 297 (475.2 seeds/m²), 103 (164.8 seeds/m²), 45 (72 seeds/m²) and 23 (36.8 seeds/m²) individuals at soil depths of 0-5; 5-10;10-15 and 15-20 cm, respectively. The differences of abundance were significant between depths of 0-5 and 10-15 (z-ratio = 3.8; p = 0.0007), 0-5 and 15-20 (z-ratio = 5.2; p < 0.0001) and 5-10 and 15-20 (z-ratio = 2.98; p = 0.02) (Figure 3a). Thus, for abundance there was no difference between two adjacent depths. The total abundance was 468 seedlings. *Cecropia pachystachya* (Rosales, Urticaceae) was the most abundant species (190 individuals), especially in 0-5 cm, with 160 individuals (Appendix 1).

Functional diversity

The functional richness (FRic) varied between depths ($F = 5.8_{3,28}$; p = 0.003), with significant difference only between 0-5 and 10-15 (LSM: z-ratio = 2.7; p = 0.04) and between 0-5 and 15-20 cm (LSM: z-ratio = 3.6; p = 0.002) (Figure 3b). There was no variation in functional evenness (FEve) and functional dispersion (FDis) between depths (Figures 3c and 3d, respectively).

Species diversity

We recorded 44 species of 16 families. The species richness varied between depths, 33 species occurred at 0-5 cm, 28 species at 5-10 cm, 13 species at 10-15 cm and nine species at 15-20 cm (Appendix 1). For the values q = 0 and q = 1 of Hill Number we observed that the depth 0-5 and 5-10 were significantly higher than 10-15 and 15-20 cm (Figure 4). However, there were no differences between the soil depths of 0-5 and 5-10, and between the soil depths of 10-15 and 15-20 cm. In the value q = 2, there was an overlap in the confidence intervals between the soil depths of 5-10 and 10-15 cm. Thus, the inverse index of Simpson (q = 2) did not show differences between two adjacent depths (Figure 4).

DISCUSSION

Species and functional composition

Changes in composition due to depth are supported in the literature (Godefroid *et al.* 2006, Boudell & Stromberg 2008, O'Donnell *et al.* 2014). Nevertheless, we did not find significant differences in functional and species composition between depths. Most species present only near the surface
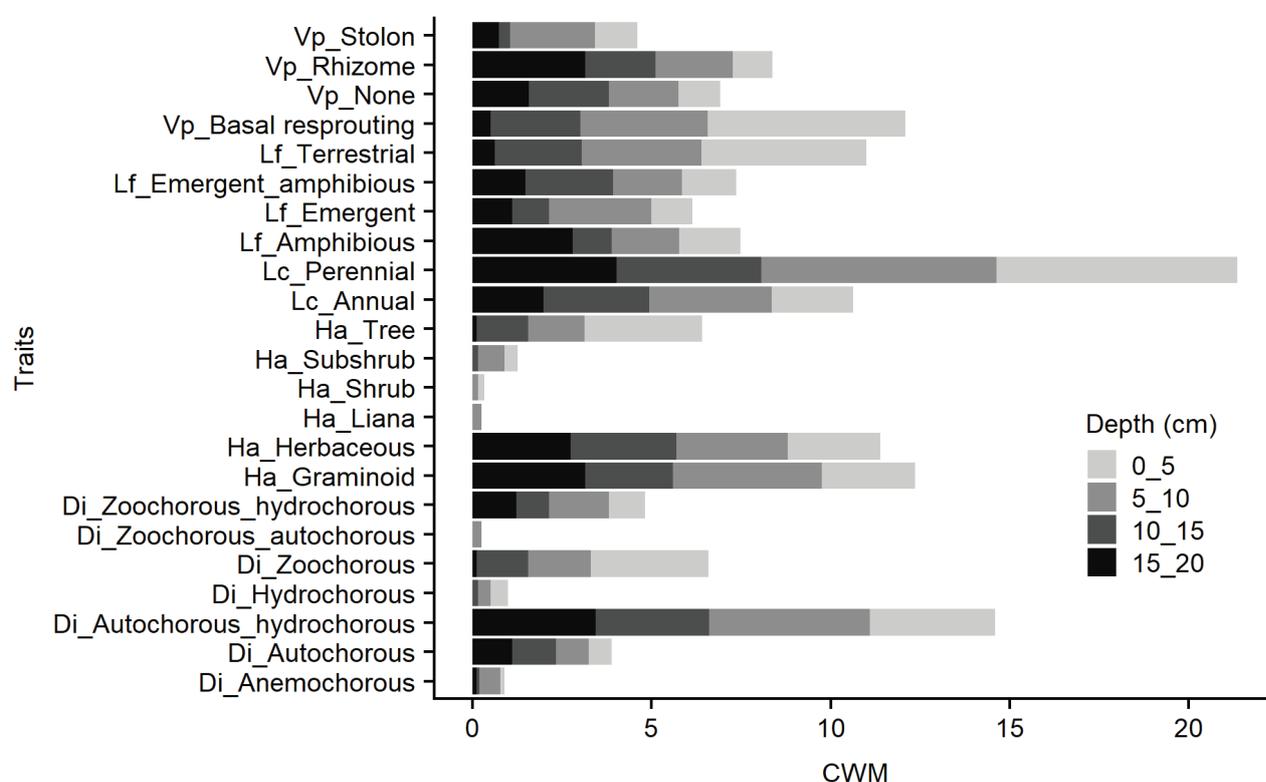

Figure 2. Values of the community-weighted trait means (CWM) of the soil seed bank in the depth gradient in Neotropical riparian forest of the Pantanal floodplain, Brazil. Vp = vegetative propagation; None = without vegetative propagation; Lf = Life form; Lc = life cycle; Ha = habit; Di = dispersal.
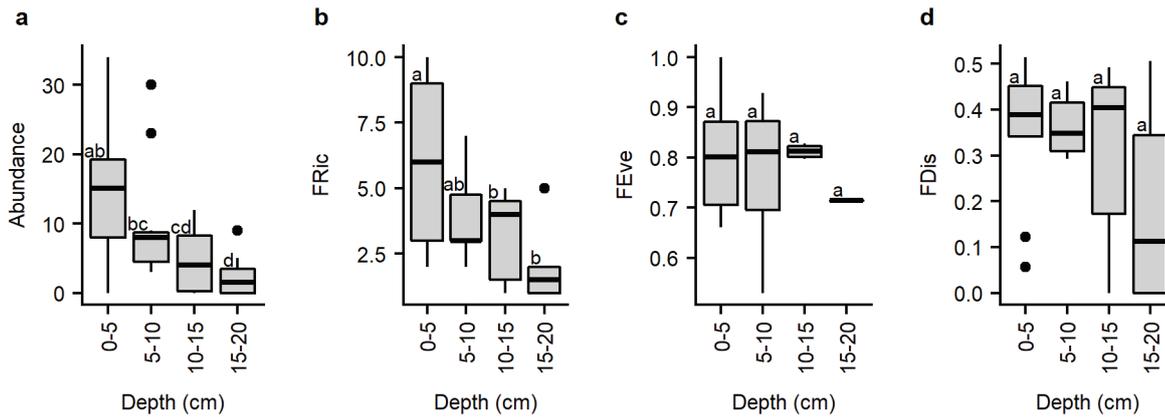
Figure 3. Boxplot of abundance (**a**) and functional diversity (**b**, **c**, **d**) of the soil seed bank in riparian forest of the Pantanal floodplain, Brazil. Boxes = second and third quartile, horizontal line = median; vertical line = first and fourth quartiles; points = outliers.
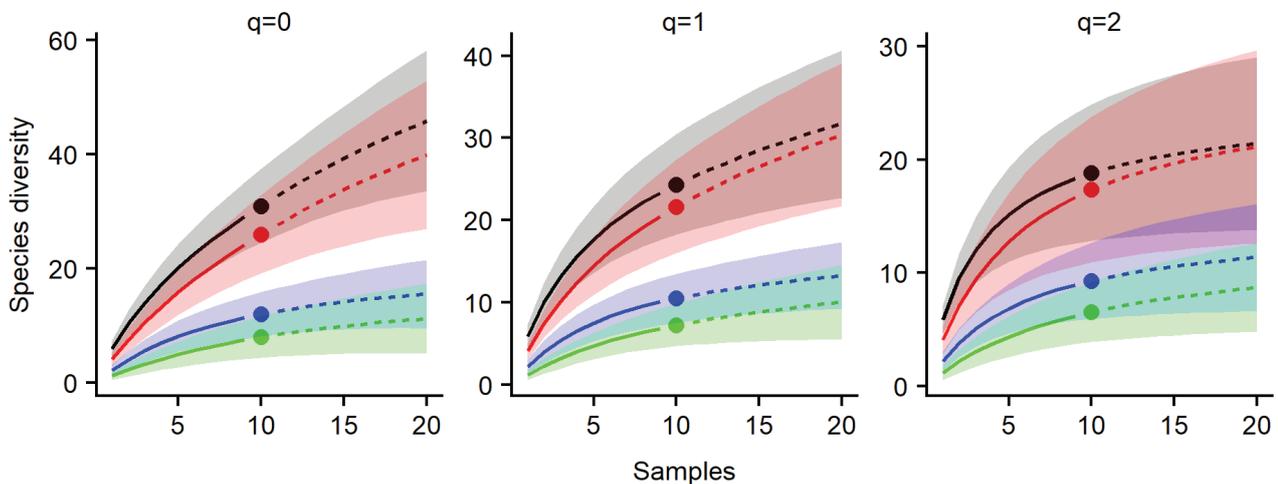

Figure 4. Sample-based rarefaction for Hill Numbers (q = 0, q = 1 and q = 2) of seed bank diversity in riparian forest of the Pantanal floodplain, Brazil. Full line = interpolation, dashed line = extrapolation up to double number of samples. Black line = 0-5 cm depth, red line = 5-10 cm depth, blue line = 10-15 cm depth and green line = 15-20 cm. Shaded area = 95% confidence interval.

can be potentially less capable of regenerating after flood or fire. Species occurring at deeper soils and over the entire profile, such as *C. pachystachya*, *Rotala ramosior* (Myrtales, Lythraceae), *Cyperus gardneri* (Poales, Cyperaceae), *Cyperus haspan*, *Scoparia dulcis* (Lamiales, Plantaginaceae), *Conyza bonariensis* (Asterales, Asteraceae), *Spermacoce glabra* (Gentianales, Rubiaceae) and *Ludwigia decurrens* (Myrtales, Onagraceae), can have important role in the resilience of the community, regenerating post-flood probably due to their higher persistence and to the continuous and numerous seeds production (Brock 2011). We can also consider the species *Steinchisma laxum* (Poales, Poaceae), *Euphorbia hirta* (Malpighiales, Euphorbiaceae), *Eleocharis minima* (Poales, Cyperaceae), *Acalypha*

communis (Malpighiales, Euphorbiaceae) and *Hymenachne amplexicaulis* (Poales, Poaceae), that occurred along the soil profile of 0-15 cm, also demonstrating some persistence in the soil seed bank. It is important to note that seeds of species found in deeper layers may not become available due to the lack of sediment removal (Beas *et al.* 2013). However, this indicates which species may be kept longer in the soil. For example, finding a species in a deep layer indicates that if it has seeds in superficial layers it is more likely to germinate after a long period if these seeds are not buried in depths that prevent germination.

We can consider that the species mentioned above with potentially persistent seed bank have divergent functional traits. For instance, *R. ramosior*

can produce hundreds of seeds per individual and requires water level fluctuations to complete its life cycle, with flowering and seed dispersal when the water recedes (Pott & Pott 2000), what provides the necessary conditions for germination (Souza *et al.* 2016). Other species also have traits related to aquatic environments such as emergent and amphibious habits (*C. gardneri, C. haspan, S. glabra* and *L. decurrens*). Nonetheless, some possess opposite traits such as terrestrial life form and differ in dispersal syndrome (Appendix 1). This trait variability imposes flexibility at community level under several situations, especially in pluriannual cycles

Although a major part of the species with potentially persistent seed bank is annual (Capon & Brock 2006), we found that 66% of the species occurring between 10 and 20 cm were classified as perennial, this being the most expressive functional trait (Figure 2). Among them are *C. pachystachya, C. haspan, H. amplexicaulis, S. glabra* and *S. laxum*. Besides a potentially persistent seed bank, which can be considered one of the main regeneration strategies (Rosbakh *et al.* 2018), our result indicates that most of these species have additional persistence niche strategies such as stolon, rhizome and basal resprouting. These strategies provide them higher capacity to persist in the community or to regenerate after rare events, such as long periods of drought or extreme floods (Capon & Brock 2006). One result that supports the evidence of flexibility in maintenance and regeneration of the vegetation is the lack of difference in functional composition between depths, with species sharing similar traits related to regeneration and persistence niches in different soil layers.

Abundance

Our results support the hypothesis that significant changes in species abundance occurred at least every 10 cm depth. This indicates that most seeds can stay viable during the time required to accumulate up to 10 cm of sediment on the margins of the Paraguay River. One hypothesis to explain the lower seed density in the deeper layers could be the germination or the loss of seed viability due to a longer time of storage in the soil (Thompson *et al.* 1997, Brock 2011). High intensity-floods can cause increased rates of sedimentation and erosion (Andrade *et al.* 2013), what influences the

stratification of the seed bank in the soil (O'Donnell *et al.* 2014). Carvalho *et al.* (2005) demonstrated that generally in the upper Paraguay River, the sediment deposition could vary between 0.062 and 0.33 mm a year, reaching a maximum rate of 8.26 mm year^{-1} in some places. In 1995 after an exceptional flood, depositions of up to 5 cm of sediment were observed in the Paraguay River (G. A. Damasceno-Junior, personal communication). Although, if we consider the deposition of 0.33 mm/year reported by Carvalho *et al.* (2005), each 5 cm layer of our sampling will correspond to 15 years. Therefore, a 20 cm of soil layer could represent to up to 60 years of deposition. The survival of these seeds in the soil for such a long time can ensure high resilience to the community.

In grasslands, the sediment deposition is slower, so the seed bank is more superficial, with the number of viable seeds decreasing more rapidly with increased depth due to the mortality over time (Goodson *et al.* 2001, Oliveira *et al.* 2015). On the other hand, the fast deposition of sediments in the riparian forests of the Paraguay River can explain why even non-persistent seeds can appear in deeper layers. However, the margins can be more prone to erosion depending on the intensity of floods and on the position and shape of the margins (Andrade *et al.* 2013). In spite of general pattern of abundance reduction with increased depth reported in the literature, some works in wetlands did not find this pattern in the distribution of seeds along depths up to 10 cm (Berge & Hestmark 1997, Abernethy & Willby 1999), agreeing with our result of difference only every 10 cm layer in relation to soil depths.

Functional diversity

The functional richness was highest in the soil depth 0-5 cm compared with 10-15 and 15-20 cm soil depths, which implies in a higher amplitude of niche of the community present in the superficial layers. The number of species can influence FRic. So, the seeds in the topsoil, besides maintaining the species diversity, also maintains the reserve richer in functional attributes than the deeper layers. One of the factors contributing to such difference is the occurrence of species with either regenerative or persistence niche traits in the top layer. Another factor is the occurrence of annual species with a persistent seed bank as much in surface soil as deeper, what differs from species with a transitory

bank, generally restricted to the surface (Bekker *et al.* 1998). That also was noticed in our work with annual species present almost in all layers.

The functional uniformity (FEve) did not vary between depths. That indicates that the distribution of the abundance of functional traits is similar between depths. This way, there is no difference in the degree of heterogeneity (or homogeneity) in the utilization of the niche space (Villéger *et al.* 2008). One of the consequences of such lack of difference of FEve between layers is that they can have similar levels of productivity and be under the same degree of susceptibility to the income of weedy species (Dukes 2001).

The FDis were not different between depths either. The similar values of FDis between layers indicate that the species are similarly dispersed in the multivariate space of the functional traits. In areas where the community is more stable, such as in forests, the effect of competition can be higher (Lohbeck *et al.* 2014). However, the opposite can occur in habitats with strong seasonal environmental filters, where the plant community is more prone to such filters than to competition (Lohbeck *et al.* 2014). Therefore, the smaller effect of competition in the plant communities of the Pantanal can occur due to the recurrence of seasonal floods and fire events (Arruda *et al.* 2016), that set the vegetation back to initial succession stages.

Therefore, we can infer that due to the presence of species functionally distinct in all layers, when these species are present in the vegetation the competition effect diminishes equally in relation to the influences of environmental filters. Thus, the community of the seed bank is similarly under strong environmental filters in all soil layers. This flexibility of the seed bank confers capacity for persistence (persistence niche; Bond & Midgley 2001) or regeneration (regeneration niche; Grubb 1977) of the community under the principal environmental filters in the Pantanal such as fire and flood.

Species diversity

The species diversity decreased with the increase of soil depth, supporting our hypothesis. We found higher diversity in the superficial soil layers (0-10 cm) than in the deeper layers (10-20 cm). Such a decline has been found in most studies on stratification of the soil seed bank in floodable areas (Bekker *et al.* 1998, O'Donnell *et al.* 2014). The higher

richness in more superficial soil layers can occur due to differences in seed persistence. Nevertheless, such as abundance, O'Donnell *et al.* (2014) found this pattern only in the floodplains, contrasting with more richness in deeper soil layers of river bar and banks. This pattern could be due to the lower sediment erosion rate on plains than on the river banks. However, in our results, the higher richness in the upper layer (0-5 cm) indicates that even when erosion occurs in the floodplain removing seeds from the surface, this removal would not exceed the amount of inputted seeds. This seed income and increase of the diversity could be caused mainly by hydrochory which facilitates long-distance dispersal (O'Donnell *et al.* 2014)

In addition, higher richness in the surface, as found in our work, allows most species in the seed bank to be readily available to regenerate the vegetation, needless sediment rotation for species supplementation. In a similar situation, in floodable grassland in the northern Pantanal, a study with the stratification of the seed bank in layers of 2 cm to 10 cm deep reported a higher species richness up to 4 cm depth without litter (Oliveira *et al.* 2015). When richness distribution has an inverse pattern, with lower richness in the upper layers, a typical situation of erosive environments, a smaller number of species would be available to regenerate the vegetation (Berge & Hestmark 1997, Abernethy & Willby 1999, O'Donnell *et al.* 2014).

Our work demonstrated that the superficial layers in Pantanal riparian forests might represent a more important demographic and genetic reservoir, increasing the probability of population regeneration after a disturbance or environmental stochasticity (flood or fire). The species that are likely to maintain a persistent seed bank also have several functional traits related to persistence niche, such as vegetative propagation, evidencing the important role of these species to community resilience. The species abundance and diversity, and functional richness are higher in the top soil layers. Thus, albeit the similarity in functionality, the superficial layers sustain higher abundance and richer reserve of functional attributes. Thereby, this 0-10 cm superficial layer can represent an essential reserve of seeds for the community, increasing the chances to face environmental variations. The lack of difference in functional and species composition indicates that the functions exerted by the community are similar

throughout the 0 to 20 cm depth, with species sharing traits related to both regeneration and persistence niches in different soil layers.

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Appendix 1. Species abundance and functional traits of the soil seed bank in Paraguay River, Pantanal riparian forest, Brazil. Ha = habit; Vp = vegetative propagation; Lf = Life form; Lc = life cycle; Di = dispersal; Te; terrestrial; Em = emergent; Am = amphibious; stol = stolon; rhiz = rhizome; None = without vegetative propagation; BR = basal resprouting; P = perennial; A = annual; Tr = tree; Ssh = subshrub; Sh = shrub; He = herbaceous; Gr = graminoid; Zo = zoochorous; Hy = hydrochorous; Au = autochorous; An = anemochorous. Depths = 0-5, 5-10, 10-15 and 15-20 cm.

Species	Ha	Lc	Di	Vp	Lf	0-5	5-10	10-15	15-20
Acalypha communis Müll. Arg.	Ssh	P	Au	BR	Te	0	0	1	0
Alchornea discolor Poepp.	Tr	P	Zo	BR	Te	1	0	0	0
Aspilia latissima Malme	Ssh	P	Au_Hy	BR	Am	0	1	0	0
Bacopa salzmannii (Benth.) Edwall	He	P	Au_Hy	St	Em	2	0	0	0
Byttneria aculeata Jacq.	Sh	P	Au_Hy	BR	Am	2	0	0	0
Cecropia pachystachya Trécul	Tr	P	Zo	BR	Te	190	9	4	1
Conyza bonariensis (L.) Cronquist	He	A	An	None	Te	2	2	1	1
Cyperus gardneri Nees	Gr	P	Au	Rh	Em	2	7	8	3
Cyperus haspan L.	Gr	P	Au_Hy	Rh	Am	14	14	8	9
Cyperus virens Michx.	Gr	P	Au_Hy	Rh	Am	0	3	0	0
Eleocharis minima Kunth	Gr	P	Au_Hy	St	Em_Am	0	0	1	0
Eriochloa punctata (L.) Ham.	Gr	A	Au_Hy	BR	Am	6	0	0	0
Euphorbia hirta L.	He	A_P	Au	BR	Te	3	0	1	0
Euphorbia thymifolia L.	He	A	Au	BR	Te	1	0	0	0
Fimbristylis dichotoma (L.) Vahl	Gr	P	Au_Hy	Rh	Am	2	1	0	0
Hymenachne amplexicaulis (Rudge) Nees	Gr	P	Hy	BR_St	Em	6	1	1	0
Hyptis brevipes Poit.	Ssh	A	Au_Hy	BR	Te	2	8	0	0
Leersia hexandra Sw.	Gr	P	Au_Hy	Rh_St	Em	3	0	0	0
Lindernia dubia (L.) Pennell	He	A_P	Au_Hy	St	Em	0	2	0	0
Ludwigia decurrens Walter	He	A	Zo_Hy	None	Em_Am	12	21	8	3
Ludwigia leptocarpa (Nutt.) H. Hara	He	P	Zo_Hy	BR	Em_Am	0	2	0	0
Ludwigia nervosa (Poir.) H. Hara	Ssh	P	Zo_Hy	BR	Em_Am	3	0	0	0
Ludwigia octovalvis (Jacq.) P.H. Raven	He	A	Au_Hy	None	Am	1	0	0	0
Ludwigia tomentosa (Cambess.) H. Hara	sh	P	Au_Hy	BR	Am	1	0	0	0
Melanthera latifolia (Gardner) Cabrera	Ssh	A	Au_Hy	None	Em_Am	2	1	0	0
Mimosa sensibilis Griseb.	Sh	P	Au	BR	Te	1	0	0	0
Oryza latifolia Desv.	Gr	A	Zo_Hy	St	Em	0	2	0	0
Panicum dichotomiflorum Michx.	Gr	A_P	Au_Hy	Rh	Em	0	1	0	0
Paspalum sp.	Gr	P	Au_Hy	St_Rh	Em	2	6	0	0

Appendix 1. ...Continued

Species	Ha	Lc	Di	Vp	Lf	0-5	5-10	10-15	15-20
Phyllanthus orbiculatus Rich.	He	P	Au	None	Te	2	0	0	0
Psychotria carthagenensis Jacq.	Sh	P	Zo	BR	Te	0	1	0	0
Pycreus polystachyos (Rottb.) P. Beauv.	Gr	P	Au_Hy	Rh	Am	1	0	0	0
Rhynchanthera novemnervia DC.	He_Ssh	P	Au_Hy	BR	Am	0	1	0	0
Rhynchosia minima (L.) DC.	Liana	P	Zo_Au	BR	Te	0	2	0	0
Rhynchospora sp.	Gr	P	Au_Hy	Rh	Em	4	1	0	0
Rotala ramosior (L.) Koehne	He	A	Au_Hy	None	Em_Am	1	1	5	1
Rugoloa hylaeica (Mez) Zuloaga	Gr	P	Au_Hy	St	Am	0	2	0	0
Scoparia dulcis L.	He	A	Au_Hy	BR	Te	4	4	6	2
Sida rhombifolia L.	He	P	Au	BR	Te	1	0	0	0
Solanum nigrescens M. Martens & Galeotti	Ssh	P	Zo_Hy	BR	Te	0	1	0	0
Spermacoce glabra Michx.	He	P	Au_Hy	St	Am	4	5	0	3
Steinchisma laxum (Sw.) Zuloaga	Gr	P	Au_Hy	St	Em_Am	5	4	1	0
Stemodia verticillata (Mill.) Hassl.	He	A_P	Au_Hy	BR	Am	4	0	0	0
Urochloa panicoides P. Beauv.	Gr	P	Au_Hy	St	Te	13	0	0	0