Effect of Flood Pulse on the Functional Diversity and Traits Composition of Birds With Different Degrees of Wetland Dependence in the Brazilian Pantanal

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TITLE PAGE

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Abstract: Hydrological dynamics of the Pantanal wetland drive the availability of resources and niche for aquatic and terrestrial fauna. We consider that changes in the hydrological regime of this floodplain can affect species richness, abundance and functional structure of waterbirds, wetland birds and non-wetland birds. Our study aimed to assess whether the degree of wetland dependence influences the response of bird groups to the flood pulse. We conducted the bird survey in the Paraguay River floodplain system, in five sampling sites, covering the periods of drought, flooding, full flood and ebb of the 2017–2018 hydrological cycle. Species richness and abundance were higher for non-wetland birds than waterbirds and wetland birds. On the other hand, we found that the higher the degree of wetland dependence by birds, the higher the differences in the functional-trait values. Species richness, abundance and all metrics of functional diversity varied significantly when there was an interaction between the degree of wetland dependence and the hydrological period. In all hydrological periods, bird groups occupied distinct niches. Traits such as foraging around or below the water surface were among the dominant functional traits in all hydrological periods. We emphasize the need to consider the functional traits of species in ecological studies of wetlands since measuring only species richness may not reflect the characteristics inherent to this type of ecosystem. In addition, the conservation of wetlands directly implies the maintenance of various niches throughout the hydrological periods, either for dependent or non-dependent bird species in wetlands.

Key words: Hydrological regimes, Floodplain, Freshwater, Functional richness, Seasonality, Waterbirds

1. INTRODUCTION

Inland wetlands formed by riverine floodplains are considered one of the most diverse and productive ecosystems in the world (Tockner and Stanford 2002), providing multiple regulating ecosystem services as well as economic and social benefits (Mitsch et al. 2015). Their relevance is recognized by the intergovernmental treaty of the Ramsar Convention (1971), which provides a framework for action to the sustainable use and conservation of wetlands of international importance (Ramsar sites). However, these areas have been widely devastated by human activities and climate change (Gupta et al. 2020), which negatively affects biodiversity in freshwater ecosystems (Albert et al. 2020).

The fluvial system of the Paraguay River in Brazil is one of the main contributors to the largest floodplain in the world, the Pantanal wetland. This system is characterized by annual and pluriannual hydrological regimes of the monomodal type, having a low amplitude and long duration, also known as flood pulse (Junk and Da Silva, 1996). Flood pulses are predictable disturbances that change the dynamics of floodplain communities, enabling the formation of a dynamic, complex and heterogeneous landscape (Junk et al. 1989; Miranda et al. 2018). Changes in hydrological conditions between the terrestrial and aquatic phases, with fluctuations in rainfall and accumulated water level, promote the input, output and lateral interaction of water, nutrients and organisms between rivers or lakes and connected flooded areas (Junk et al. 1989). The different hydrological periods (flooding, full flood, ebb and drought) (Lázaro et al. 2020) are fundamental for the formation of functional units (e.g., central channel, floodplain forest, oxbow lake, pond, swamp) that make up permanent or temporary aquatic habitats (Wantzen et al. 2005) and the various wetland macrohabitat types (Junk et al. 2014) that influence the availability of resources and niche for aquatic and terrestrial fauna (Figueira et al. 2011; de Deus et al. 2020a; de Deus et al. 2020b).

Recently, fires in the Brazilian Pantanal devastated about 30% of this ecosystem and gained worldwide repercussion due to the magnitude of vegetation devastation, extreme drought and animal deaths in protected and unprotected areas, which also affected the indigenous territories and traditional communities in the region (Libonati et al. 2020; Mega 2020). In addition, the landscape changes caused by “arc of native vegetation loss” at the surrounding floodplain plateau (Guerra et al. 2020), as well as the reduction in water mass and precipitation in recent years, can cause severe changes in biodiversity and ecological functions (Lázaro et al. 2020). Thus, it is imperative to understand the structure and dynamics of biological communities in the Brazilian Pantanal.

Birds play a fundamental role in wetlands by contributing to the flow of matter and energy in the environment and the cycling of nutrients as they have great mobility and participate in a wide range of ecosystem services (Whelan et al. 2008; Green and Elmberg 2013; Luck et al. 2013). Wetland ecosystems such as Pantanal, in turn, provide ideal places for breeding, resting, feeding, and are an important stopover and route for migratory bird species (Somenzari et al. 2018; Jahn et al. 2020). In addition, wetland dependence can drive the turnover of bird species depending on the water level in floodplains (Lorenzón et al. 2020). However, the ecosystem functions of birds in wetlands are often overlooked due to the lack of essential information on their interactions in these environments (Green and Elmberg 2013).

Some studies conducted in the Pantanal demonstrated the importance of environmental heterogeneity and seasonality for the diversity of plants (Catian et al. 2018; Olivo-Neto et al. 2020),

mammals (Lázari et al. 2013), birds (Deus et al. 2020, Thomas et al. 2020), snakes (Piatti et al. 2019), anurans (Pansonato et al. 2011), fish (Penha et al. 2017) and invertebrates (Aranda and Aoki 2018; Battirola et al. 2018). Nevertheless, due to recurrent environmental changes, there are still gaps in the understanding of events related to seasonality in species diversity (Tonkin et al. 2017). Moreover, knowledge on the ecological role that bird species play in the Pantanal should be explored, as it can support more effective decision-making for the wetland's conservation (Frota et al. 2020b).

Functional diversity measures have been widely used to understand the role of natural processes and environmental disturbance on the structure of biological communities (Mouillot et al. 2013). This approach allows evaluating the organism's response to environmental change, as well as the organism's effect on the functioning of the ecosystem, becoming useful for conservation (Luck et al. 2012). Functional diversity estimates the differences between species or functional groups that coexist in a community based on their functional characteristics (i.e., morphological, physiological and behavioral traits) (Tilman 2001; Petchey and Gaston 2006), determining the impact of biodiversity on the functioning of the ecosystem and the structure of biological communities (Tilman 2004). Although the number of studies approaching functional diversity measures has increased recently, the subject is considered poorly discussed for freshwater environments (Calaça and Grelle 2016). Some studies conducted in aquatic ecosystems demonstrate the strong relationship between functional traits and structural or seasonal environmental characteristics for vertebrates and invertebrates that depend on or are associated with wetlands (Almeida et al. 2016; Cardoso et al. 2017; Almeida et al. 2018; Liu and Wang 2018; Almeida et al. 2019; de Deus et al. 2020b).

In this study, we evaluated whether the degree of wetland dependence influences the response of bird groups (waterbird, wetland bird and non-wetland bird) to the Paraguay River's flood pulse. For this, we tested the hypothesis that the environmental change generated with variations in the water level should cause considerable differences in the composition of bird assemblage over the hydrological cycle, changing species richness, abundance of individuals and their functional structure. We predict that: (1) waterbirds and non-wetland birds are more influenced by the periods of the hydrological cycle, as they have a greater and lesser affinity for wetlands, respectively; (2) the group of waterbirds and wetland birds should have higher values of species richness and abundance of individuals, as well as of diversity of ecological characteristics, in the high-water season (flooding and full flood), whereas non-wetland birds should present greater diversity during low water (ebb and drought); (3) Functional trait composition varies among the three bird groups in each hydrological period, avoiding niche overlap and enabling resource partitioning. Besides that, functional trait proportion also changes between hydrological periods since, in the high waters, birds that feed on items associated with waterbodies should be favored, while in the low waters, non-wetland birds will be favored because there is more availability of resources for land birds.

2. MATERIAL AND METHODS

2.1. Study area

The system of our study includes the fluvial-lacustrine sector of the Paraguay River, Northern floodplain of the Pantanal wetland, in the state of Mato Grosso, Paraguay watershed, Brazil (Figure 1). This location includes the Ramsar site *Estação Ecológica de Taiaí* (EET), a fully protected area by Federal Law nº 9.985/2000, as well as its buffer zone protected by the State Resolution *CEPESCA* nº 02/2018, and a Private Reserve of Natural Heritage protected by the same federal legislation. The climate is equatorial savanna with dry winter (Aw) according to the Köppen classification, with an average annual rainfall of 1500 mm and annual average temperature ranging from 32° C to 20° C (Kottek et al. 2006). The region's vegetation is classified as Semi-Deciduous Seasonal Alluvial Forest (Veloso *et al.* 1991).

Fig. 1 Location of the sampling sites in the Paraguay River floodplain, Pantanal wetland, Brazil.

EET is characterized by different types of wetland macrohabitats consisting predominantly of aquatic areas, such as the channels of the Paraguay and Bracinho rivers, and *baías* (ponds); swampy areas, such as floating islands and meadows that diversify in their successional stage with various biological forms (e.g., floating, emergent); and aquatic-terrestrial transition zones, which consist of flooded forests and flooded grasslands (Frota et al. 2017). The buffer zone consists of floodplain channels interconnected to irregular depression lakes (Wantzen et al. 2005) and open areas consisting of flooded grasslands and aquatic macrophytes; it also presents patches of flooded forests on the banks of the river channel.

2.2. Bird survey

We sampled birds in five areas of the Long-Term Ecological Research site “*Dinâmicas Ecológicas na Planície de Inundação do Alto Rio Paraguai*” (Figure 1), covering the protected area (EET) and its buffer zone. Sampling was carried out along the river channel and access to the aquatic and terrestrial

transition zones occurred with a smaller boat (license SISBIO – nº 59399). We conducted four campaigns, which matched the four hydrological periods, viz., drought (August - October), flooding (November - January), full flood (February - April), and ebb (May - July), of the 2017-2018 cycle (Figure 2).

Fig. 2 Hydrological cycle 2017-2018 showing average rainfall (mm) and average water level (cm) in the Paraguay River, Cáceres hydrological station, Paraguay watershed, Brazil. Arrows indicate the four bird-monitoring campaigns carried out during the cycle, covering the hydrological periods drought, flooding, full flood, and ebb. Source of telemetric data: *Agência Nacional das Águas* (2019).

We established ten point-count stations in each area to sample bird assemblages following the methodology of Blondel et al. (1970). The minimum distance between points was 500 meters to distribute the effort and avoid overlapping records. At each point-count, the bird species and the number of observed and/or heard individuals were recorded for 15 minutes considering a 50-meter radius from the observer. Data collection occurred from 6 am to 10 am, with each site being visited for two days in each campaign, totaling a sampling effort of 100 hours of observation.

2.3. Classification of birds according to the degree of wetland dependence

For the classification of birds groups, we followed Lorenzón et al. (2020), who categorize birds into three groups according to the degree of wetland dependence: (1) waterbirds, birds that have morphological adaptations to live in aquatic environments; (2) wetland birds, species that depend on resources or habitats in wet systems for food or reproduction; and (3) non-wetland birds, for those associated with terrestrial habitats, such as forest and savanna environments, or generalist habits, but that are not wetland-dependent. For the taxonomic classification of bird species, we followed Piacentini et al. (2015) and, for the migration category, we followed Somenzari et al. (2018).

2.4. Functional traits

To measure the functional structure of bird assemblages in relation to hydrological periods and degree of wetlands dependence, we considered 18 functional traits obtained from the EltonTraits database (Wilman et al. 2014), which reflect the use of resources and functional role in natural ecosystems (Luck et al. 2012; Wilman et al. 2014). The functional matrix consisted of 18 traits located in the columns and species in the lines. We used the following functional traits: diet, defined as the proportion of each consumed food item (1 - invertebrates; 2 - endothermic vertebrates, such as mammals and birds; 3 - ectothermic vertebrates, such as reptiles and amphibians; 4 - fish; 5 - carrion or carcasses; 6 - vertebrates in general or unknown, when there is no clear identification of what kind of vertebrate was consumed; 7 - fruits; 8 - nectar; 9 - seeds; 10 - other plants materials); foraging stratum, treated as the estimated percentage of time spent in each stratum (11 – below water surface; 12 – around water surface; 13 - ground; 14 - understory; 15 - mid to high levels of vegetation; 16 - canopy; 17 - aerial); and 18 - biomass (in grams) as a continuous variable.

2.5. Data analysis

To understand how bird diversity is influenced by the flood pulse, we calculated for each bird group (“waterbirds”, “wetland birds”, “non-wetland birds”) in each hydrological period (Drought, Flooding, Full Flood, Ebb), species richness and abundance of individuals. We also calculated four complementary functional diversity measures based on the multivariate functional-trait space (Villéger et al. 2008): functional richness (FRic), which represents the functional space filled by the community; functional evenness (FEve), describing the regularity of abundance distribution in the functional space, where values close to zero indicate very irregular functional distances between species and values close to 1 indicate very constant distances; and functional divergence (FDiv), defines how far the abundances of the species are from the center of the functional space (Mason et al. 2005). FDiv values increase if the most abundant species have extreme values of functional characteristics. High functional divergence indicates low niche overlap and low competition between species (Mouchet et al. 2010). We also calculated functional dispersion (FDis), which is the average distance of individual species to the community centroid in a multidimensional characteristics space (Laliberté and Legendre 2010), which is high when niche complementarities increase. Increases in FDis mean that abundances of species with trait values further away from the centroid increased, indicating higher use of the margins of the functional space (Almeida et al. 2019). Also, we calculated community-weighted means (CWM) for each trait of the community. CWM represents the community’s functional composition and constitutes average values of the weighted traits at the community level (Lavorel et al. 2008) and enables to assess the association between trait dominance and environmental gradients for a set of communities (Duarte et al. 2018). Functional metrics were calculated considering the three levels of wetland dependence by birds and the four hydrological periods. FRic, FEve, FDiv, FDis and CWM values were calculated using the dbFD function in the FD package of R (Laliberté et al. 2015).

To test differences in species richness, individual abundance and functional diversity between hydrological periods for each bird group, we performed generalized linear mixed models (GLMM) at the sampling-site level. We evaluated isolated effects and interactions between hydrological periods

(categorical variable with the levels Drought, Flooding, Full Flood and Ebb) and the three groups classified according to the degree of wetland dependence (categorical variable with the levels Waterbirds, Wetland birds, Non-wetland birds). Hydrological period and bird groups were considered in the analyses as fixed factors and sampling site was inserted as a random factor to control the independence of the samples (Zuur et al. 2009). We used Poisson distribution for models evaluating richness and abundance with the link function = “log”. For functional diversity measures, we used the Gaussian distribution with the link function = “identity”. Model fit was defined using the corrected Akaike Information Criterion (AICc) for small samples, and the best model was the one with the lowest value of AICc. We used the Maximum Likelihood (ML) method to estimate the fitted model values. Null models with no effect were included for comparison. Models were compared using the “F” test for data with normal distribution and the “Chisq” test for non-normal distribution using a significance level of 5% ($p \leq 0.05$). For these analyses, we used the lme4 package and glmer and lmer functions in R (Bates et al. 2015). Then, for models with significant results, we performed multiple comparisons with Tukey's post-hoc test using the glht function of the multcomp package in R (Hothorn et al. 2008).

To assess which functional traits are the most representative for Waterbirds, Wetland birds and Non-wetland birds in each hydrological period, we performed a Principal Component Analysis (PCA). We calculated the variables' dimensions and evaluated the combined variation of the traits using the cumulative proportion of the two main axes. Values were established according to the average of each trait's community-weighted means (CWM). To verify which variables were the most correlated in each axis, we evaluated the description of the dimensions using the function dimdesc. In this analysis, we used the FactoMineR package (Husson et al. 2007). For graphic design, we use the ggplot2 package (Wickham et al. 2013). We conducted all statistical analyses in the R environment (R Core Team, 2019).

3. RESULTS

3.1. Overview

We recorded 15,714 individuals belonging to 162 species, of which 35 are waterbirds ($n = 3,425$), 29 wetland birds ($n = 4,147$) and 98 non-wetland birds ($n = 8,142$). Species were distributed in 21 orders and 48 families (33 non-Passeriformes and 15 Passeriformes). Families with the largest number of species were Tyrannidae (15), Thraupidae (10), Ardeidae (9) and Psittacidae (9). Of the total bird records, 21 are species of total or partial migratory behavior and one species (*Crax fasciolata*) is in a global threat category (Table 1).

3.2. Influence of the hydrological period on the diversity of waterbirds, wetland birds and non-wetland birds

3.2.1. Waterbirds

Waterbirds group, showed no differences in species richness between hydrological periods (Pseudo-F: 3.46; $p = 0.32$). There was a difference in abundance between periods (Pseudo-F: 322.76; $p <$

0.001), with the largest number of individuals observed during flooding (mean = 261.4, SD = 278.66) and the smallest during drought (mean = 117; SD = 59.81). In the pairwise comparisons, we found similar abundance of waterbirds in the flooding and ebb periods ($p = 0.40$). On the other hand, flooding presented a larger number of individuals than full flood (mean = 147.2; SD = 94.82), ebb (mean = 159.4; SD = 57.74) and drought (mean = 117; SD = 59.81), with significant differences ($p < 0.001$ in all cases). Drought also had a smaller number of individuals than ebb ($p < 0.001$) and full flood ($p < 0.001$).

We found no difference in functional richness between hydrological periods for waterbirds (Pseudo-F: 3.62; $p = 0.30$), while full flood had lower FEve (mean = 0.53; SD = 0.04) than drought (mean = 0.65; SD = 0.06) and flooding (mean = 0.65; SD = 0.11) (full flood vs. drought: $p = 0.03$; full flood vs. flooding: $p = 0.02$). FDiv was low during the full flood period (mean = 0.66; SD = 0.07) when compared to drought (mean = 0.83; SD = 0.07) ($p < 0.001$). We also observed a decrease in FDiv from the flooding period (mean = 0.80; SD = 0.05) to full flood ($p = 0.008$) and an increase from the full flood period to ebb (mean = 0.83; SD = 0.08) ($p < 0.001$). In contrast, FDis values did not vary between hydrological periods for the waterbird assemblage (Pseudo-F: 6.13; $p = 0.10$).

3.2.2. Wetland birds

Similarly to waterbirds, species richness of wetland birds also did not vary between hydrological periods (Pseudo-F: 1.15; $p = 0.76$). Abundance varied in pairwise comparisons of all periods (ebb vs dry, flooding vs dry, flood vs ebb, flooding vs ebb, flooding vs flood, $p < 0.001$ in all cases, Table 2). Although full flood had a higher average abundance of wetland birds (mean = 192.4; SD = 91.85) than drought (mean = 174.6; SD = 24.57), this difference was not significant ($p = 0.16$). As for the functional structure, FRic did not vary between hydrological periods (Pseudo-F: 7.09, $p = 0.06$), and neither did FEve (Pseudo-F: 6.38, $p = 0.09$) and FDis (Pseudo-F: 6.13, $p = 0.10$). There was difference only in FDiv (Pseudo-F: 9.58, $p = 0.02$), this difference being observed between flooding and drought ($p = 0.04$) and flooding and flood ($p = 0.02$). The lowest value was recorded in flooding (mean = 0.75; SD = 0.04) compared to the other two periods.

3.2.3. Non-wetland birds

Although species richness of non-wetland birds showed the highest average during the drought period (mean = 34.8; SD = 10.05), we did not find a significant difference between the evaluated periods for this metric (Pseudo-F = 4.38; $p = 0.22$). On the other hand, abundance varied between periods (Pseudo-F = 230.65, $p < 0.001$) being the highest in the drought period (mean = 494.8; SD = 225.30), while ebb had a higher number of individuals (mean = 452.8; SD = 163.43) than flooding (mean = 348.2; SD = 78.76) ($p < 0.001$) and full flood (mean = 332.6; SD = 41.91) ($p < 0.001$). Flooding and full flood, in contrast, did not show difference in abundance for this bird group ($p = 0.538$). Regarding the functional structure, FRic, FEve and FDiv were similar between periods ($p = 0.91, 0.35$ and 0.30 , respectively; Tables 2 and 3), while FDis was higher in flooding (mean = 0.39; SD = 0.02) compared to ebb (mean = 0.33; SD = 0.04; $p = 0.02$).

3.2.4. Interaction between bird groups and hydrological periods

Comparisons of the predicted values in our models with the null model showed that species richness, abundance and the four functional diversity measures varied significantly when there was an interaction of the fixed effects “degree of wetland dependence” and “hydrological period” (Figure 3; Table 4). When assessing the isolated effects, we found that FDiv and FDis did not show significant variation for the degree of wetland dependence, but rather for species richness, abundance, FRic and FEve between bird groups (Table 5). On the other hand, abundance was the only metric that was significantly affected by hydrological period, with differences in the bird assemblages between full flood vs drought ($z = -6.680$; $p < 0.001$), flooding vs drought ($z = 3.785$; $p < 0.001$), full flood vs ebb ($z = -9.044$; $p < 0.001$), and flooding vs full flood ($z = 10.435$; $p < 0.001$).

Table 4: Comparison of the generalized linear mixed model (GLMM) with the null models, showing the Variance and Standard Deviation (SD) of the random effect “Site”, and the degree of freedom (df), test value (X^2) and the significance level (p-value) of the fixed effects “hydrological period” (drought, flooding, full flood, ebb) and “degree of wetland dependence” (waterbirds, wetland birds, non-wetland birds) on species richness, abundance and functional diversity (FRic, FEve, FDiv and FDis) of birds in the Paraguay River floodplain, Pantanal wetland, Brazil.

Response variable	Fix Effect	Random	Variance	SD	df	X^2	p value
Species Richness	Group				2	257.89	< 0.001
	Period				3	3.31	0.34
	Group*Period				11	266.89	< 0.001
		Site	0.01	0.11			
Abundance	Group				2	2335.6	< 0.001
	Period				3	127.77	< 0.001
	Group*Period				11	2957	< 0.001
		Site	0.01	0.12			
FRic	Group				2	50.27	< 0.001
	Period				3	1.34	0.71
	Group*Period				11	57.71	< 0.001
		Site	< 0.001	0.01			
FEve	Group				2	14.69	< 0.001
	Period				3	2.96	0.39
	Group*Period				11	33.72	< 0.001
		Site	< 0.001	0.08			
FDiv	Group				2	0.43	0.80
	Period				3	5.05	0.16
	Group*Period				11	29.34	0.002
		Site	< 0.001	0.07			
FDis	Group				3	0.37	0.82
	Period				2	6.21	0.1
	Group*Period				11	38.28	< 0.001
		Site	0.01	0.03

Fig. 3 Variations in species richness, abundance of individuals and functional diversity measures of waterbirds, wetland birds and non-wetland birds between hydrological periods in the Paraguay River floodplain, Pantanal wetland, Brazil. Boxplots show the median values (thick centerline), quartiles (bottom and top of the boxes), maximum and minimum values (whiskers) and outliers (circles). a) Species richness; b) Abundance; c) Functional richness (FRic); d) Functional evenness (FEve); e) Functional divergence (FDiv), f) Functional dispersion (FDis).

3.3. Functional composition

The first two PCA axes explained 67.50% of the variation in the set of functional traits in the drought period. On axis 1, the most representative traits were foraging around the water surface ($R^2 = 0.96$; $p < 0.001$) and fish diet ($R^2 = 0.84$; $p < 0.001$). On axis 2, the most representative were invertebrates diet ($R^2 = -0.76$; $p < 0.001$) and foraging on the ground ($R^2 = -0.85$; $p < 0.001$). In the flooding period, the first two PCA axes explained 68.05% of the variation in the functional traits, being fish diet ($R^2 = 0.96$; $p < 0.001$) and foraging around the water surface ($R^2 = 0.89$; $p < 0.001$) the most representative characteristics on axis 1, and plant diet ($R^2 = -0.65$; $p = 0.008$) and foraging on the ground ($R^2 = -0.79$; $p < 0.001$) the most representative on axis 2. In the full flood period, the first two axis explained 70.25% of the variation in the traits, highlighting foraging around the water surface ($R^2 = 0.95$; $p < 0.001$) and fish diet ($R^2 = 0.94$; $p < 0.001$) as the most representative on axis 1. On axis 2, invertebrate diet ($R^2 = -0.87$; $p < 0.001$) and foraging on the ground ($R^2 = -0.71$; $p < 0.001$) stood out. In the ebb period, the first two axes explained 66.12% of the variation, with foraging around the water surface ($R^2 = 0.95$; $p < 0.001$) and diet of ectothermic

vertebrates ($R^2 = 0.89$; $p < 0.001$) being the most associated with axis 1, while invertebrate diet ($R^2 = 0.74$; $p < 0.001$) and foraging in the aerial stratum ($R^2 = 0.76$; $p < 0.001$) were the most representative on axis 2.

The ordination diagrams of the principal components generated with CWM values (Figure 4) showed that functional traits such as a diet of fish and ectothermic vertebrates, foraging around the water surface and the weighted average of biomass were positively associated with waterbirds in all hydrological periods. Functional traits of wetland birds seem to be more similar to those of non-wetland birds than those of waterbirds. Invertebrate diet and foraging in the understory were more associated with wetland birds, while fruit diet and foraging in the canopy were more associated with non-wetland birds. This was evidenced mainly in the flooding period when there seemed to be a greater distinction between groups. In the ebb period, however, there was apparently a niche overlap between these two groups regarding a diet of invertebrates and endothermic vertebrates.

Fig. 4 Ordination diagram of the principal components analysis (PCA) showing the variation in the set of community-weighted mean (CWM) trait value of the waterbirds, wetland birds and non-wetland birds for each hydrological period (a) Drought, b) Flooding, c) Full flood and d) Ebb) in the Paraguay River floodplain, Pantanal wetland, Brazil.

4. DISCUSSION

4.1. Influence of the hydrological period on the diversity of bird groups

The degree of wetland dependence influenced the birds' response to the flood pulse in the Pantanal wetland. Species richness and abundance of individuals were higher for non-wetland birds than waterbirds and wetland birds, a result similar to that found in another South American river system (Lorenzón et al. 2020). Such results can be attributed to the fact that most neotropical bird species, in general, live in forest

or non-forest habitats (~88%), while a much smaller number (~12%) is directly associated with wetlands or aquatic habitats (Stotz *et al.* 1996).

Flood pulse did not affect species richness and functional richness of the three considered bird groups, revealing that the functional space filled by the bird assemblages remains constant throughout the hydrological periods. The lack of difference in the FRic values suggests that the species within each evaluated group use similar resources throughout the hydrological periods. According to Figueira *et al.* (2011), factors such as the abundance of different resource types are regulated by environmental heterogeneity and seasonality in the Pantanal, which can allow the coexistence of a larger number of ecologically similar bird species. Similarly, De Deus *et al.* (2020b) found that the functional diversity of birds was not significantly affected by seasonality in the northern Pantanal, but habitat type (forest x savanna) had a strong influence on structure and functional diversity.

The abundance of individuals varied between the hydrological periods for the three groups, and we found that waterbirds showed the highest abundance values during flooding and the lowest in the drought period. On the other hand, non-wetland birds predominated during ebb and drought, and were less abundant in flooding and full flood, corroborating our initial hypothesis. This agrees with the study of Lorenzón *et al.* (2020), which also found higher abundance values for non-wetland birds during the low-water period.

Waterbird FEve was low during full flood, showing that during this period the functional distances were less regular, which indicates that some parts of the niche, even if occupied, are underutilized (Villéger *et al.* 2008; Almeida *et al.* 2016). FEve did not vary for wetlandbirds or non-wetland birds between the evaluated periods, indicating that the functional distribution of these bird groups remains throughout the hydrological cycle.

FDiv varied between periods considering waterbirds, being lower during the full flood period than during drought. We also noticed an FDiv decrease in the flooding period in relation to full flood and an increase in the period of full flood in relation to ebb. Such results reveal that there is a low niche differentiation between species in the assemblage during the high-water period, as the most abundant species are ecologically very similar and can compete for resources (Mason *et al.* 2005; Mouchet *et al.* 2010). This may also reflect the reduced niche availability during the flood season, favoring species that are adapted to these conditions, such as birds of the Family Ardeidae, which can forage among wetlands connected to river channels. For wetland birds, the lowest FDiv value was observed in the flooding period compared to drought and full flood, evidencing a low degree of niche differentiation among species during flooding, which can cause greater resource competition during this period. This measure did not vary for non-wetland birds possibly because they took refuge in non-flooding environments, use resources in higher strata of vegetation, or even because of behavioral factors such as migration. According to Pinho *et al.* (2017), some birds can have seasonal or occasional movements looking for better conditions and greater availability of resources throughout the year.

Functional dispersion of the waterbirds was greater during drought when compared to flooding and full flood, suggesting that there are more complementary niches in this period (Laliberte and Legendre 2010). In turn, FDis did not vary between the hydrological periods for the wetland bird assemblage, while non-wetland birds showed higher FDis in flooding compared to ebb, which indicates greater niche

complementarity during flooding (Laliberte and Legendre 2010). In general, a previous study observed that the bird community was functionally overdispersed throughout the seasons in flooded areas (de Deus et al. 2020b). However, in the present study, we found that there is a variation in the functional dispersion for bird groups considering their degree of wetland dependence.

Our results showed that the fluctuation from different hydrological periods combined with the degree of wetlands dependence by species influences the richness, abundance and functional diversity of birds in the Pantanal. The isolated effect of hydrological periods on bird assemblages influenced only abundance. However, when assessing the combined effect of period and different bird groups, significant differences were observed for all considered diversity measures. This result indicates that evaluating only the general species assemblage can mask important wetland-dependent responses of birds, as observed for forest-dependent birds (Matuoka et al. 2020). This is so because birds in wetlands can be affected differently by disturbances due to their response to water level (Lorenzón et al. 2020) throughout the seasons (Che et al. 2019), as well as regarding the wetland type, degree of environmental conservation (Almeida et al. 2020) and degree of connectivity of the water-bodies (Almeida et al. 2016). Still, biotic factors such as functional characteristics can be considered the main determinants of ecosystem processes, regardless of the hydrological regime (Setubal et al. 2020).

In general, we observed that birds with a higher degree of wetland dependence (waterbirds and wetland birds) showed greater differences in trait values (i.e., functional richness) in the Paraguay River floodplain compared to non-wetland birds (Figure 3; Table 5). In contrast, species richness and abundance of non-wetland birds showed higher values compared to the two other groups (Figure 3). Diversity measures with this inverse response reveal that a larger number of non-wetland birds have similar characteristics. It is noteworthy that less diverse but abundant resources in environments with different annual hydrological regimes can enable increased efficiency of resource exploitation by most species with similar ecological characteristics (Setubal et al. 2020). In addition, this variation demonstrates the relevance of natural wetland ecosystems toward maintaining the diversity of ecological functions.

4.2. Trait composition

Changes in the trait composition between hydrological periods were observed for wetland birds and non-wetland birds. Bird composition usually varies depending on the available macrohabitat types in each hydrological period (Frota et al. 2020a). Our result also highlights the importance of the flood pulse for the maintenance of the functional role of these birds, here demonstrated by the functional composition based on dominant traits of bird assemblages. We evaluated a river system that harbor mostly of non-passerine species, which can directly contribute to a greater variety of functional traits due to the evolutionary distance of these organisms, which can or can not share ecological characteristics.

Waterbirds presented a distinct ecological niche in relation to wetland and non-wetland birds in the four evaluated hydrological periods. The most characteristic traits of waterbirds were food items obtained in the aquatic environment (e.g., fish) and foraging around or below the water surface, which was already expected, considering their adaptations to aquatic habitats or aquatic-terrestrial transition zones. Also, we highlight that these traits were predominant even in the drought and ebb periods possibly due to

the predominance of permanent aquatic habitats, such as swamps and marshes, in this floodplain sector (Wantzen et al. 2005; Frota et al. 2017).

Waterbirds (e.g., Ciconiiformes, Pelecaniformes) are organisms with high mobility and biomass, so they require a large amount of energy, which can be provided via the consumption of fish. The relationship between aquatic birds and the fish fauna in the Pantanal seems to be little studied (Keppeler et al. 2016), even though they are important regulators of these taxa in freshwater ecosystems, especially in the flooding and full flood periods, which were the periods in which we detected the highest abundance of waterbirds, corroborating the study of Kantek et al. (2020). These periods coincide with the “dequada” process in the region, which occurs due to limnological changes, such as the depletion of dissolved oxygen in the aquatic system, and causes greater vulnerability and mortality of fish (Oliveira et al. 2013) and, consequently, enables a high food supply for piscivorous birds or those that occasionally feed on fish.

Waterbirds also showed a dominance of plants materials in their diet. We highlight here that some waterbird species can be important vectors of endozoochory (Wilkinson et al. 2017; Lovas-Kiss et al. 2020) not only secondarily but also primarily (Van Leeuwen et al. 2017). This group can disperse viable seeds or plant propagules over long distances (Kleyheeg et al. 2019). Dispersion by waterbirds can depend on species and season, being of fundamental importance for aquatic, amphibious and terrestrial plants to connect to wetlands at different scales (Silva et al. 2020).

In floodplains, forests and grasslands are essential to ensure plant resources such as fruits, seeds and flowers for species associated with these traits in their diet, as observed for wetland birds and non-wetland birds. Resource maintenance for these bird groups often generates an interdependent relationship, through mutualistic interactions. Such interactions can highlight the role played by these birds in the seed dispersal and pollination processes, enabling the plant species recruitment and colonization of new areas (García 2016). This is especially importante for plants that are more tolerant to flooding and that establish themselves in environments with greater sediment deposition during the alternation of aquatic and terrestrial phases of the hydrological cycle. Among these plants, we can mention the trees *Erythrina fusca* Lour. (Fabaceae) and *Calophyllum brasiliense* Cambess (Calophyllaceae) (Olivo-Neto et al. 2020) that are commonly observed in the area of the presente study.

In general, bird groups occupied distinct niches in all hydrological periods. We observed that wetland birds and non-wetland birds share some traits such as invertebrate and endothermic vertebrate diet in the ebb period. During flooding and full flood, non-wetland birds were more restricted to the highest strata of vegetation. Still, foraging on the ground showed a strong negative relationship in these periods, which reveals that, when the water level is high, the foraging in this stratum decreases. During ebb and drought, foraging on mid to high levels of vegetation and in the understory was also associated with the non-wetland group, thus favoring the exploitation of a greater variety of resources in more structured environments such as forests. According to de Deus et al. (2020b), forest areas, in contrast to savannas, may have a larger number of potential niches and allow a greater co-occurrence of species.

Insectivorous birds are highly diverse in tropical ecosystems and have important coexistence mechanisms (Sherry et al. 2020). This is a possible explanation for the predominance of the invertebrate diet found in our results, which was mainly associated with wetland birds and non-wetland birds in all hydrological periods. We emphasize that birds with this diet trait play an important regulatory role in

controlling insect populations and reducing plant damage, and the loss of this functional group can lead to negative consequences in trophic cascades (Sekercioglu et al. 2004).

4.3. Threats to bird diversity in natural wetlands

The conservation status of wetland-dependent species has decreased at higher rates than that of species associated with other ecosystems (Davidson 2016) and the goal of the Ramsar Convention to contain wetland degradation has not been achieved yet (Davidson et al. 2019). Although freshwater wetlands play a major role in maintaining ecosystem services (Mitsch et al. 2015), these are considered “exploitable” areas and are, consequently, highly threatened. Studies show that wetlands and biodiversity in freshwater ecosystems are much more threatened than marine and terrestrial ecosystems, due to emerging threats such as use of natural resources, climate change and contamination by microplastics and biochemicals (Reid et al. 2019).

In the Pantanal wetland, loss of water mass in the past 10 years has already been observed due to climate changes aggravated by anthropogenic pressures (Lázaro et al. 2020), and the reduction of these floodplains can drive the loss of the functional diversity of waterbirds and wetland-dependent birds. These conditions occur due to the impact of the agricultural and energy sectors in the ecological system of the Pantanal. Agriculture, represented by land use, generates pressures such as the conversion of natural ecosystems and the loss of macrohabitats and biodiversity. Energy, represented by the hydroelectric power production matrix, which is characterized by many large (UHs) and small hydroelectric plants (PCHs) in the Upper Paraguay basin, affects longitudinal and lateral hydrological connectivity (Da Silva et al. 2015). Human pressure established in natural ecosystems, such as the loss of native vegetation (i.e., deforestation, burning), degradation of water quality, modification in the hydrology patterns, and draining of wetlands (Gupta et al. 2020), is the cause of an ongoing decline in avian diversity due to habitat loss and also affects ecological functions (Sekercioglu et al. 2004; Sekercioglu 2006; Sekercioglu 2012).

4.4. Conclusion and implications for conservation

In our study, we accessed bird diversity and functional structure in the Brazilian Pantanal considering the degree of wetland dependence by avian groups. We emphasize the need to evaluate functional metrics in ecological studies of the region and in assessments of environmental impact on wetlands since measuring only species richness may not reflect the characteristics inherent to this ecosystem type. In this way, it is also possible to assess more effectively the conservation status of wetland ecosystems. The results presented here provide subsidies to encourage decision-making for environmental policies in the Paraguay River floodplain and other lowland river systems.

Furthermore, wetland conservation directly implies the maintenance of different niches throughout hydrological periods, whether for species that are dependent or not on wetlands. The loss of important functional groups can result in greatly modified ecological communities regarding structure and function (Norris et al. 2020). Moreover, integrated terrestrial-freshwater planning can guarantee benefits for the aquatic biodiversity without losses on the terrestrial biodiversity (Leal et al. 2020).

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Conflicts of interest/Competing interests

There are no conflicts of interests.

Availability of data and material

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Code availability

Not applicable

Authors' contributions

Conceptualization: AVBF and BDV; Methodology and Investigation: AVBF, BDV and SMA; Data curation and analyses: AVBF; Writing – original draft: AVBF; Writing – review and editing: AVBF, BDV, SMA, JRSN and CJS. All authors revised and approved the final version this manuscript.

Ethics Approval

This study follows the license from the responsible authority for carrying out the research in the respective area. The permission activities with a scientific purpose are under authorization number 59399 of Biodiversity Authorization and Information System - SISBIO/ICMBio.

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Figures

Figure 1

Location of the sampling sites in the Paraguay River floodplain, Pantanal wetland, Brazil. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

Figure 2

Hydrological cycle 2017-2018 showing average rainfall (mm) and average water level (cm) in the Paraguay River, Cáceres hydrological station, Paraguay watershed, Brazil. Arrows indicate the four bird-monitoring campaigns carried out during the cycle, covering the hydrological periods drought, flooding, full flood, and ebb. Source of telemetric data: Agência Nacional das Águas (2019).

Figure 3

Variations in species richness, abundance of individuals and functional diversity measures of waterbirds, wetland birds and non-wetland birds between hydrological periods in the Paraguay River floodplain, Pantanal wetland, Brazil. Boxplots show the median values (thick centerline), quartiles (bottom and top of the boxes), maximum and minimum values (whiskers) and outliers (circles). a) Species richness; b) Abundance; c) Functional richness (FRic); d) Functional evenness (FEve); e) Functional divergence (FDiv), f) Functional dispersion (FDis).

Figure 4

Ordination diagram of the principal components analysis (PCA) showing the variation in the set of community-weighted mean (CWM) trait value of the waterbirds, wetland birds and non-wetland birds for each hydrological period (a) Drought, b) Flooding, c) Full flood and d) Ebb in the Paraguay River floodplain, Pantanal wetland, Brazil.