**Bird dependence on wetlands determines functional responses to flood pulse in the Brazilian Pantanal**

Angélica Vilas Boas Frota1 · Breno Dias Vitorino1 · Sara Miranda Almeida2 · Josué Ribeiro da Silva Nunes1 · Carolina Joana da Silva1

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**Abstract**

Hydrological regimes in floodplains are essential to support biodiversity that depend on wetlands, and understanding how these organisms are associated to this ecosystem could be useful, as they can act as important agents for the maintenance of diversity and natural processes. We aimed to assess the bird functional responses to the Pantanal flood pulse, considering the hydrological periods and three bird groups with different degrees of wetlands dependence. For this, bird survey was conducted in the Paraguay River floodplain system, covering the hydrological periods of the 2017–2018 cycle. We considered species richness, abundance, four functional diversity measures, and functional trait composition as ecological responses. Species richness was higher for bird group with lower degree of wetland dependence, mainly in drought and ebb periods. 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 over periods. Abundance was affected by the variation of the hydrological periods for all bird groups. Bird groups had distinct niches, and functional traits associated with waterbirds were dominant in all periods. We found that degree of wetland dependence is driving the response of birds to changes in hydrological periods. Measuring only species richness may not reflect the inherent characteristics of this ecosystem. Bird groups such as waterbirds and wetland birds showed greater functional diversity throughout the hydrological periods, evidencing the importance of the flood pulse regime for species that are highly dependent on these environments and that perform many ecological services.

**Keywords** Floodplain · Functional diversity · Hydrological regimes · Seasonality · Waterbirds

**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). River floodplain systems are characterized by annual and pluriannual hydrological regimes — flood pulse concept — wherein fluctuations of 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). However, the loss of wetlands due to human activities and climate change (Gupta et al. 2020) has negatively affected biodiversity in freshwater ecosystems (Albert et al. 2021). Worldwide, wetland-dependent species have declined at higher rates than species associated with other ecosystems (Davidson 2016). Estimates by the organization Wetlands International reveal the steady decline of waterbird populations, highlighting the large gaps in knowledge in the Neotropics and losses of wetlands in South America (Wetlands International 2012; Davidson 2016). Thus, understanding how these organisms are associated with flood pulses in floodplains could be useful, as they can act as important agents for the maintenance of diversity and natural processes, being efficient bioindicators of ecosystem changes.
The seasonal dynamics of wetlands allows a fluctuation in the availability of resources for biodiversity according to their annual conditions of floods and droughts. In this ecosystem, birds play a key role, contributing to the flow of matter and energy in the environment and the cycling of nutrients, as they are highly mobile and participate in a wide range of ecosystem services (Whelan et al. 2008; Green and Elmberg 2013; Luck et al. 2013). Wetland ecosystems, 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). Nevertheless, 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).

Birds are one of the most diverse biological groups, and some species being more dependent on wetlands than others, such as waterbirds, which have morphophysiological characteristics (e.g., legs, feet, beak, and uropygial gland size) and behavior adapted for direct use of resources in aquatic habitats (Vieira 2017; Almeida et al. 2018). This dependency gradient may also include species that, although they do not have the mentioned morphophysiological characteristics, present behavioral aspects directly related to the dependence on resources or habitats in wetlands, whether for food or reproduction, such as species that inhabit swamps or marshes. On the other hand, more generalist species or those that are more associated with terrestrial habitats may also use habitats in wetlands. In this context, birds can be classified into three groups: waterbirds, those with a higher degree of dependence on wetlands; wetland birds, those with an intermediate degree of dependence on wetlands; and non-wetland birds, those with a lower degree of dependence on wetlands (Accordi 2010; Wetlands International 2012; Billerman et al. 2022). This dependence on wetlands by birds drives temporal turnover of species along water variation in floodplains, in which the periods of higher and lower waters favor the occurrence of more or less dependent groups, respectively (Almeida et al. 2016; Lorenzón et al. 2020).

To assess the ecological responses of birds in wetland ecosystems, many measures of diversity can be considered. In addition to classical measures such as number of species and distribution of abundance (Whittaker et al. 2001), metrics of functional diversity have been widely used to understand the role of natural processes and environmental disturbances in 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 (Luck et al. 2012). Functional diversity estimates the differences between species or functional groups that coexist in a community based on their morphological (e.g., body mass), physiological (e.g., metabolism), and behavioral (e.g., foraging strategies and diet items) functional traits (Tilman 2001; Petchey and Gaston 2006). The use of functional traits in ecological studies allows a more accurate view of natural processes and, although there is little information, standardized data have been made available and help to understand the role that species play in their environment (Wilman et al. 2014). Such characteristics are related to species niches (Tilman 2001) and may also be determinants of ecosystem processes in environments with different hydrological regimes (Setubal et al. 2020).

The Pantanal wetland is one of the largest continuous floodplains in the world and presents hydrological regimes with a monomodal, low amplitude, and long duration flood pulse (Junk and Da Silva 1996). 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, and marshes) that make up permanent or temporary aquatic habitats (Wantzen et al. 2005) and are essential for biological groups that depend on wetlands (Junk et al. 2006). Recently, extreme drought and fires in the Brazilian Pantanal gained worldwide repercussion due to the magnitude of the devastation of biodiversity (Libonati et al. 2020; Mega 2020). 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 Pantanal floodplain.

In the present study, we aimed to assess the bird functional responses to the Pantanal flood pulse, considering the effects of hydrological periods on bird groups with different degrees of wetlands dependence. For this, we tested the following predictions: (1) the variation of hydrological periods will affect each group of birds differently, as the species richness and abundance of birds with a high degree of wetlands dependence tend to be greater in periods of high-water level (Lorenzón et al. 2020); (2) measures of functional diversity between hydrological periods should vary more for bird assemblages that depend on wetlands, as they are strongly influenced by seasonal factors in floodplains, and these differences will be more pronounced between flood and drought periods (Almeida et al. 2016, 2019); and (3) we expect a turnover in the composition of functional traits between hydrological periods, because the flood pulse allows a wide variety of resources for aquatic and terrestrial fauna in each period (Figueira et al. 2011; de Deus et al. 2020a, b). Then, in higher waters, traits associated with the dependence of birds on wetlands will be more representative, and in low waters, traits associated with a group less dependent on wetland will predominate.
Methods

Study area

The system of our study includes the Paraguay River floodplain, Northern Pantanal wetland, in the state of Mato Grosso, Paraguay watershed, Brazil (Fig. 1). This location includes the Ramsar site Taiamá Ecological Station (TES), 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 protected area under the same federal legislation. It presents an elevation between 93 and 118 m of altitude (Brasil 2017). The climate is tropical 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 to 20 °C (Alvares et al. 2013). In the Pantanal, the landscape is characterized by a mosaic of semi-deciduous seasonal alluvial forest formation, non-forest natural formations, water bodies, agriculture, and pastures (Souza et al. 2020).

Characterized by different types of Brazilian wetland macrohabitats (Junk et al. 2014), the TES is formed by a river island (16°48′S–16°58′S and 57°24′W–57°40′W) and consisting predominantly of aquatic areas, such as the channels of the Paraguay and Bracinho rivers, and baías (ponds); marshes areas, such as floating vegetation islands and meadows that diversify in their successional stage, with aquatic plants of various biological forms (e.g., floating and emergent); and aquatic-terrestrial transition zones, which consist of flooded forests (e.g., forest dominated by *Erythrina fusca* Lour.) 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 marshes; it also presents patches of swamps on the banks of the river channel.

Bird survey

We sampled birds along five sites, each one 5 km long, located within the Long-Term Ecological Research area (LTER) “Dinâmicas Ecológicas na Planície de Inundação

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**Fig. 1** Location of the study area and sampling sites (T1, T2, T3, T4, and T5) in the Paraguay River floodplain, Pantanal wetland, Brazil
do Alto Rio Paraguai” (Fig. 1). Sampling was carried out along the river channel and access to the macrohabitats occurred with a small boat (license SISBIO–nº 59,399). We conducted four field expeditions, which matched the four hydrological periods: drought (August–October), flooding (November–January), full flood (February–April), and ebb (May–July), of the 2017–2018 cycle (Fig. 2).

To sample the bird communities, we established ten point count stations in each site, following the protocol for bird assemblage surveys in wetlands ecosystem (Accordi 2010). The minimum distance between points at each site was 500 m to distribute the effort and avoid overlapping records. At each point count station, we recorded the bird species and the number of observed and/or heard individuals during 15 min considering a 50-m radius from the observer. Data collection occurred from 6 to 10 a.m., and each site was visited for 2 days in each hydrological period of flood pulse, totaling a sampling effort of 100 h of observation.

Bird species were classified according to their degree of dependence on wetlands, based on information available in the literature (Accordi 2010; Wetlands International 2012; Billerman et al. 2022) and our personal knowledge of the species in terms of morphophysiological and behavioral characteristics. In this way, the birds were categorized into waterbirds, wetland birds, and non-wetland birds (see in Supplementary Material Table S1 for details). Analyses were performed for each group of birds separately. Thereby, for each site, we summed the number of species and the abundance of individuals of each bird group for each hydrological period, totaling 60 samples (5 sites × 3 bird groups × 4 periods). Taxonomic classification of the bird species followed Pacheco et al. (2021), and for the migratory status, we followed Somenzari et al. (2018).

### Functional traits

To measure the functional structure of bird assemblages in relation to hydrological periods and bird groups with different degrees of wetlands dependence, we considered three functional traits distributed in 18 categories obtained from the EltonTraits 1.0 database (Wilman et al. 2014) that reflect resource use and functional role in natural ecosystems (Luck et al. 2012; Wilman et al. 2014). We organized a functional matrix, where rows were species and lines were functional traits. 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 plant 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.

### Data analysis

We calculated the mean and standard error (SE) of species richness and abundance of individuals for bird assemblages and for each bird group (waterbirds, wetland birds, non-wetland birds) classified according to the degree of wetland dependence in each hydrological period (drought, flooding, full flood, ebb). 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 (FDs), 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 FDs imply that abundance of species with trait values further away from the centroid increased, indicating higher use of the margins of the functional space (Laliberté and Legendre 2010; Almeida et al. 2019). In addition, we calculated community-weighted means (CWMs) 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 (Garnier et al. 2004; 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 values were calculated in each sampled site and for each bird group and hydrological period using the dbFD function in the FD package (Laliberté et al. 2015).

We performed generalized linear model (GLM) and linear models (LMs) at the sampling-site level to evaluate how the hydrological period affects species richness, number of individuals, and functional diversity of bird groups with different degrees of wetland dependence. The predictor “hydrological period” was a categorical variable with the four levels (drought, flooding, full flood, and ebb), and “bird groups” was a categorical variable with three levels (waterbirds, wetland birds, non-wetland birds). We evaluated the isolated effects of hydrological periods on diversity metrics in first model. Then, we performed a second model with the interactions between the hydrological periods and bird groups. Null models with no effect were also included for comparison. 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 for small samples (AICc), and the best model was the one with the lowest value of AICc. For this, we use the AICctab function from the package bbmle (Bolker and R Development Core Team 2020). Subsequently, we graphed the confidence intervals of the selected model and performed pairwise comparisons of the models’ predictors for each diversity measure using the emmeans and contrast functions of the emmeans package (Russell et al. 2022). Tukey was the adjustment method for the \( P \) values of tests of contrasts, considering confidence intervals 95% level.

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 community-weighted trait mean (CWM). To verify which variables were the most correlated in each axis, we evaluated the description of the dimensions using the dimdesc function. In this analysis, we used the FactoMineR package (Le et al. 2008). For graphics design, we use the ggplot2 package (Wickham 2016). We conducted all statistical analyses in the R environment (R Core Team 2019).

**Results**

**Overview**

We recorded 15,714 individuals belonging to 162 species, of which 38 are waterbirds (3,499 individuals), 26 are wetland birds (3,588 individuals), and 98 are non-wetland birds (8,627 individuals). 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 spp.), Thraupidae (10 spp.), Ardeidae (9 spp.), and Psittacidae (9 spp.). Among the birds, 21 are migratory species (13 non-wetland birds; 5 waterbirds; 3 wetland birds). Of total species, 12 were recorded exclusively in the full flood period (9 non-wetland bird; 3 waterbirds), 10 only in the ebb period (4 waterbirds; 6 non-wetland birds), 7 only in the flooding period (5 non-wetlands; 1 wetland bird; 1 waterbird), and 4 only in the drought period (all non-wetland birds) (Supplementary Material Table S1). Regarding bird assemblages, species richness (\( z = 51.76; P < 0.0001 \)) and abundance (\( z = 319.28; P < 0.0001 \)) were higher in the drought period. In general, the functional diversity measures were also higher in the drought period for bird assemblages, except for functional richness, which showed no differences between periods (Supplementary Material Tables S2 and S3).

**Effects of hydrological periods on bird groups**

Comparisons of the values in our models with the null model showed that species richness, abundance, and two of the four measures of functional diversity (FRic and FDs) were explained by the interaction of the predictors hydrological
period and bird groups. Unlike the other measures, species richness and abundance were better explained by the isolated effect of the hydrological period when compared to the null model. FEve was better explained by the variation of the hydrological period when compared to the combined model of predictors (Fig. 3; Table 1). The estimated values in the models and the pairwise comparisons revealed that non-wetland birds showed higher species richness and abundance, and lower functional diversity when compared to waterbirds and wetland birds (Supplementary Material Tables S3 and S5). During the flooding, waterbirds showed a higher abundance than the wetland birds ($z = 4.82; P < 0.001$), while in the ebb period, the abundance values were higher for wetland birds ($z = -2.61; P = 0.009$). These two bird groups also differed in functional evenness during the drought, with the highest values observed for waterbirds ($z = 2.54; P = 0.010$). We found lower functional dispersion for waterbirds than for wetland birds in the flooding, full flood, and ebb periods. In the drought and ebb periods, we found greater functional dispersion of waterbirds and wetland birds compared to non-wetland birds (Supplementary Material Table S5).

Specifically, waterbirds showed no differences in species richness between hydrological periods. However, there was a difference in abundance between periods for this group, with the highest number of individuals observed during flooding (mean = 266; SE = 125.63) and the lowest during the ebb (mean = 163.60; SE = 26.48). In the pairwise comparisons, we found similar abundance of waterbirds in the full flood and ebb periods ($z = 1.58; P = 0.11$). On the other hand, flooding presented a greater number of individuals than full

![Fig 3](image-url) 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. Graphs show the 0.95 confidence interval and pairwise comparisons. a Species richness; b abundance; c functional richness (FRic); d functional evenness (FEve); e functional divergence (FDiv); f functional dispersion (FDIs). Significance level: “***” $P < 0.001$; “**” $P < 0.01$; “*” $P < 0.05$.
flood \( z = 12.42; P < 0.001 \), ebb \( z = -10.93; P < 0.001 \), and drought \( z = -16.28; P < 0.001 \). The drought also had a lower number of individuals than ebb \( z = -5.87; P < 0.001 \) and full flood \( z = -4.31; P < 0.001 \). We found no difference in functional richness and functional divergence between hydrological periods for waterbirds, but there was greater functional evenness during the drought than in the other periods (Supplementary Material Tables S2 and S4). Functional dispersion values for waterbirds were significantly higher in the drought when compared to the full flood period \( z = 2.08; P = 0.03 \).

Species richness of wetland birds also did not vary between hydrological periods. However, the abundance of this group was low in drought period compared to the other hydrological periods (Supplementary Material Tables S2 and S4). Regarding the functional structure of wetland bird assemblage, we found variation only in the functional richness from the full flood to ebb \( z = -2.30; P = 0.02 \). For non-wetland birds, we found higher species richness in the drought than in the full flood period \( z = 2.17; P = 0.02 \). The abundance of this group was higher in the drought when compared to the other periods (Fig. 3), as well as when comparing the ebb period with full flood \( z = 9.76; P < 0.001 \) and flooding \( z = 8.37; P < 0.001 \). There were greater functional divergence and functional dispersion for non-wetland birds during the flooding than in the drought and ebb periods (Supplementary Material Tables S2 and S4).

### Functional trait composition

The first two PCA axes explained 74.2\% 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 \( R^2 = -0.87; P < 0.001 \). On axis 2, we observed a high representation of species that feed on invertebrates \( R^2 = -0.85; P < 0.001 \) and foraging on the ground \( R^2 = -0.85; P < 0.001 \). In the flooding period, the first two PCA axes explained 69.4\% of the variation in the functional traits, being fish diet \( R^2 = -0.95; P < 0.001 \) and foraging on mid to high levels of vegetation \( R^2 = 0.92; P < 0.001 \) the most representative traits on axis 1, and nectar diet \( R^2 = 0.72; P = 0.002 \) and foraging on the ground \( R^2 = -0.75; P = 0.001 \) the most representative on axis 2. In the full flood period, the first two axes explained 76.6\% of the variation in the trait composition, where foraging on mid to high levels of vegetation \( R^2 = 0.96; P < 0.001 \) and fish diet \( R^2 = -0.91; P < 0.001 \) were the most representative on axis 1. On axis 2, invertebrate diet \( R^2 = -0.97; P < 0.001 \) and foraging on the ground \( R^2 = -0.62; P = 0.013 \) were the dominant functional traits. In the ebb period, the first two axes accounted for 68.1\% of the bird trait composition, being foraging around the water surface \( R^2 = -0.95; P < 0.001 \) and ectothermic vertebrates diet \( R^2 = -0.89; P < 0.001 \) the most associated with axis 1, while invertebrate diet \( R^2 = -0.88; P < 0.001 \) and foraging on the ground \( R^2 = -0.84; P < 0.001 \) were the most representative on axis 2.

The ordination diagrams of the principal components generated with CWM values (Fig. 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 associated with waterbirds in all hydrological periods. Functional traits of wetland birds seem to be more similar to those of non-wetland birds than to 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.

### Discussion

We found that degree of wetland dependence is driving the response of birds to changes of hydrological periods in floodplain systems. The hydrological periods combined

| Response variable | Model       | AICc  | ΔAICc | df | AICc  |
|-------------------|-------------|-------|-------|----|-------|
| Richness          | Period      | 604.6 | 236   | 4  | <0.001|
|                   | Period*Group| 368.6 | 0     | 12 | 1     |
|                   | Null        | 601.3 | 236.1 | 1  | <0.001|
| Abundance         | Period      | 6637  | 3557  | 4  | <0.001|
|                   | Period*Group| 3080  | 0     | 12 | 1     |
|                   | Null        | 6758.2| 3678.1| 1  | <0.001|
| FRic              | Period      | -447.3| 11.1  | 5  | 0.0037|
|                   | Period*Group| -458.4| 0     | 13 | 0.9531|
|                   | Null        | -452.2| 6.2   | 2  | 0.0432|
| FEve              | Period      | -113.3| 3.6   | 5  | 0.1429|
|                   | Period*Group| -103.5| 13.4  | 13 | 0.0011|
|                   | Null        | -116.9| 0     | 2  | 0.856 |
| FDiv              | Period      | -130  | 1     | 5  | 0.26  |
|                   | Period*Group| -130.2| 0.7   | 13 | 0.3   |
|                   | Null        | -131  | 0     | 2  | 0.44  |
| FDis              | Period      | -298  | 35.6  | 5  | <0.001|
|                   | Period*Group| -335.5| 0     | 13 | 1     |
|                   | Null        | -298  | 32.2  | 2  | <0.001|
with bird groups with different degrees of dependence on wetlands affected species richness, abundance, functional richness, and functional dispersion of bird assemblages in the Pantanal. The isolated effect of hydrological periods on bird assemblages affected species richness, abundance, functional evenness, functional divergence, and functional dispersion. Functional structure presented higher values and varied more to waterbirds than for the other bird groups, evidencing the importance of the flood pulse for the maintenance of species functions highly dependent on wetlands.

Our results indicate that evaluating only the general species assemblage can mask important responses of wetland-dependent birds, as observed for forest-dependent birds (Matuoka et al. 2020). This is 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 in relation to the type of wetland, degree of environmental conservation (Almeida et al. 2020; Daniel et al. 2021), and degree of connectivity of water bodies (Almeida et al. 2016). Here, we included that the degree of dependence on wetlands by birds and their functional traits consisting of the type of feeding, the method and habitat of obtaining the food, and body size can be considered the main determinants of species responses to natural changes in river floodplains. This highlights the importance of biotic factors in the ecosystem processes that occur in floodplains, regardless of the hydrological regime (Setubal et al. 2020).

Based on the classification adopted for the bird groups and functional traits used in our study, we found a pattern in which non-wetland birds have greater taxonomic diversity, while birds with a higher degree of wetland dependence (waterbirds and wetland birds) have greater functional diversity in all hydrological periods evaluated in this floodplain. That is, when the bird community is more dependent on wetlands, it presents greater variation in the values of ecological characteristics (for example, functional richness), evidencing that floodplains provide different conditions and resources for the maintenance of complementary niches. In contrast, non-wetland bird species have more similar characteristics to each other. However, we emphasize that abundant resources in environments with an annual flood

Fig. 4 Ordination diagram of the principal components analysis (PCA) showing the variation in the set of community-weighted mean (CWM) trait value of 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.
pulse can increase the efficiency of resource exploitation by most species with similar ecological characteristics (Setubal et al. 2020). Furthermore, this variation in the response of bird groups demonstrates the relevance of natural wetland ecosystems to maintaining species diversity and ecological functions.

**Ecological responses of bird groups**

In general, the variation of hydrological periods in this floodplain did not affect species richness and functional richness of bird groups, revealing that the functional space filled by bird assemblages remains constant throughout the cycle. The lack of difference in FRic values suggests that species within each evaluated group use similar resources in all hydrological periods. Likewise, de Deus et al. (2020b) found that the functional richness of understory birds is maintained throughout the hydrological seasons in the northern Pantanal, but habitat type (forest or savanna) had a strong influence on functional structure of these communities. The variety and abundance of resources, therefore, are regulated by the environmental heterogeneity that is made possible by the seasonality of the Pantanal (Figueira et al. 2011), structurally modifying the habitats that form this landscape and allowing for greater species diversity (Tews et al. 2004).

The abundance of individuals varied between the hydrological periods for the three groups, and we found that waterbirds presented the highest values of abundance 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. Our results are in agreement with Lorenzón et al. (2020), who also found higher abundance values for non-wetland birds during the low-water period. We emphasize that the drought period favors the occurrence of understory birds in flooded forests (de Deus et al. 2020a; Thomas et al. 2020) which are more active due to the reproductive activity at this time (Pinho and Marini 2014), while in the flooding period, waterbirds are favored due to the increase of aquatic habitats and connection of water bodies. Non-wetland birds were also more abundant compared to the other bird groups in each period, showing that this floodplain has macrohabitats available for these individuals to share over the periods (Frota et al. 2017, 2020), but for those birds that depend on wetlands, it is necessary to maintain the dynamic of water.

Waterbird assemblages tend to show variation in the functional distribution of abundance across years and seasons (Almeida et al. 2019). In our study, we found that the abundance of this group is functionally more evenly distributed in the drought period, as shown by the values of FEve. The other groups did not vary along the hydrological cycle in relation to evenness. We also observed that waterbirds had higher FEve values during the drought period than wetland birds, showing that their functional differences are less variable at this period (Villéger et al. 2008). The low values of FEve during full flood for waterbirds may indicate that in this period the functional distances were less regular, suggesting that some parts of the niche, even when occupied, are underutilized (Villéger et al. 2008; Almeida et al. 2016). Regarding non-wetland birds, the low FDiv and FDis in the drought and ebb periods reveal that there is a low niche differentiation between the species of these groups during the low-water period, as the most abundant species are ecologically very similar and may compete for resources (Mason et al. 2005; Mouchet et al. 2010). On the other hand, we found higher and more constant FDiv and FDis values throughout the hydrological cycle for waterbirds and wetland birds. This may also reflect the reduced availability of niches in floodplains for non-wetland birds, favoring species that are more adapted to these conditions, such as birds of the Ardeidae Family, which can forage in wetlands connected to river channels.

FDiv and FDis functional measures did not vary for wetland birds, possibly because they have less extreme functional traits than waterbirds. Non-wetland birds showed greater niche divergence during flooding and full flood periods. This result may be because this group can take refuge in non-flooding environments, use resources in higher strata of vegetation, or even because of behavioral factors, such as migration due to seasonal changes. According to Pinho et al. (2017), some birds may perform seasonal or occasional movements in search of better conditions and greater availability of resources throughout the year in the Pantanal. Functional dispersion of the waterbirds was greater than non-wetland birds during drought, suggesting the coexistence of functionally dissimilar waterbirds species through niche complementarity in this period (Laliberte and Legendre 2010). Understory bird community can remain functionally overdispersed throughout the seasons in flooded areas (de Deus et al. 2020b), but communities with higher FDis values support more ecological functions due to a wide range of characteristics (Almeida et al. 2018). We emphasize that the period of lower water coincides with the breeding or wintering of many species of waterbirds, such as Rynchops niger, and after the first rains, flood events contribute to connecting habitats and promoting a foraging niche for species dependent on these wetlands, demonstrating the importance of the Pantanal hydrological cycle to species dynamics.

**Bird functional traits in wetlands**

Functional traits associated to waterbirds were more representative in all periods, contrary to our assumption. Trait composition for wetland birds and non-wetland birds revealed that these groups share some resources, such as invertebrates during the ebb period. Although the bird...
composition usually varies with habitat type and hydrological period (Frota et al. 2020; Thomas et al. 2020), our findings corroborate that the traits composition is maintained over periods (de Deus et al. 2020b) showing a trend to stability of ecological functions in the Pantanal wetland. We highlight 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. We evaluated a river system that houses mostly non-passerine birds, which can directly contribute to a greater variety of functional traits due to the evolutionary distance of these organisms, which can or cannot share ecological characteristics.

Waterbirds presented a distinct ecological niche in relation to wetland and non-wetland birds in the four evaluated hydrological periods. The traits more associated to waterbirds were food items obtained in the aquatic environment (e.g., fish) and foraging around or below the water surface, which was expected, considering their adaptations to aquatic habitats or aquatic-terrestrial transition zones. Also, we highlight that these traits were more representative even in periods of drought and ebb, possibly due to the predominance of permanent aquatic habitats, such as baiás and marshes, in this river floodplain system (Wantzen et al. 2005; Frota et al. 2017).

Waterbirds (e.g., Ciconiiformes and 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 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 birds that occasionally feed on fish.

Waterbirds also showed a dominance of plant 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 the species that use these items in their diet, as observed for wetland birds and non-wetland birds. The maintenance of resources for these bird groups often generates an interdependent relationship, through mutualistic interactions. Such interactions may evidence the role played by these birds in the processes of seed dispersal and pollination, enabling the recruitment of plant species and colonization of new areas (García 2016). This is especially important for trees that are more tolerant to flooding and that are adapted to environments with greater sediment deposition during the hydrological cycle. Among these trees, we can mention Erythrina fusca Lour. (Fabaceae) and Calophyllum brasiliense Cambess (Calophyllaceae) (Oliveo-Neto et al. 2020) that are commonly observed in the area of the present study.

Insectivorous birds are highly diverse in tropical ecosystems and have important coexistence mechanisms (Sherry et al. 2020). In our results, we found predominance of the invertebrate diet, which was mainly associated with wetland birds and non-wetland birds in all hydrological periods. Insect-eating birds play an important role in controlling insect populations, reducing plant damage, and therefore, the loss of this functional group can lead to negative consequences in trophic cascades (Sekercioglu et al. 2004).

In general, bird groups occupied distinct niches and consumed different resources, regardless of the hydrological period. We observed that wetland birds and non-wetland birds share some traits such as invertebrates as one of the main components of the diet in the ebb period. During flooding and full flood, non-wetland birds were more restricted to the highest strata of vegetation. Furthermore, foraging on the ground showed a strong relationship in the evaluated periods, showing that despite the high-water level in the area, birds more adapted to foraging in wetlands can use this stratum. During ebb and drought, foraging on mid to high levels of vegetation was also associated with the non-wetland birds, thus favoring the exploitation of a greater variety of resources in environments with a greater complexity of vegetation and vertical stratification of resources such as forests. According to de Deus et al. (2020), forest areas, in contrast to savannas, may have a larger number of potential niches and allow a greater co-occurrence of species. We emphasize that seasonal changes also influence the behavior of species, such as reproduction or territoriality, which are not represented in this type of analysis, but if considered could elucidate these patterns.

Conclusions and implications for conservation

In our study, we assessed bird diversity and functional structure considering the hydrological periods of flood pulse and degree of wetland dependence by bird groups. We found
that the response of bird community structure and functional trait composition to different hydrological periods depends on the degree of dependence of the species on wetlands. We emphasize that the low amplitude and long duration of the flood pulse (Junk and Da Silva 1996), the fluvo-lacustrine characteristics of this aquatic system (Wantzen et al. 2005), and the functional traits chosen to represent the use of resources by birds (Wilman et al. 2014) were key factors in interpreting the ecological response of species. Our results reflect only a part of the entire floodplain system, so we recommend larger-scale studies to better understand these processes.

We recommend considering functional measures in ecological studies in the region and in assessments of environmental impact on wetlands since measuring only species richness may not reflect the characteristics inherent to this ecosystem. In this way, it is also possible to assess in a more effective way the particulars of floodplains, because the bird groups with a high degree of dependence on wetlands showed greater functional diversity throughout the hydrological periods. The results presented here provide subsidies to encourage decision-making for environmental policies in the Paraguay River floodplain and other lowland river systems, take into account the importance of the flood pulse regime for species that are highly dependent on wetlands and that provide many ecological services. The last few years have been marked by extreme droughts, with river levels reaching extremely low values due to climate changes associated with human activities (Lázaro et al. 2020; Marengo et al. 2021; Pivello et al. 2021). 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, such as waterbirds and wetland birds, can result in ecological communities greatly modified in structure and function (Norris et al. 2020). Furthermore, integrated terrestrial-freshwater planning can guarantee benefits to aquatic biodiversity without losses in terrestrial biodiversity (Leal et al. 2020).

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

Declarations

Conflicts of interest The authors declare no competing interests.

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