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Avian Beta Diversity in a Neotropical Wetland: the Effects of Flooding and Vegetation Structure

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Abstract
Habitat heterogeneity in the Pantanal results from flood dynamics and vegetation characteristics. Considering that these impacts affect landbird nesting conditions and food resource availability, species turnover and richness should respond to them. We conducted this study in the northeastern Pantanal, in two dominant habitats, savanna and forest, covering two annual cycles. The objectives were: (1) evaluation of trophic structure, (2) analyses of species dissimilarity patterns, and (3) investigation of whether seasonal changes in the flood regime and/or vegetation characteristics drive these patterns. We used mist nests to acquire data on bird species composition, abundance, and guilds. Insectivore and omnivore species were the predominant guilds. The bird community showed very high overall dissimilarity, with a Jaccard Index of 0.86, with 86% attributed to species replacement and 14% to species nestednesss. This high dissimilarity reflects the reduced number of shared species, mainly between some savannas and forests (12%). Our analyses also showed that habitat characteristics, specifically the differences in vegetation structure and composition, mostly explained the species turnover. Flood seasonality was also an important driver of bird community spatial variability, in which dissimilarities in species composition increased from the terrestrial to the aquatic phases, with the wettest phase being the most dissimilar.

Keywords Pantanal · Neotropical landbird communities · Dissimilarity · Nestedness · Vegetation structure

Introduction

Unlike terrestrial ecosystems, tropical river floodplains are marked by temporal and spatial transitions between aquatic and terrestrial phases (Junk et al. 2014). Flood and flow pulses determine these conditions, affecting the degree of landscape connectivity, habitat heterogeneity, and productivity, which, in turn, have an impact on biodiversity (Junk et al. 1989; Tockner et al. 2000). The South American Pantanal is the world's largest floodplain wetland (approximately 150,000 km^2) and is subjected to a monomodal inundation cycle determined by annual variation in river discharge and precipitation. The Pantanal is made up of a mosaic of forest and savanna physiognomies, where species experience the phytogeographical influences of three major biomes, i.e., the savannas, such as the *Cerrado* and *Chaco*, and the Amazonian rainforest (Adamoli 1982; Nunes da Cunha et al. 2007). The Pantanal is considered a biodiversity hotspot (Mittermeier et al. 2005) and a major avian migration destination from the Nearctic and Austral regions (Junk et al. 2006a). Approximately 463 bird

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species have been recorded in the Pantanal (Tubelis and Tomas 2003; Petermann 2011). One quarter of these species are wetland-dependent, and three-quarters are upland species (Junk et al. 2014). Many bird species depend on the flood rhythm and dynamics of the tropical wetlands for reproduction and feeding or escaping from the severe weather conditions in the temperate zone (Antas 1994). The seasonal disruption of terrestrial habitat connectivity during flooding affects bird mobility, mainly for the species that are land specialists (Saunders et al. 1991).

Knowledge about the ecological processes that shape species composition variation across the habitats provides important information for biodiversity conservation and management (Kraft et al. 2011; Ruhí et al. 2017). The species diversity and distributions across the large river floodplains may be driven by many ecological forces, such as habitat conditions and structure, temporal changes in food supply mediated by evolutionary factors that affect the environmental tolerance and competitive ability of certain species, or neutral processes, such as limited dispersal and speciation (Hubbell 2001; Zhou and Zhang 2008). According to the habitat heterogeneity hypothesis, an increase in habitat heterogeneity leads to an increase in alpha and beta diversity. Previous studies have supported this hypothesis, showing that at landscape scales, a strong positive correlation exists between vegetation structure and diversity (i.e., habitat heterogeneity) with bird species diversity (Mac Nally et al. 2002). On the other hand, at local scales, vegetation structure seems to have a larger role than floristic composition in driving landbird compositional variation (MacArthur et al. 1966; Rotenberry and Wiens 1980; Rotenberry 1985). Disturbances caused by annual flood and flow pulses are responsible for strong seasonal gradients in floodplains (Tockner et al. 2000), profoundly changing the food supply and nesting conditions for reproduction within a single habitat (Figueira et al. 2006). Consequently, these changes marked by the flood pulse might affect the temporal dynamics of landbird communities, which are the subject of this study, causing seasonal fluctuations in species richness, identity, and abundance across the landscape (Shoo et al. 2005; Rahayuningsih et al. 2007; Scherer et al. 2010; Katuwal et al. 2016).

Analysis of the causes of the ecological processes driving biodiversity demands looking beyond local avian species richness and paying attention to the patterns generating between area variation in assemblage species composition (Baselga 2010). Studies about beta diversity have become more common in the last 20 years (Anderson et al. 2011), with a variety of statistical approaches applied to its analyses (Legendre et al. 2005; Anderson et al. 2006; Tuomisto and Ruokolainen 2006; Qian and Ricklefs 2007; Vellend 2010). These studies have shown that variations in species composition between habitats may trace to two antagonistic processes, species turnover and nestedness, or species loss (Baselga 2010).

The spatial replacement of species by others (i.e., species turnover) may be caused by geographical barriers, speciation, historical factors, niche amplitudes, or human impacts (Condit et al. 2002; Tuomisto et al. 2003; Qian et al. 2005). Other factors can cause spatial replacement, such as limited dispersal of the species, habitat isolation, and limited habitat capacity; however, antagonistic species interactions will occur when resource availability becomes seasonally limited (Jankowski et al. 2009; Baselga 2010).

Vegetation structure is a main factor in determining bird species distribution in the environment (Aleixo 1999), and the seasons in the Pantanal directly affect the phenology of plants, determining the resources that are available to the animals. Compared with other habitats, forest habitats are expected to have a higher diversity of plant species and consequently a higher diversity of landbirds. The abundance and richness of these bird species increase with the increasing complexity of the vegetation structure, as plant diversity provides additional resources and different habitats (Boncina 2000; Tews et al. 2004; Nájera and Simonetti 2009; Khanaposhtani et al. 2012; Baláž and Balážová 2012).

Considering beta diversity, the expectation is that when landscape heterogeneity is low and consists of similar plant communities, the avian landbird assemblages will be smaller subsets of the species found in other places (nestedness). Conversely, when habitat heterogeneity is high and marked by diverse and structurally complex plant communities, we would expect the variation in bird composition between the sites to result from the species replacement (Baselga 2010). However, if species with broad environmental requirements dominate the area (i.e., generalists), as in the case of the Pantanal landbird community (Signor and Pinho 2011), a reduction in beta diversity is expected because most species will be able to occupy the entire landscape (Kessler et al. 2009).

The aim of this study was to examine the trophic structure and patterns of the distribution of landbirds in the mosaic of savanna and forest physiognomies that are subjected to annual flood cycles in the northeastern Pantanal, Mato Grosso, Brazil. The seasons and habitats may be important factors for determining the temporal and spatial distribution of bird species, but in this dynamic ecosystem, the species can also adapt to survive in all different environmental conditions. The goals were to (i) evaluate the influences of flood seasonality and habitat heterogeneity on spatiotemporal variation in bird composition, abundance, and trophic structure; (ii) understand the impact of species turnover and nestedness on patterns of beta diversity; and (iii) analyze whether beta diversity patterns are shaped by spatial processes (e.g., limited dispersal) or by differences in vegetation structure and composition that cause the floodplain vegetation mosaic.

Materials and Methods

Study Area

Our study was carried out in the northeastern Pantanal in the SESC (Serviço Social do Comércio) Pantanal area, Mato Grosso, Brazil (16°39’S, 56°47’W) (Fig. 1). This region covers approximately 4200 ha and is located on the floodplain of the Cuiabá River, one of the major tributaries of the Paraguay River within the Pantanal.

The regional climate is tropical humid with marked seasonality between the winter and summer periods. The precipitation varies between 1000 and 1500 mm and decreases in winter, resulting in a very dry season (Junk et al. 2006b). Following the seasonal trends in precipitation during the Austral summer and the changes in river discharge, the river floodplains of the northern Pantanal annually experience a transition from terrestrial to aquatic ecosystems caused by the river water overflow, local precipitation events, and/or water seepage connections (Junk 1993). These annual flood cycles may be divided into four seasons: dry, which is the terrestrial phase caused by the strong hydric deficit from July to September; rising water, which is when the rain starts from October to December; wet, which is during the highest levels of inundation from January to March; and the receding water season, which is when the level of the water declines from April to June (Heckman 1998). The characteristics of the flood pulse vary annually depending on the volume of water coming from the Cuiabá River and the changes in precipitation, which are often associated with climatic anomalies (e.g., El Niño) (Ropelewski and Halpert 1987).

The Pantanal vegetation is considered a hyperseasonal savanna because of the prolonged inundation in an area where savanna vegetation types predominate (Silva et al. 2000). This ecosystem displays floristic elements of three important morphoclimatic and phytogeographic domains: the *Cerrado*, Amazonia, and the *Chaco*, making it a zone of ecological tension (Silva et al. 2000; Junk et al. 2006b). Different drainage patterns, flooding characteristics, and geomorphologic features create the conditions for a large variety of alluvial ecosystems. The savanna vegetation types are the dominant physiognomies (67.0%), followed by the swamp (7.4%), dry forest (3.9%), pioneer formation such as monodominant *Vochysia divergens* (Vochysiaceae) Cambarazal forest (3.1%), gallery forest (2.4%), *Chaco* (0.5%), and other (15.7%) physiognomies (Silva et al. 2000; Nunes da Cunha

Fig. 1 Study site in the northeastern Pantanal, Mato Grosso, Brazil

et al. 2007). The area studied represents this rich mosaic of different forest formations (e.g., monodominant forests, semideciduous forests) and savannas (e.g., bushed savanna, low tree and shrubby savanna, and steppic savanna), with significant variations in floristic components and structural vegetation.

Sampling design and data collection

Birds

We conducted data collection from July 2014 to July 2016 during two annual flood cycles. Eight sample sites, which were separated by at least 1 km, were established in the landscape. To capture the variation in vegetation components, we selected four savanna sites (*Cerrado*), which were characterized by scattered trees and a large proportion of grassland and shrubs, and four forest sites, which were characterized by a high proportion of large trees forming a mostly developed canopy structure. Forests were sampled 26 times and savannas 25 times over the 24 months of data collection.

To acquire data on bird species abundance, we used mist nets (Bibby et al. 2000) that were 9 m long by 2.7 m high with 20 mm × 20 mm mesh; the nets were opened for 5 h starting at sunrise (6 am to 11 am) and for 2 h before sunset (3 pm to 5 pm), which are periods corresponding with high bird activity (Robbins 1981). A total of 10 nets, which were 200 to 250 m apart, were established in each of the eight areas for six consecutive days per season. The captured species were identified and assigned according to the literature (Wilman et al. 2014) into their main trophic positions (guilds), as follows: insectivores (INS), omnivores (OMN), frugivores (FRU), nectarivores (NEC), granivores (GRA), piscivores (PIS), and carnivores (CAR). Avian nomenclature followed the South American Classification Committee (Remsen et al. 2009).

Vegetation data

We analyzed the influences of vegetation on bird community structure in two ways: first, by evaluating the effect of the physiognomic aspects of vegetation, represented by two habitat types, forest and savanna; and second, by assessing the role of plant compositional and structural gradients on beta diversity patterns. The plant compositional gradients were represented by a few axes of the principal coordinate analysis (PCoA) (Legendre and Legendre 2012) that summarized the variation patterns in the abundance of plant species. We ran the PCoA using the Bray–Curtis dissimilarity index, based on quantitative (abundance data) matrices of the plant species composition for the community analyses. Vegetation data were acquired using the point-centered quarter method (Mitchell 2007). This method consisted of the random establishment of 10 central points in each of the eight sample sites, functioning as the center of a Cartesian plane defining four quadrants. In each of the four quadrants, we measured the smallest distance from the central point to the three closest individuals in the three different life forms: trees (large and middle size), shrubs, and palm trees. Thus, in each quadrant, we obtained four measures of distance and used them to calculate the absolute density of each plant species in each site. Middle-sized trees were those with diameters greater than 10 cm and lower than 30 cm at breast height; large trees were those with diameters greater or equal to 30 cm. All species were identified through comparisons with specimens in the Central Herbarium of the Federal University of Mato Grosso, Cuiabá, Brazil. Scientific names were confirmed using the reflora website (http://reflora.jbrj.gov.br).

Statistical Analyses

Measuring Beta Diversity

To quantify the general pattern of dissimilarity in species composition between sampling areas, total beta diversity (BDTotal) was calculated using the Jaccard dissimilarity indices of the presence/absence species matrices considering the two years of data sampling. The BDTotal is computed as the total sum of squares of the distances between all sampling pairs multiplied by n (n-1), producing the total variance, or total beta diversity (BDTotal) (Legendre 2014). BDTotal varies between 0 (no difference in species composition) and 1 (completely different set of species). Because beta diversity covers different aspects of the community variation (Tuomisto 2010), total beta diversity was broken down into replacement and nestedness components (Baselga 2010). The replacement or turnover represented the proportion of unshared species among all sampling units (Anderson et al. 2011), while the richness difference (i.e., nestedness) indicated that the bird community of a certain area is a smaller subset of the species found in another area (Legendre 2014). We conducted this analysis in the R software using the *beta.multi* function of the *betapart* package.

The analysis of the local contribution to beta diversity (LCBD) was used to examine the degree of uniqueness of the species composition of each sampling unit. The LCBD is an index that shows how much each site contributes to the total dissimilarity between sites. It is calculated as the diagonal values of the Gower-centered dissimilarity matrix computed using PCoA. The furthest sites relative to the graph centroid are the most exceptional or unique (De Cáceres and Legendre 2013; Legendre 2014). We tested the significance of the LCBD using random and independent permutations of the species matrix, which test whether species are randomly and independently distributed between the sampling sites. The LCBD indices were also extended to replacement and nestedness, indicating that underlying ecological processes were driving site differences (Legendre 2014). Next, the Spearman correlation was applied to investigate the relationship between the LCBD indices and species richness, thus elucidating whether the higher LCBD indices represented sites with high or low numbers of species.

Effects of Flood Season and Habitat Type on Landbird Community Structure

To evaluate the effects of seasonality (i.e., rising, wet, receding, and dry seasons) and the two habitat types (i.e., savanna and forest) on the variation in the abundance of landbird species, we used permutational multivariate analysis of variance (PERMANOVA). PERMANOVA was run with 9999 permutations using the Bray–Curtis dissimilarity measurement to calculate the pseudo-F that shows the differences in dissimilarity between the treatments (Anderson and Walsh 2013). Next, we applied the SIMPER test (similarity percentage analysis) to examine the contribution of each species to the average similarity within groups (Clarke 1993). This method consisted of calculating the Bray–Curtis dissimilarity among all pairs of samples and examining the relative dissimilarity contributed by each species.

Spatial and Environmental Drivers of Beta Diversity

To investigate changes in landbird community structure along spatial (sample geographic location) and environmental gradients (vegetation–PCoA axes) in the floodplain, we applied a generalized dissimilarity model (GDM) with the Bray–Curtis bird dissimilarity matrix (Ferrier et al. 2007). The GDM is a nonlinear matrix regression technique for analyzing spatial patterns in the compositional dissimilarity between pairs of locations as a function of environmental dissimilarity and geographic distance. We used the default setting of the three I-spline basis functions per predictor. The I-splines show the rate of biological changes that is an estimate of beta diversity and represented by the partial ecological distance, according to the geographic distances (i.e., geographic coordinates) and the plant composition gradient (PCoA axes) (Ferrier et al. 2007). The I-spline represents the total amount of compositional replacement associated with each variable, and as a partial regression, it works as an indication of the importance of each variable in determining patterns of beta diversity. The shape of the curves generated by the I-spline indicates the variation rate of species replacement and the contribution of the species to the ecological distances between sites (Ferrier et al. 2007). We performed analyses using the *gdm* function in the R package (Manion et al. 2014). Before doing so, we applied the Mantel test to identify correlations between time (i.e., date of data collection) and bird species dissimilarity, thus avoiding mistakes in interpretations as a result of temporally autocorrelated data (Legendre and Fortin 2010; Legendre and Legendre 2012; Legendre et al. 2015).

Results

Landbird Community Structure and Composition

Over the two annual cycles (2014–2016), we captured 2.107 individuals (landbirds: 2.028 ind., 96.26%; (semi)aquatic birds (three kingfisher species and one heron were considered for this study; Online Resource 2): 79 ind., 3.74%) from 135 species, 107 genera, and 28 families. The most representative families were Tyrannidae (34 spp.; 25%; 400 ind.), Thraupidae (17 spp.; 13%; 452 ind.), and Furnariidae (15 spp.; 11%; 276 ind.), followed by Thamnophilidae (11 spp.; 8%; 241 ind.) and Trochilidae (9 spp.; 6%; 223 ind.). The numbers of bird species and individuals in the savannas and forests for each of the four flood seasons are summarized in Fig. 2. The savanna areas were richer and more abundant in species (1589 ind.; 120 spp.) than were the forest areas (518 ind.; 65 spp.) (Fig. 2). Of the total number of species (135) in the study site, 69 were exclusive to savanna and 15 to forest areas. Unlike in the savanna habitats, the variation in flood conditions affected the community structure in forests to a greater degree, with the number of individuals and species dropping by half from the rising season (205 ind.; 46 spp.) to the receding period (46 ind.; 20 spp.). The general trend throughout the two years of the flood cycles was a decrease in the landbird species richness from the rising season (44 spp.) to the receding period (20 spp.).

The most abundant species in the study areas were *Ramphocelos carbo* (131 ind.), an omnivorous species, and the insectivorous *Synallaxis albilora* (103 ind.). Insectivore birds (961 ind.; 46%) were the most representative group during the four flood seasons during the two studied years, followed by omnivores (587 ind.; 28%), nectarivores (223 ind.; 10.6%), and granivores (186 ind.; 8.8%). All trophic guilds were prevalent in savanna habitats (Fig. 3), except frugivores and piscivores, which dominated the forest habitats. Frugivores increased in numbers during the first rains, while nectarivores were most abundant during the rising and wet seasons in savanna habitats.

Patterns of Beta Diversity Affected by the Flood Cycle and Habitat Type

The bird assemblage showed very high overall dissimilarity, with a Jaccard index of 0.86, with 86% attributed to species replacement and 14% to species nestedness. This high dissimilarity reflects the reduced number of species shared between some habitats, in particular

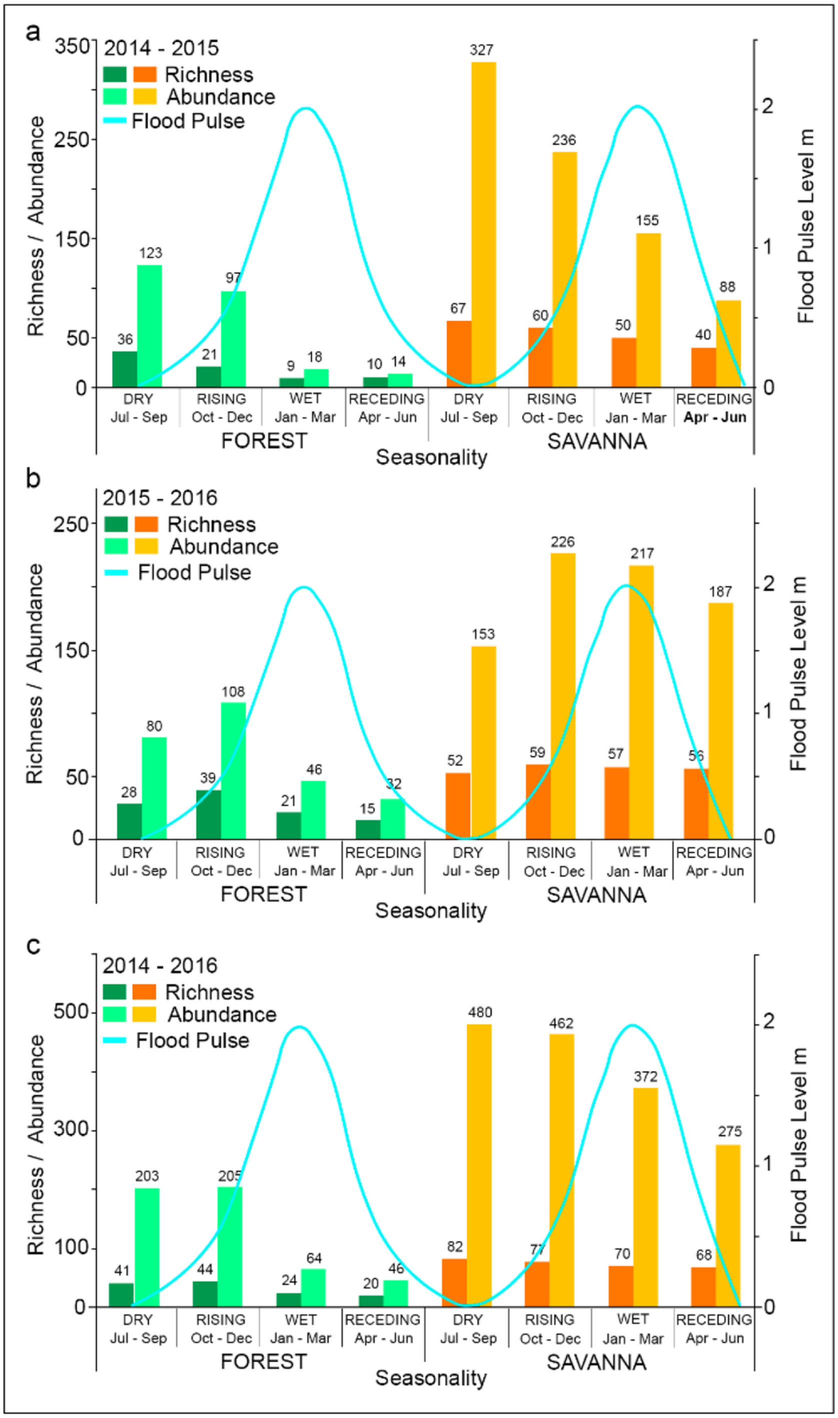

Fig. 2 The variance in avian species richness and abundance during the four hydrological stages (dry, rising, wet, and receding) of the annual flood cycle and between the two phytophysiognomic groups: forest (left side) and savanna (right side) in the northeastern Pantanal, Mato Grosso, Brazil. The dataset covers two annual flood cycles: (**a**) 2014–2015 and (**b**) 2015–2016. The pattern of variability in avian richness and abundance over the whole two years (2014–2016) is shown in (**c**). The annual flood cycle is marked by a peak of flooding, when the water level may reach approximately 2 m in height and a dry period after flooding recedes (blue line)

between some savannas and forests that represented 11% of shared species. On the other hand, low values of dissimilarity were also found, especially among savanna habitats, indicating up to 80% of shared species, with a Jaccard index of 0.42. In general, forest habitats shared fewer species with other areas. Nevertheless, the proximity between some of the forest and savanna sites (sites 7 and 8) might have increased their similarities, with 73% of species shared.

The dissimilarities in species composition between sites increased from the dry season (J = 0.89) to the wet season throughout the flood cycle, with the wet season as the most dissimilar (J = 0.93) (Fig. 4). Species replacement remained the main process that explained the patterns of beta diversity across all seasons. Nevertheless, during the wet season, when the flooding achieved a maximum, nestedness began to play a major role, with the contribution increasing from 15% to 19% of the observed beta diversity pattern. In the wet season, there

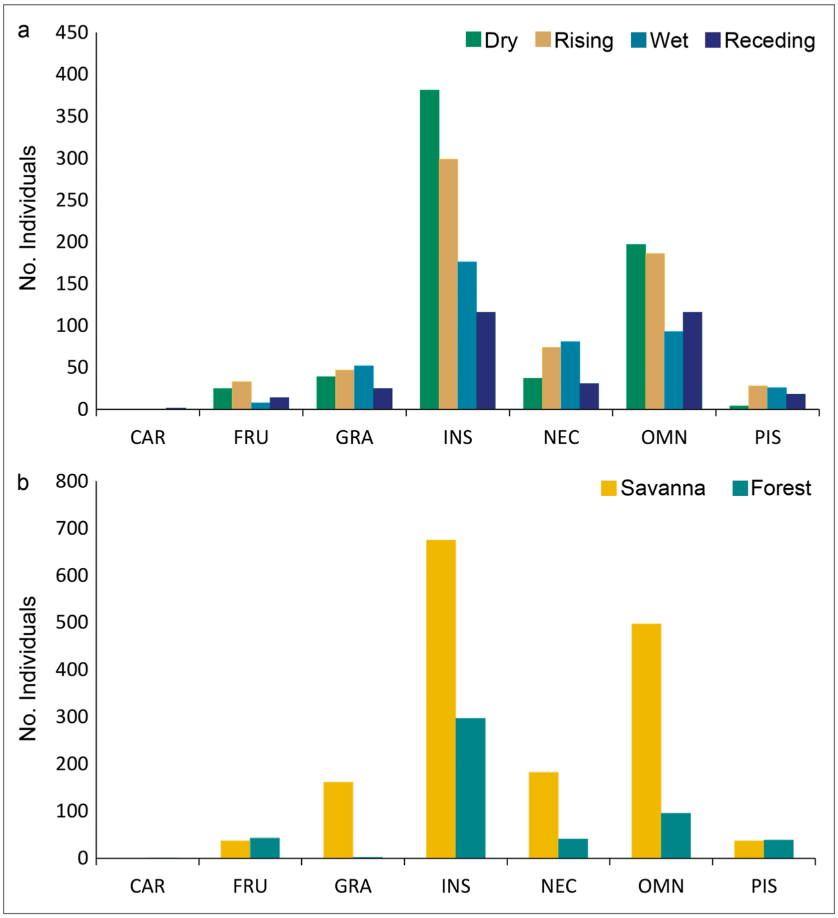

Fig. 3 The number of avian guild members between seasons and habitats in the northeastern Pantanal, Mato Grosso, Brazil, over the seasons from 2014 to 2016. Guilds: CAR: carnivores, FRU: frugivores, GRA: granivores, INS: insectivores, NEC: nectarivores, OMN: omnivores, PIS: piscivores

seemed to be a departure of species with specific requirements from the forest habitats, resulting in decreased species richness and increased overall community dissimilarities. The beginning of the rainy season, when flood water rose, was the period of greatest similarity between the bird assemblages. At that time, the species richness increased the novelty of community composition within each site and decreased the overall dissimilarity in the floodplain. This increase might have been related to niche expansion during a period of higher food supply for frugivorous and piscivorous birds. After the wet season, when floodwater receded, site connectivity started to re-establish, but the long-term flooding for some sites (site 7) had a significant impact on biodiversity, causing species loss.

The local contributions to beta diversity (LCBD) ranged from 0.0 to 0.18 and negatively correlated with species richness ($r = -0.45, p < 0.001$) in all flood seasons (Fig. 4). This result indicated that in general, sites with higher uniqueness presented a lower number of species. This was the case for site 3, a forest habitat that occasionally flooded and had a restricted distribution in the floodplain. Such uniqueness was then more attributable to the low number of bird species (fewer than 5 in site 3) than to the existence of an exclusive set of species, as demonstrated by the high number of shared species in this area (70% to 90%). Nevertheless, site contribution to beta diversity patterns varied among flood seasons, particularly during the two extremes of the flood cycle at the ends of the dry and wet seasons. Site 6, for instance, was a savanna that experienced a high flood intensity and was dominated by a very small number of shrub species, which introduced many novel species into the bird community, mainly during the wet season, when it maintained an elevated richness (32 species) related to a high species turnover. Similarly, site 7, which was a forest site that flooded for more than 5 months, was one of the richest forest sites but, unlike site 6, had a high richness that was present during both the dry and rising water seasons. In contrast, during the wet and receding seasons, this site presented a high LCBD associated with a substantial drop in the number of bird species. In summary, although the differences in richness in a small pool of birds were mostly determined by differences in the bird communities in the forest habitats, species turnover explained the differences between the bird-rich savanna habitats.

The PERMANOVA analysis confirmed that the structure and composition of the bird communities varied significantly throughout the seasons ($F = 1.593$, $p = 0.01$, 7% of contribution) and to a greater extent between habitat types ($F = 11.059$, $p = 0.0001$, 17% of contribution). According to the SIMPER test, the 16 species with the highest average contributions to

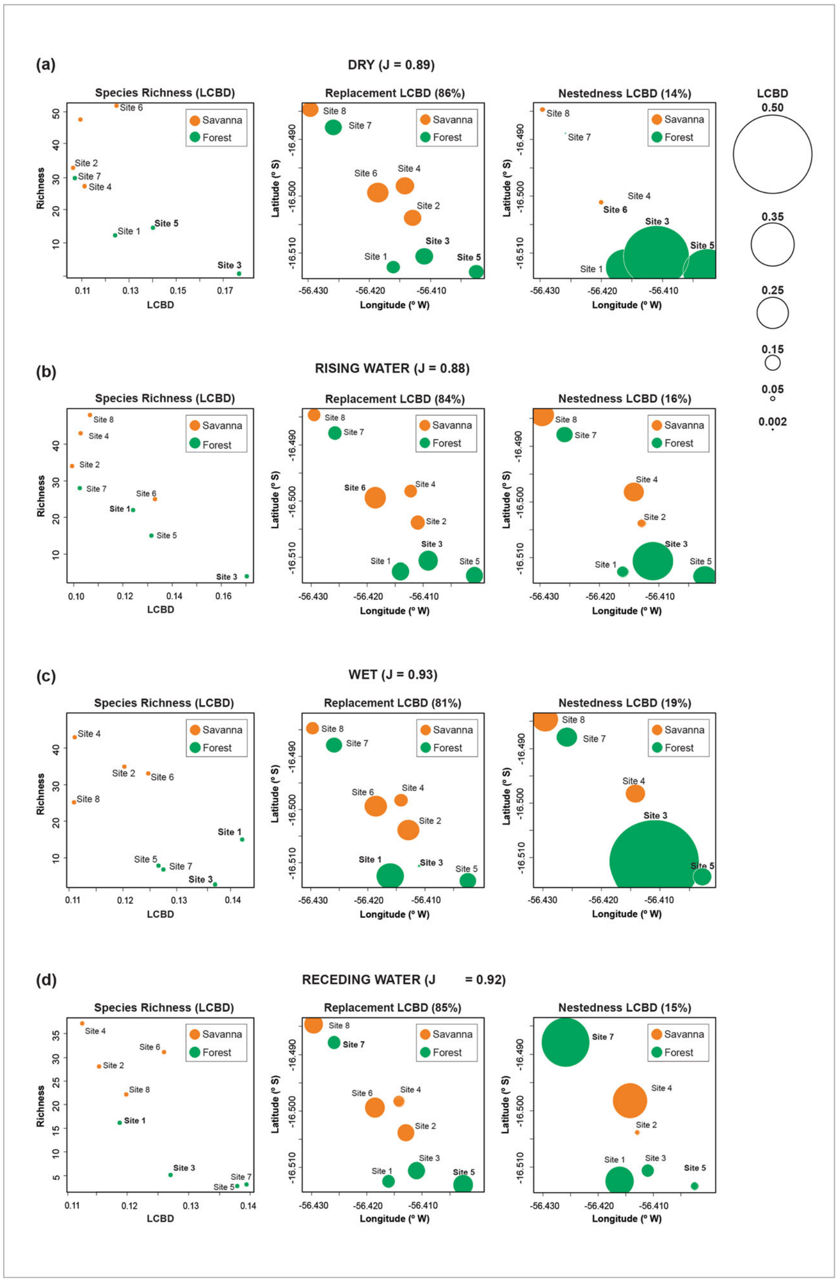

Fig. 4 Local contribution to avian beta diversity (LCBD) in the northeastern Pantanal, Mato Grosso, Brazil, over the seasons from 2014 to 2016. Each of the eight sampling sites is shown, indicating their degree of uniqueness in species composition to the total dissimilarity. The geographic positions of the savanna (orange) and forest sites (green) are displaced. The relation between the LCBD values and species richness is shown in (first column). The site contributions to beta diversity (circle size) in each flood season (i.e., dry (**a**), rising (**b**), wet (**c**), receding (**d**)) were divided into replacement (second column) and nestedness components (third column). Sites with LCBD <0 are not shown

the overall dissimilarity between seasons and habitats were *Amazilia fimbriata* (NEC), *Cercomacra melanaria* (INS), *Chloroceryle aenea* (PIS), *Cnemotriccus fuscatus* (INS), *Coereba flaveola* (OMN), *Columbina talpacoti* (GRA), *Dysithamnus mentalis* (INS), *Elaenia chiriquensis* (OMN), *Hemitriccus margaritaceiventer* (INS), *Hypocnemoides maculicauda* (INS), *Phaethornis nattereri* (NEC), *Pipra fasciicauda* (FRU), *Ramphocelos carbo* (OMN), *Saltator coerulescens* (OMN), *Sporophila angolensis* (GRA), and *Synallaxis albilora* (INS) (Online Resource 1). The changes in the abundances of these 16 species were responsible for up to 50% of the average dissimilarity between habitat types and flood seasons. *Synallaxis albilora* and *R. carbo* were the most abundant species in the dry season (average of 3.41 and 3.16 individuals, respectively). *Chloroceryle aenea* (American Pigmy Kingfisher), which lives and feeds close to riverbanks, almost disappeared during the dry season (0.25 ind.), and presented its highest population during the rising season (1.73 ind.) and was seemingly insensitive to habitat type. The nectarivores *A. fimbriata* and *P. nattereri* were found in all seasons in similar proportions and in both habitats but predominated in the savannas. *Columbina talpacoti* was exclusive to savanna habitats, with increased abundance during the rising season. The savanna-restricted tyrannid *E. chiriquensis* was present in the receding season, when it jumped from 0 to 2.83 individuals.

The Effects of Plant Composition and Geographic Distances on Beta Diversity

The Mantel test indicated that there was no significant temporal autocorrelation between the bird assemblages sampled at the 90-day intervals, which corresponds to the interval found between the four flood seasons. According to the GDM, geographic distance and plant composition gradients explained 58% of the deviance in observed bird community dissimilarities (Fig. 5a). The relative importance of the predictor variables differed strongly, showing a higher importance of plant compositional gradients on bird compositional replacement, whereas geographic distance was of considerably less importance, as indicated by the sum of the I-spline coefficients (Fig. 5b). The maximum height of each spline indicates the magnitude of the total biological change along that gradient (Fig. 5c and d). The sites that were separated from each other by up to 600 m showed the most pronounced rates of biological replacement (Fig. 5c). In contrast, we expected that the closer sites presented lower turnover rates because of the limited dispersal of birds, but the high habitat heterogeneity at short distances might have enhanced the landscape diversity. A quick and significant change in bird assemblages was related to the changes in both vegetation structure and composition, with these differences marked by a transition from shrub-dominated plant communities to tree-rich forest communities (Fig. 5d). The most pronounced changes in bird communities were observed within the forest habitats, highlighting the roles of habitat isolation and food supply on the differences found among the four forest habitats: the wetter forests had the richest and most distinct bird compositions.

Discussion

Studies have shown the importance of vegetation heterogeneity and flooding cycles on the structure and dynamics of the bird community of the Pantanal (Cintra and Yamashita 1990; Figueira et al. 2006). The present study deepens the discussion of the ecological processes involved in the landbird strategies for dealing with seasonality that result in the annual spatial (re)organization of bird community members. Despite the low bird endemism in the Pantanal, where 60% of the birds are considered generalists that live in a wide variety of geographic areas (Brown 1986), the spatial and seasonal variation in habitat conditions resulted in high species turnover. The habitat

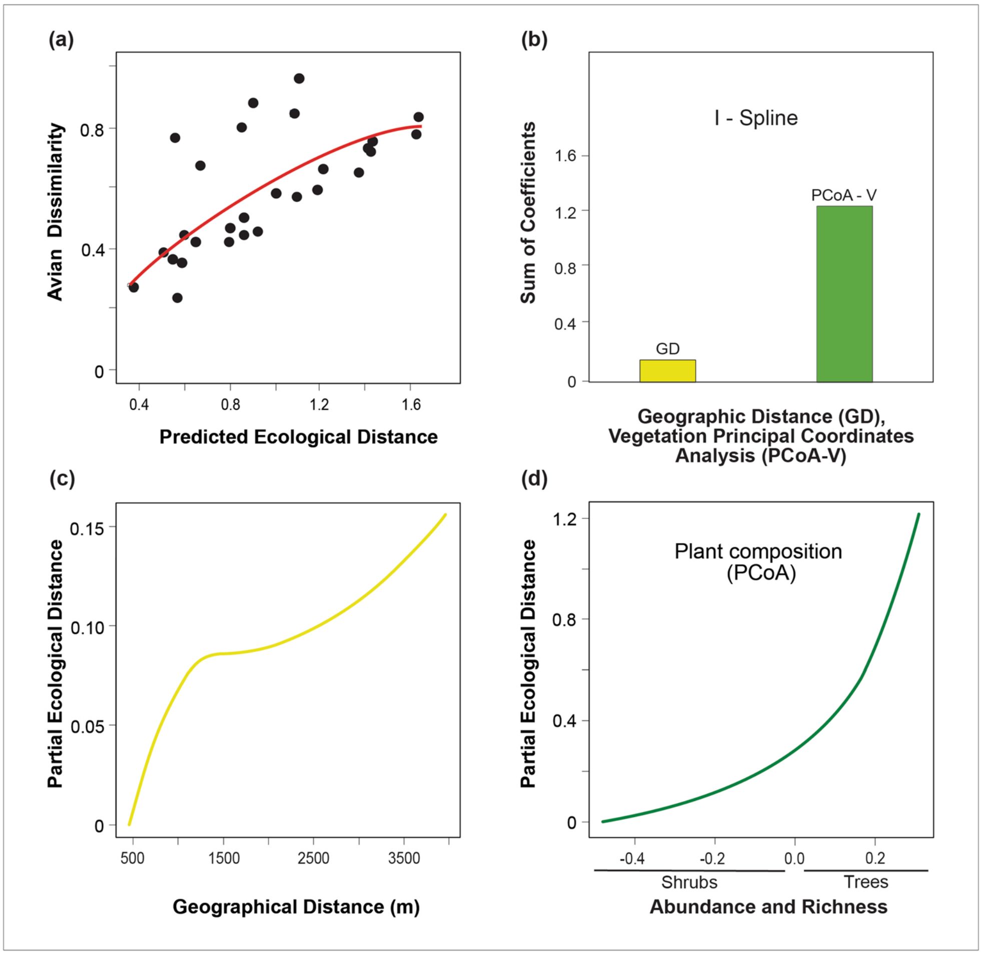

Fig. 5 Generalized dissimilarity model (GDM) of the avian community in the northeastern Pantanal, Mato Grosso, Brazil, over the seasons from 2014 to 2016. (**a**) The relationship between observed compositional dissimilarity of each site-pair for all avifauna and the linear predictor of the regression from the GDM (predicted ecological distance between site-pairs), (**b**) proportion of total explained deviation attributable to the geographic distances (GDs) and vegetation principal coordinates analysis (PCoA-V), (**c** and **d**) GDM-fitted I-splines (partial regression fits) for variables significantly associated with bird beta diversity for all eight sites (savanna and forest). The ecological partial distance indicates the relative importance of the predictor to the turnover

preference, diversification of bird diet, and seasonal migratory behavior lead to niche partitioning due to the fluctuation in resource availability (Figueira et al. 2006; Riegert et al. 2011; Signor and Pinho 2011; Pinho et al. 2017).

A total of 463 bird species have been identified in the Pantanal (Petermann 2011). At our study site, we recorded a total of 135 species, which comprise approximately 40% of all landbird species known to be found in the Pantanal. The birds with the most diverse habitat preferences within the forest strata were captured in the mist nets. According to the definitions of Stotz et al. (1996) for avian species strata preference, the following 11 preference categories were represented among the 135 species captured in this study: canopy, 38 spp. (28.15%); midstory, 5 spp. (3.71%); midstory to canopy, 14 spp. (10.37%); terrestrial, 9 spp. (6.67%); terrestrial to canopy, 7 spp. (5.19%); terrestrial to midstory, 2 spp. (1.49%); terrestrial to understory, 5 spp. (3.71%); terrestrial and aquatic, 1 sp. (0.74%); understory, 23 spp. (17.04%); understory to canopy, 14 spp. (10.37%); and understory to midstory, 17 spp. (12.60%). In view of these observations, the mist nets not only sampled understory species but also species from all other strata, showing that the mist nets were not a limiting methodology in surveying the local avifauna.

In this study, 11% of species were forest-exclusive, 51% preferred savanna habitats, and 38% occurred in both habitats. Insectivores, such as *Attila bolivianus*, *Celeus flavus*, *Coccyzus euleri*, *Dendrocolaptes platyrostris*, *Leptopogon amaurocephalus*, *Monasa nigrifrons*, *Pyriglena leuconota*, and *Thamnophilus amazonicus,* occurred exclusively in forest habitats. Forest-dependent species are particularly susceptible to land conversion and are the first groups to decline in forest landscapes with a reduced amount of habitat (Devictor et al. 2008; Yabe et al. 2010; Morante-Filho et al. 2015). The loss of forest habitats in the Pantanal affects migratory routes for foraging and reproduction, threatening bird species with local extinction (Pinho et al. 2017). *Attila bolivianus*, for instance, occurs in the wet forests along the Amazon River and accesses the Pantanal through riverine forests (Sigrist 2009), making it highly susceptible to land-cover changes.

Habitat heterogeneity emerged as the major factor over flood seasonality for explaining variation in species composition and bird community structure. In contrast to expectations, savannas showed a higher number of bird species compared with that in forests, which also presented higher values of nestedness (Fig. 6). These results suggest that the sparse understory vegetation of some forest habitats may have contributed to the lower number of bird species. The spatial distribution pattern of birds implies both their preferences for specific vegetation structure and for specific floristic associations according to availability of foods such as fruits and flowers over the seasons (Power 1975; Rotenberry 1985). Some studies have shown that the spatial distribution of frugivorous, granivorous, and nectivorous birds may have direct associations with certain plant species (Trainor 2002; Fleishman et al. 2003; Díaz 2006; Gil-Tena et al. 2007; Hanzelka and Reif 2016). In general, granivorous and nectivorous birds occurred mainly in savanna physiognomies (i.e., shrubby savanna, steppic savanna) in areas where the grass coverage was high, especially during the aquatic phase (Rebellato and Nunes da Cunha 2005). This association indicates the importance of these birds for conserving natural pastures that are subjected to seasonal flooding. In agreement with our results, the diversity and abundance of this guild is considered to be higher in open *Cerrado* vegetation than in forest areas (Motta-Júnior 1990; Silva 1992; Piratelli and Pereira 2002). This pattern probably traces to the sparse understory with few grasses in seasonally flooded forest habitats (Arieira and Nunes da Cunha 2006).

The predominance of insectivorous and omnivorous species in the floodplain, however, is considered to be less influenced by plant specificity because insectivores do not respond directly to plant species but to the arthropods living above and on the ground (MacArthur et al. 1966; Rotenberry and Wiens 1980; Rotenberry 1985). The omnivores might respond to habitat heterogeneity and climate seasonality by switching food options and using strategies to coexist, such as moving between vegetation patches (Tubelis and Tomás 1999; Figueira et al. 2006). The ability of the birds to move among habitat fragments depends on the degree of landscape fragmentation (i.e., isolation and patchy areas) and varies according to the body mass of each species (Figueira et al. 2006; Yabe et al. 2010). Larger birds will need more resources and consequently will explore larger areas, while smaller birds as Passerines may be adapted to explore smaller natural fragmented landscapes (Yabe et al. 2010). In our study, we found a weak effect of spatial processes on beta diversity, suggesting that dispersal limitations might not strongly affect patch occupancy. This finding emphasizes the predominant effect of habitat heterogeneity on species segregation.

The annual flood pulse may drastically change ecosystem characteristics by switching them from terrestrial to aquatic systems, increasing primary productivity and changing biodiversity (Junk et al. 2006b). The seasonality in the availability of food resources such as fruits, nectar, or arthropods helps to explain seasonal patterns in bird distribution and abundance, forcing some bird species to alternate between resources over the seasons or migrate to find better conditions (Terborgh and Winter 1983; Bodmer 1990; Adis et al. 2001; Adis and Junk 2002; Marques et al. 2007; Battirola et al. 2007; Battirola et al. 2010). Some evidence suggests that several bird species of the Pantanal engage in either seasonal or occasional movements between the Pantanal and the surrounding plateau (Pinho et al. 2017). This dynamic may explain the changes in the richness, abundance, and patterns of beta diversity during the flood seasons and among the habitats and

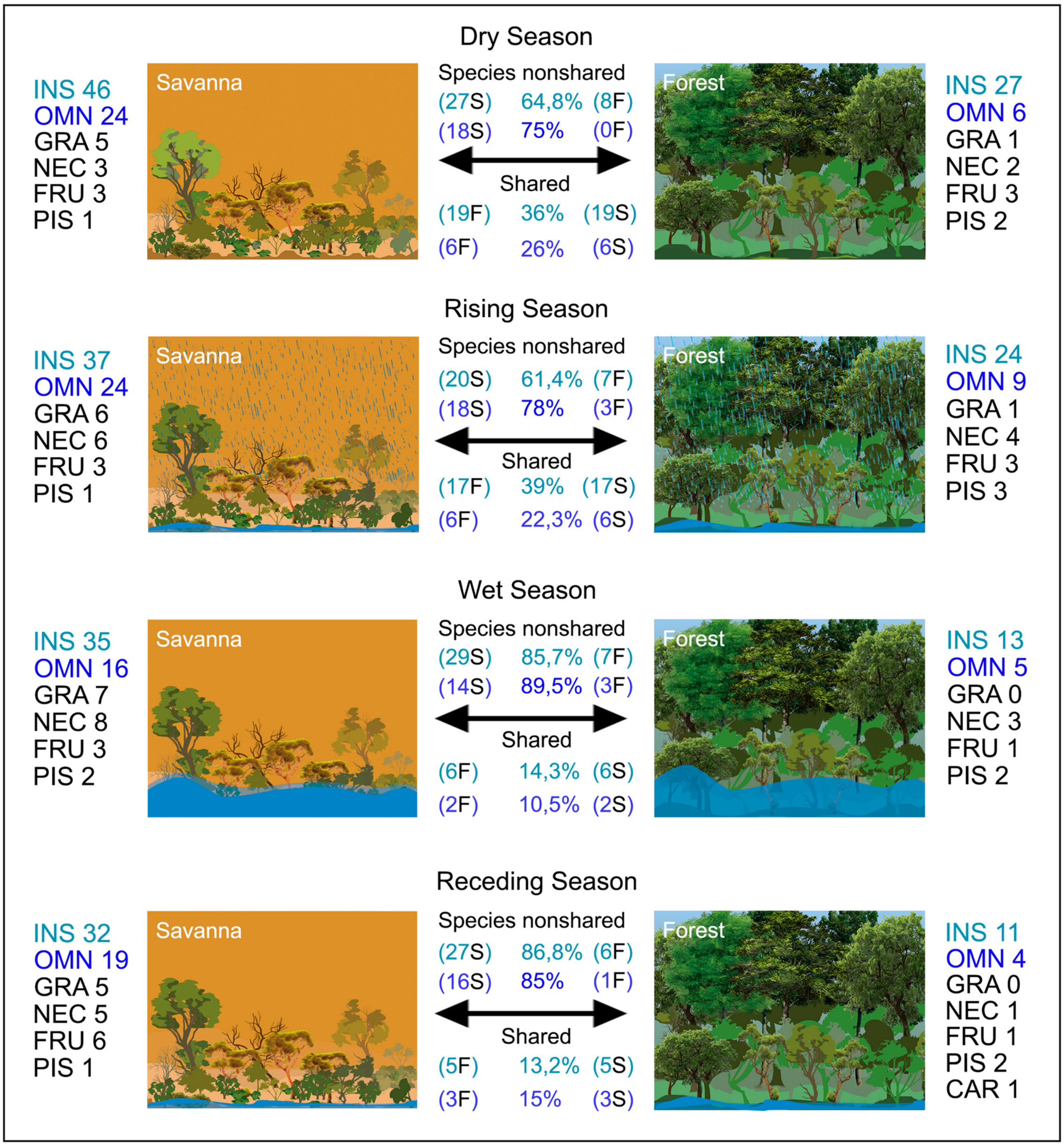

Fig. 6 Number and percentage of nonshared and shared species in trophic guilds between savanna and forest habitats over the four seasons (dry, rising, wet, receding) from 2014 to 2016 in the northeastern Pantanal, Mato Grosso, Brazil. Highlighted information in light blue indicates data on insectivores, and in dark blue indicates data on omnivores. The total number of species for each guild is presented in far left and right of the graphs. Guilds: INS: insectivores, OMN: omnivores, GRA: granivores, NEC: nectarivores, FRU: frugivores, PIS: piscivores, CAR: carnivores

indicates the occurrence of niche partition over space and time (Miyazaki et al. 2006; Riegert et al. 2011).

The annual and historical climatic and resource instability has been associated with the predominance of resident and omnivore species in the Pantanal (Willis 1979; Figueira et al. 2006; Signor and Pinho 2011). Corroborating these findings, we found 118 spp. of resident birds (87%), a result similar to that found by the work of Cintra and Yamashita (1990) (73% resident species), which used mist nets together with field observations. Resident species, such as the omnivores *Ramphocelus carbo* and *Saltator coerulescens*, that remain in the floodplain regardless of the season might explore a variety of food resources when resources are abundant, and competition is reduced. This response might also occur during the rising season; a similar but opposite trend of a narrowing diet when competition is high and food availability is lower might occur in the dry and wet seasons, which requires to further research. These species are known as 'imperfect generalists' because they may switch from being food generalists to using specific resources in response to resource availability. Some species from the most abundant guilds of insectivores also may behave like imperfect generalists, such as *Celeus* *flavus*, which occasionally feeds on small fruits (Sigrist 2009). Despite their diet plasticity and wise use of habitat heterogeneity, flood pulse affects many species (Figueira et al. 2006), decreasing or increasing their abundances in response to annual changes at the beginning and end of each of the four flood seasons, which are controlled by climate fluctuations (Fig. 2). The higher number of seasonal migrants in the Pantanal compared to that in other Neotropical forests (72% in Robinson et al. 2000, and 73% in Anjos et al. 2007) and the flexibility of these species to annual variation in timeline of the floods and droughts (Pinho et al. 2017) emphasizes the impacts of seasonal changes driven by periodic flooding.

The dry season, which corresponds to the Austral winter in the Pantanal, involves a (re)colonization of the floodplain after a long period of food scarcity and an increase in abundance of resident and seasonal migratory birds (Pinho et al. 2017). The arrival of some regional migrants in the Pantanal coincides with an increase in arthropod abundance, especially in savanna habitats (Lopes et al. 2016). Regional migrants, which comprised 17 of the recorded bird species in the present study (13%), may show flexible migratory behavior by exploring favorable times of the year to feed or reproduce in the Pantanal wetland (Figueira et al. 2006; Pinho et al. 2017). High bird density in savanna habitats increases interspecific competition, resulting in species segregation among different habitats and explaining species turnover as the main component of beta diversity (Figueira et al. 2006; Signor and Pinho 2011). Compositional differences among forest habitats, in contrast, are more affected by species loss, offering evidence of the low resource availability (Fjeldså 1999; Khanaposhtani et al. 2012). Despite the low number of species at these sites, forests contributed the most to the spatial differences in species composition throughout the floodplain.

The rising water season is associated with the fruiting of many forest trees and the germination and reproduction of many grasses, forbs, and aquatic macrophytes (Pott and Pott 2000). This period coincides with a gain in specialized guilds such as frugivores, nectarivores, graminivores, carnivores, and piscivores at the expense of insectivores and omnivores. The increase in plant resources for frugivores at this time increased the differences in community composition among the different forest types, i.e., evergreen and seasonal forests, increasing species turnover among these areas compared to that in the dry season. At the same time, at the peak of food resources in the floodplain, high food supply and low competition might have favored a broad diet, reducing habitat segregation (Riegert et al. 2011). The direct response of the guild specialists to increased food resources promoted by the rainy period demonstrates the strong impact that climate change may have on bird population dynamics. Reduction or alteration of fruiting periods could strongly affect frugivores such as the regional migrant *Pipra fasciicauda* (Terborgh and Winter 1983; Terborgh 1986; Peres 1994), leading them to lose their seasonal migratory habitat during flooding (Pinho et al. 2017).

The receding and wet seasons presented the highest average compositional dissimilarity, illustrating a reduction in habitat availability and food resource abundance when a great part of the floodplain becomes waterlogged. These changes caused an increase in the nestedness component of beta diversity, mainly when the flood water level was highest and the quantity of available resources might have a major effect on bird community dissimilarities. During the wet period, the numbers of bird species decreased, especially in forest habitats, probably because the inundated forest becomes restrictive for foraging and nesting, particularly by understory birds (Pinho et al. 2017). In addition, the sparse vegetation in the understory is thought to decrease bird diversity in these habitats (Fjeldså 1999; Khanaposhtani et al. 2012). Despite the loss of species richness as an explanation of the differences among forest habitats, seasonal flood migrants, i.e., *Dysithamnus mentalis* (Pinho et al. 2017), appeared in the wet season, bringing uniqueness to riverine forest sites (site 1).

Figueira et al. (2006) stated that forest habitats are richer and more stable than savannas like the *Cerrado* based on the ratio of seasonal versus resident species. Here, we consider community resilience as the changes in the species composition and structure of the overall community affected by environmental variation caused by the annual flood cycle (Ives and Carpenter 2007). From this perspective, the Pantanal landbird community is not stable but is instead very dynamic, with ecological processes varying among the different habitat types. Thus, the replacement of food resources in savanna habitats throughout the year was associated with greater stability in terms of species richness. However, the replacement of a generalist avian community with more specialized species assemblages highlights the transitional quality of these communities, changing the nature and strength of interactions among species (Ives and Carpenter 2007).

Forest habitats may be considered susceptible to landscape changes because of the presence of many forest-restricted bird species and the high pattern of nestedness structuring the bird assemblages. The loss of species within the forest patches will make later species replacement difficult in the severely fragmented areas because of dispersal limitations (Baselga 2010), indicating that the habitat type has lower resilience to disturbance. On the other hand, in savannas, drier climate conditions are thought to have a great impact on bird richness and species turnover because an increase in fire frequency would change the structure and the composition of the vegetation (Durigan and Ratter 2015; Van Langevelde et al. 2003). Wet forests may show greater resilience to climate fluctuations in the short term because the soil moisture levels remain more constant during the dry season. Thus, the conservation of the birds of the Pantanal depends on the maintenance of the high spatial habitat heterogeneity pinned to hydrological seasonality.

The pronounced turnover rate of landbirds in different habitats that was observed in the northeastern Pantanal indicates the importance of the different environmental drivers triggered by the flood pulse, which, in turn, affects the availability of the resources and dispersal capacities of the local avifauna. These ecological processes generate differences in the distribution of species throughout the seasons in response to environmental and habitat heterogeneity gradients. Insectivorous and omnivorous species were the predominant guilds during the seasons. The dry and rising seasons experienced increases in species richness and abundance in savannas, whereas forests, despite being less rich in bird species, offer specific habitat conditions related to food availability during the wet season in which a new set of forest-specialized birds appear. The type of vegetation structure was the main determinant of the dissimilarity of these areas. Forest and savanna environments presented a clear differentiation in the composition of bird species due to the structure of the vegetation. This novel information contributes to the understanding of how landbirds respond to seasonal changes in wetlands, such as the Pantanal, and allows the prediction of possible losses in avian diversity if natural environmental conditions are altered. Our study shows the importance of conserving large areas of the Pantanal with different forest and savanna physiognomies adapted to their dynamic natural hydrological cycle to ensure the protection of avian species.

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Compliance with Ethical Standards

Conflict of Interest The authors declare no conflict of interest with any data or information provided in this manuscript.

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