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Filipe Ferreira de Deus, Karl-L. Schuchmann & Marinêz Isaac Marques

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ORIGINAL ARTICLE



Seasonality in the Brazilian Pantanal influences avian functional diversity

Filipe Ferreira de Deus ^{a,b}, Karl-L. Schuchmann ^{a,c,d} and Marinêz Isaac Marques ^{a,b,d}

^aComputational Bioacoustics Research Unit (CO.BRA), National Institute for Science and Technology in Wetlands (INAU), Federal University of Mato Grosso (UFMT), Cuiabá, Brazil; ^bPostgraduate Program in Ecology and Biodiversity Conservation, Institute of Biosciences, Federal University of Mato Grosso, Cuiabá, Brazil; ^cOrnithology, Zoological Research Museum A. Koenig (ZFMK), Bonn, Germany; ^dPost-Graduate Program in Zoology, Institute of Biosciences, Federal University of Mato Grosso, Cuiabá, Brazil

ABSTRACT

Seasonality significantly affects environmental changes in the Pantanal, especially during wet and dry periods. Inundation and drought impact the onset of flowering and fruiting and the occurrence of insects. Because such resources may vary across seasons, it is expected that avian functional diversity also changes. We examine how functional diversity changed over time, as measured by functional richness and functional divergence. For functional richness, we observed a functionally overdispersed bird community over the seasons, whereas for functional divergence, two different patterns were found: (1) functionally overdispersed bird communities during the wet and receding seasons and (2) functionally clustered avian communities in the dry and rising seasons. The diversity of functional groups did not significantly vary across the seasons, as expected, but varied between forests and savannas. The environment has restricted resources in certain seasons, benefiting species with specific functional characteristics, however, bird species in the Pantanal are often generalists adapted to using a wide variety of food resources. Although the habitat turnover rate is an important factor that influences bird species composition across seasons, the changes in species composition still allowed the maintenance of certain functional characteristics, contributing to conservation of the existing functional groups in the ecosystem.

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Introduction


Functional diversity of communities is defined by grouping species according to similar biological or ecological characteristics (Tilman 2001; Petchey & Gaston 2002; Schleuter et al. 2010; Cadotte et al. 2011; Weiher 2011). This approach allows us to understand ecosystem functioning, community organization, coexistence among species, interactions among species, and environmental change (Lavorel & Garnier 2002; Folke et al. 2004; McGill et al. 2006; Díaz et al. 2007; Mason et al. 2007; Mouillot et al. 2007; Weiher 2011; Hanspach et al. 2012).

Considering that species play a role in the environment in which they coexist, environmental characteristics and life histories will determine how these interactions occur (Hagen et al. 2012; Ewers et al. 2013). Specific attributes, such as morphological, physiological, and ecological features, represent the functional attributes of species, and these features are directly affected by environmental filters (Jax 2005; Violle et al. 2007). Therefore, climatic and

environmental variations are drivers of functional diversity (Díaz et al. 2007). Limiting factors caused by environmental changes, such as fire, flooding, and drought, will determine species survival, resulting in the selection of those that are suitable and that have specific functional attributes adapted to the imposed conditions (Zobel 1997; Grime 1998; Hérault 2007; Barbosa et al. 2009). Thus, species may converge in their characteristics and have similar functions that allow them to co-occur in the environment and share the available resources (Tilman 1986; Levey 1988; Devey & Peres 2000; Ernest et al. 2000).

According to the environmental filtering hypothesis, environmental factors such as topography, soil, climatic conditions, and interactions among species are the main determinants of diversity and functional group richness (Weiher & Keddy 1995, 1999; Díaz et al. 1998; Mason et al. 2011; De Bello et al. 2013a, 2013b; Kraft et al. 2015). Therefore, environmental filters together with immigration, speciation, and competitive exclusion influence the community composition through regional and local biogeographical

CONTACT Filipe Ferreira de Deus  filipededeus88@gmail.com

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processes (Weiher et al. 1998; Loreau 2000; Shurin & Srivastava 2005; Fukami et al. 2007). Species with different or similar functional attributes will be able to coexist according to their ability to survive under imposed environmental conditions and competition (Hardin 1960; MacArthur & Levins 1967; Stubbs & Wilson 2004).

As a result of environmental changes, interactions and function may not remain constant (Kremen et al. 2007; Tremlová & Münzbergová 2007; Mouchet et al. 2010), as observed when environmental functions in bird communities are affected by anthropic activities (Fischer et al. 2007; Tschardt et al. 2008; Clough et al. 2009; Flynn et al. 2009). For example, during floods in the Pantanal, terrestrial and understory birds that feed on insects and other invertebrates move to non-inundated areas or to higher vegetation strata to find such resources (Adis et al. 2001; Adis & Junk 2002; Marques et al. 2007; Battistola et al. 2007, 2010; Donatelli et al. 2014). Therefore, understanding how species abundance, guilds, and the proportions of functional groups are affected by environmental changes is fundamental for ecology and useful for developing conservation strategies for threatened species.

Several statistical measures and indexes have been proposed to calculate functional diversity (Walker et al. 1999; Petchey & Gaston 2002; Mason et al. 2005; Villéger et al. 2008). Functional richness (FR) and functional divergence (FD) are two of the main components of functional diversity and indicate, respectively, the number of attributes the community has and how each taxon differs within the categories of each attribute (Mason et al. 2005). Using these components, it is possible to understand the degree of niche differentiation of the species and infer the resource availability in the environment. Niche diversification will determine the type of functional organization of communities, e.g., a functionally clustered bird community is expected to occur in savannas, where species have similar functional traits, in response to environments affected by frequent disturbances, such as fire and drought (Weiher & Keddy 1995; Sobral & Cianciaruso 2016). In forests, however, which are considered relatively stable and structurally complex environments, functionally overdispersed bird communities are expected, as the species dispersal capability rather than the niche is considered to be the most important factor determining functional groups (Mouchet et al. 2010; Sobral & Cianciaruso 2016). Therefore, in forest habitats, birds of different guilds with different functional attributes will supposedly be able to find resources for their survival, as these habitats do not

face drastic environmental changes, such as frequent burning and drought, as observed in some forests of the southern Pantanal where the bird community was seasonally more stable (Donatelli et al. 2014).

The Brazilian Pantanal is characterized as a dynamic ecosystem comprising several phytophysiognomies that are annually affected by floods (Nunes da Cunha et al. 2007; Junk et al. 2014). Contrasting conditions ranging from dry to flooded environments in different seasons affect resource availability. Because they are exposed to such environmental changes, bird species in the Pantanal may migrate or adapt in response to seasonality. The objective of this study was to investigate the temporal changes in the landbird community FR and FD in forest and savanna habitats across the four seasons in the Pantanal. It was expected that the functional diversity (FR and FD) would be similar between forests and savannas within each season, e.g., many different functional characteristics occurring during the dry season (higher bird diversity) and few functional characteristics in the wet season (lower bird diversity). Despite the fact that most of the bird species in the Pantanal are considered to be generalists (Signor & Pinho 2011), it was also expected that the diversity of functional groups would change across seasons because many species show migration or dispersal patterns, indicating the existence of clear species turnover in this ecosystem (De Deus et al. 2020).

Materials and methods

Sampling design and data collection

General information

Our study was conducted in the northeastern Pantanal in the SESC Pantanal area, Poconé, Mato Grosso, Brazil (16°39'S, 56°47'W) (Figure 1). This protected region comprises an area of approximately 4200 ha and is part of the Cuiabá River floodplain. The mean annual precipitation in the region of Poconé is c. 1400 mm, considering the flatter relief shape and the north position of this area the floods are shallower by 2 m depth range over the wet seasons between January to March (Nunes da Cunha & Junk 2004). Precipitation and temperature was recorded by a weather station at our study site and is shown in Figure 2. The annual flood cycles are divided into four seasons characterized as (1) wet, with the highest levels of flooding from January to March; (2) receding, when the level of the water starts to decline from April to June; (3) dry, the terrestrial phase caused by a strong hydric deficit from July to September; and (4) rising, starting with the onset of precipitation from October to December (Heckman

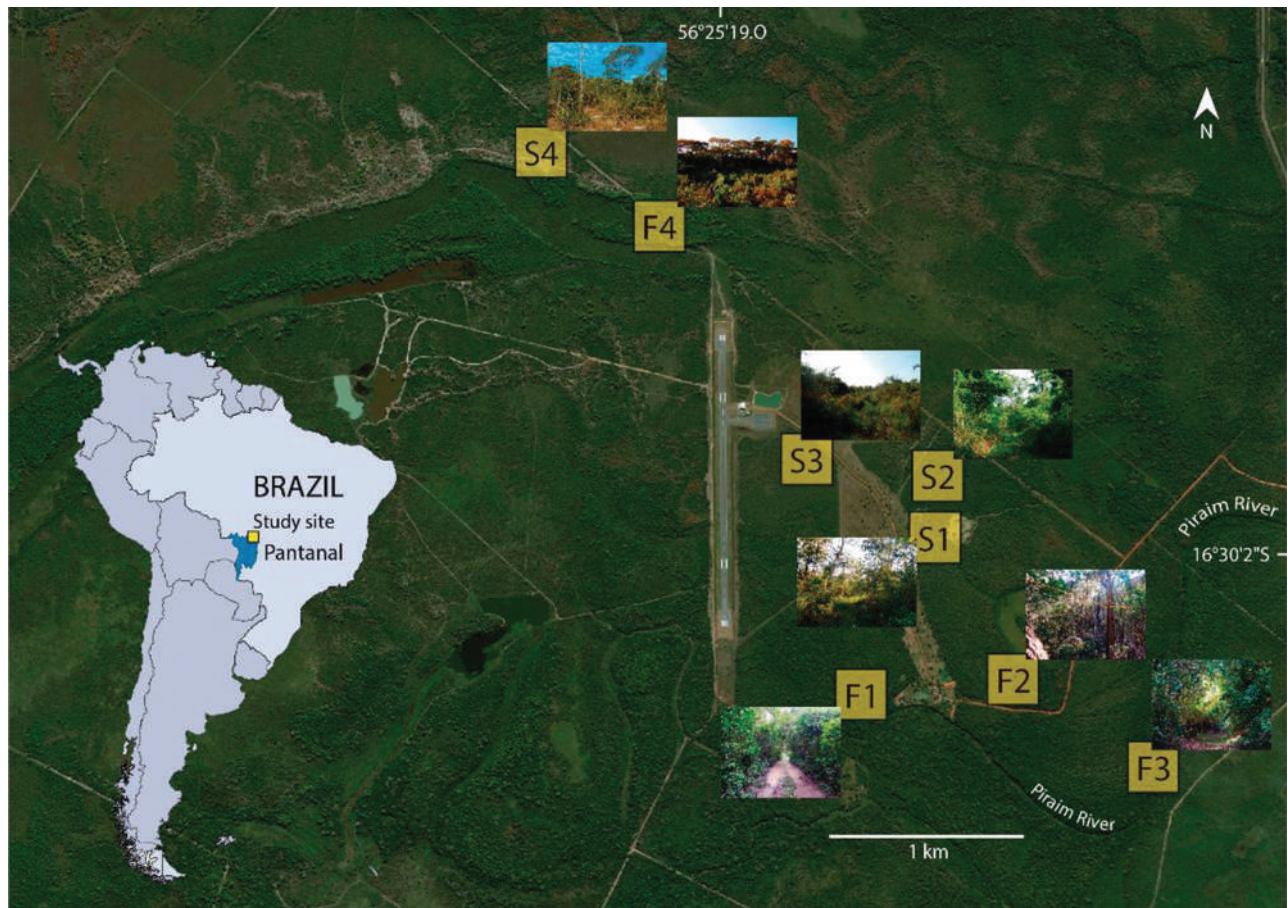


Figure 1. Study area and the mist nets sampling sites in the northeastern Pantanal, Mato Grosso, Brazil. Forests sampling sites are indicated as F1, F2, F3, F4, and savannas as S1, S2, S3, S4.

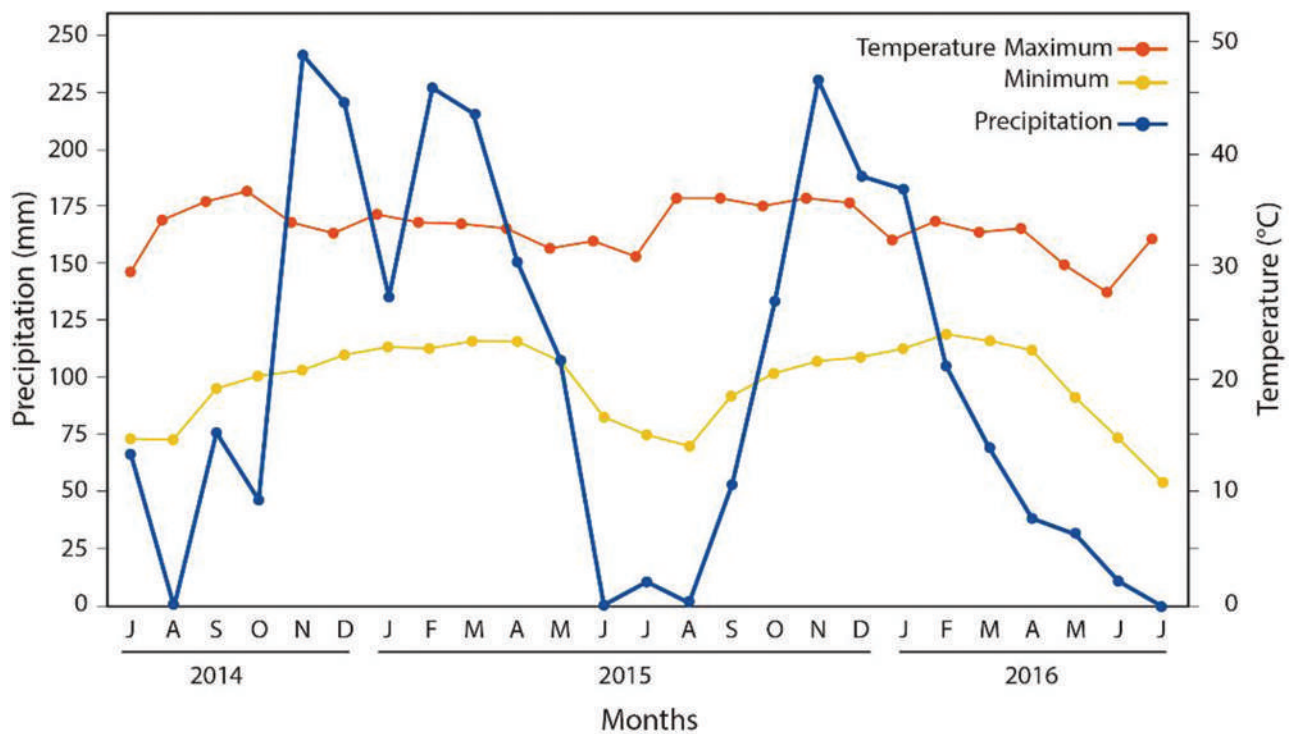


Figure 2. Precipitation and temperature over two annual cycles in one region of northeastern Pantanal, Poconé, Brazil.

1998). Eight sampling sites separated by at least 1 km were established. To capture the variation in vegetation, we randomly selected four savanna sites characterized mainly by scattered trees and a large proportion of grassland and shrubs and four forest sites defined mainly by a high proportion of large trees that form a coherent canopy structure. Forests were sampled 26 times and savannas 25 times over the 24 months of data collection from July 2014 to July 2016.

We captured birds using mist-nets (9×2.7 m, 20 mm mesh size, Bibby et al. 2000) that were open from 6:00–11:00 h and 15:00–17:00 h (Robbins 1981). Ten nets, separated by 200–250 m, were used in each site for six consecutive days each season. Avian nomenclature follows the South American Classification Committee (Remsen et al. 2009). This study is part of the biodiversity monitoring project Sounds of the Pantanal, Computational Bioacoustics Research Unit (www.cobra.ic.ufmt.br, INAU/UFMT/CNPq/INCT), conducted under SISBIO permit no. 39095 (K.-L. Schuchmann).

Functional structure

To quantify functional diversity, the following functional traits were used: avian guild, body size, and stratum that each species occupied. Guilds were insectivores, omnivores, frugivores, granivores, nectarivores, and piscivores. Species were grouped according to their dominant food resources (Wilman et al. 2014). Body size was a composite that comprised body mass, total length, bill length and width, wing length, tail length, and tarsus length. Birds were weighed on a spring balance (Pesolas®), and measured by a handheld caliper (accuracy of ± 0.1 mm). We used the average of each morphometric category of each species. Foraging strata were ground, understory, midstory, canopy, and water, and seven associations among these categories were used because birds use more than one foraging stratum: midstory to canopy, terrestrial to canopy, terrestrial to midstory, terrestrial to understory, terrestrial and aquatic, understory to canopy, and understory to midstory (Stotz et al. 1996).

Statistical analysis

Because variables were categorical and numerical/continuous, the *dist.ktab* method (distance coefficient of mixed variables) was applied, which generalizes the Gower's general distance coefficient, allowing the treatment of several statistical types of variables in the calculation of distances. This function is included in the *ade4* package of R, and we used this modified Gower distance to treat various types of variables, as our measure of functional diversity (Pavoine et al. 2009). We calculated

functional diversity following Petchey and Gaston (2002). The dendrogram generated based on the measure of functional diversity quantifies the extent of complementarity among species trait values by estimating the distances between species in trait space. We used null models and calculated the two main functional components, FR and FD, for forests and savannas across all the seasons. The null models help to identify which process, competition or environmental filtering determines the functional groups (Mason et al. 2007). To calculate the FR, we used the standardized effect size of phylogenetic diversity in communities (*ses.pd*), and the standardized effect size of mean pairwise distances in communities (*ses.mpd*) was used to calculate the FD (software package *picante*; Kembel et al. 2008). These metrics are applied to quantify the relative excess (overdispersion) or deficit (clustering) of the phylogenetic diversity of certain species groups in the pooled community (Mazel et al. 2016). These phylogenetic metrics were used to create a functional dendrogram but not to perform phylogenetic analyses in this study. These metrics were employed because phylogenetic trees and functional dendrograms have the same structure.

The calculated FR is the number of functional attributes in the community. Large values of FR indicate that many different groups use the available resources. Therefore, values farther from zero (in both the positive and negative directions) have a greater effect on functional diversity than those closer to zero. The FR test provides values of the FR, standardized by the richness and represents the functional diversity values in comparison to those expected by the null model. In other words, these FR measures represent a comparison of the existing functional diversity and the expected by chance based only on the richness of the community. Thus, positive values represent higher FR than that expected for the richness. Negative values represent a lower FR than that expected for the richness. In contrast, FD indicates how the attributes are distributed within the space of functional characteristics. For example, in the functional group represented by granivores birds, we can find species with different characteristics, such as longer or shorter beaks, and these differences in species characteristics within the same functional group are encompassed by FD.

We randomized the community data matrix with the independent swap algorithm, maintaining species occurrence frequency and sample species richness (Kembel et al. 2008). Positive values of *ses.pd* and *ses.mpd* indicate functional overdispersion, meaning the values are greater than expected based on species richness. Negative values of *ses.pd* and *ses.mpd* indicate functional clustering, with values lower than expected

on the basis of the observed species richness (Weiher & Keddy 1995). We used analysis of variance (ANOVA) with the observed functional diversity to compare habitats and seasons. 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 & Fortin 2010; Legendre et al. 2015). The analyses were performed in R (R Development Core Team).

Results

At our study site, we recorded 132 species, approximately 40% of all landbird species known in the Pantanal. We captured 2,104 individuals from 104 genera and 26 families, and 2,013 individuals were measured. Landbirds (2,025 individuals) comprised 96% of the captures, followed by semi-aquatic birds (three kingfishers, one heron, 79 individuals).

Functional richness and divergence

Considering the FR, forests had positive values in all four seasons, indicating a greater FR than that expected by chance (overdispersion) (Table 1). FR in one forest sampling unit was negative, during rising season. For savanna environments, FR was positive in all areas and seasons (Table 1). FR was large and positive when forests and savannas were analyzed together.

When the standardized effect size of the mean pairwise distance was calculated for the FD, we found that forest areas showed positive and negative values throughout all seasons except the receding season. We observed that the receding season had higher values of FD than expected based on the richness, showing that taxa differ greatly within the categories of each attribute. In savannas, positive values of FD predominated during the wet and receding seasons, and negative values predominated in the dry and rising seasons. Considering the FD in both forests and savannas,

a functionally clustered (negative values) and functionally overdispersed (positive values) bird community was observed in the dry/rising and wet/receding seasons, respectively. Negative values were found in five areas during the dry season and in six areas during the rising season. No pattern of FR and FD was detected during dry and wet season to one forest site, since the small number of captured species in these periods.

In the dendrogram, avian guilds were the main units considered in the formation of groups. Species occupying different foraging strata were found in all guild groups. Morphometric characteristics were visible in the separation of groups of species with a relatively high body mass and total length, separating them from the other species that were members of the same guild, such as *Dendrocolaptes platyrostris* (INS), *Butorides striata* (PIS), and *Crypturellus undulatus* (OMN) (Figure 3). ANOVA showed significant differences in FR among habitats, but season and the habitat/season interaction did not have significant effects (Figure 4).

Discussion

Forests

For the Pantanal forests, the predominance of positive FR values indicates a functionally overdispersed bird community, a pattern to be expected for such habitats due to the lower frequency of natural disturbances than that observed in savannas (Furley 2006; Mouchet et al. 2010; Sobral & Cianciaruso 2016). In comparison to savannas, forests are considered to be more stable environments a greater number of potential niches, allowing for the co-occurrence of species. In the rising season, a negative FR occurred in a monodominant Cambará tree forest (Cambarazal, *Vochysia divergens*). Due to the predominance of one tree species, the avian diversity was closely related to vegetation phenological patterns, such as flowering and fruiting. Cerrado forests were found to be functionally clustered by Sobral

Table 1. Data of functional richness (FR) and functional divergence (FD) expressed as ses.pd (standardized effect size of phylogeny) and ses.mpd (standardized effect size of mean pairwise distances), respectively, in forests and savannas during two annual cycles in northeastern Pantanal, Mato Grosso, Brazil. Forests sampling sites are indicated as F1, F2, F3, F4, and savannas as S1, S2, S3, S4.

		Wet			Receding			Dry			Rising		
		Species	FR	FD	Species	FR	FD	Species	FR	FD	Species	FR	FD
Forest	F1	14	0.91	0.38	14	0.72	0.07	12	0.87	-0.12	21	0.77	-0.23
	F2	1	-	-	5	2.21	0.11	1	-	-	5	1.91	0.31
	F3	8	1.27	0.23	3	2.03	0.07	14	0.88	0.11	16	0.56	0.04
	F4	7	0.70	-0.30	3	3.27	0.11	30	0.41	-0.36	28	-0.26	-0.08
Savanna	S1	35	0.84	0.03	28	1.02	0.15	32	0.57	-0.31	34	0.61	-0.12
	S2	43	0.58	0.16	37	0.85	0.11	26	0.86	0.01	43	0.28	-0.09
	S3	32	0.31	0.02	31	0.12	0.34	52	0.52	-0.28	24	0.45	-0.11
	S4	25	1.00	0.28	22	0.65	-0.26	48	0.50	-0.25	48	0.38	-0.21

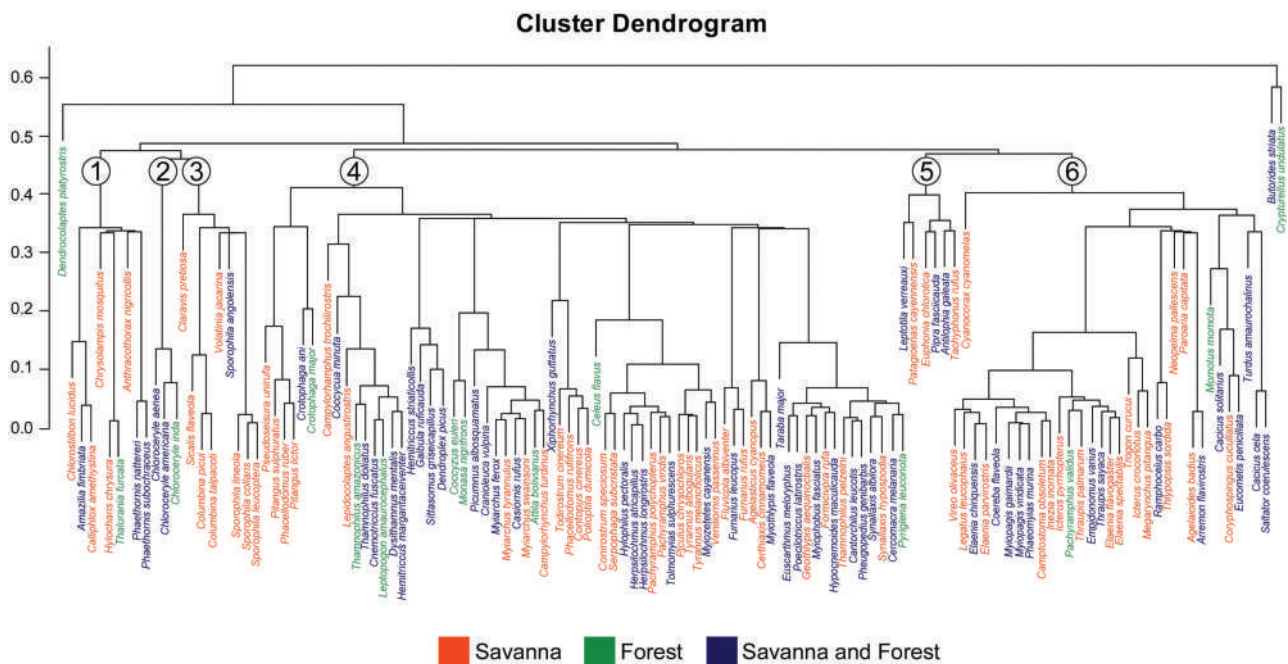


Figure 3. Dendrogram of the bird species assemblage based on functional characteristics in forests and savannas during two annual cycles in the northeastern Pantanal, Mato Grosso, Brazil. The species were grouped by guild: 1 – nectarivore, 2 – piscivore, 3 – granivore, 4 – insectivore, 5 – frugivore, and 6 – omnivore. Species captured exclusively in savannas were marked with orange, exclusively in forests with green, and in both habitats with blue.

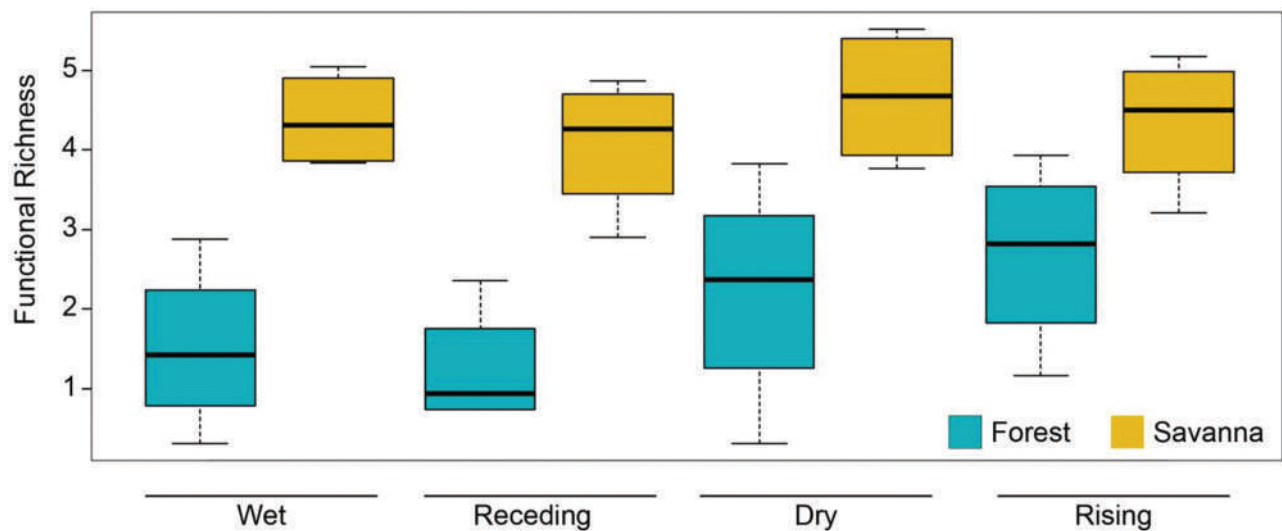


Figure 4. Boxplots of the functional richness of forests and savannas during four seasons in the northeastern Pantanal, Mato Grosso, Brazil.

and Cianciaruso (2016); however, they were found to be functionally overdispersed in our study, showing that the seasonality of the forests in the Pantanal may create environmental conditions supporting different niches, e.g., allowing the coexistence of species from different guilds over the seasons. Many avian studies from Brazilian forests showed higher diversity of species in forests or habitats associated with forests as in

veredas and cerradão (Tubelis & Cavalcanti 2000; Galina & Gimenes 2006; Tubelis 2009; Donatelli et al. 2014)

In the forests, the FD indicated the random functional distribution of the bird community during the wet, dry, and rising seasons, as indicated by the equal numbers of areas with positive and negative values. The Cambarazal showed negative values in these

three seasons in FD and FR, suggesting the selection of bird functional traits by environmental filters in this type of vegetation. The environmental conditions and the supply of resources (e.g., fruits, insects, fishes) define the certain types of niches available, resulting in use by species with preadapted characteristics. In the nature the availability of these resources may vary according to climatic conditions and seasons, affecting the distribution and abundance of guilds of various taxonomic groups as arthropods, mammals, and birds (Janzen & Schoener 1968; Levey 1988; Devey & Peres 2000; Post & Forchhammer 2002; Battirola et al. 2007, 2010).

Therefore, avian species belonging to similar functional groups will not have accentuated differences in their trophic characteristics in the Cambarazal. In addition, one of the forest areas in our study displayed few avian species across the seasons, and they were mainly insectivores and omnivores, while other forests contained additional groups (piscivores, nectarivores, and frugivores); these differences in the number of functional groups may have affected the functional distribution of the Pantanal bird community. In cases in which positive values were found for FD, the differences in species functional traits are more pronounced, reflecting a bird community with niche differentiation (Mouchet et al. 2010). However, in our study, most species of each guild had similar morphological and body mass characteristics, and few species were large (total length) or had a high body mass. The species with these characteristics were clearly isolated at the extremes of the dendrogram (Figure 3).

Savannas

According to Sobral and Cianciaruso (2016), the natural fires and long dry periods in the Cerrado savanna are environmental filters that select for generalist species adapted to the environment, constituting functionally random communities. However, our study indicates that the avian community in the Pantanal savanna sites analyzed is functionally overdispersed in terms of FR and FD during the wet and receding seasons and functionally clustered during the dry and rising seasons. Even in some sites with a high number of species, negative values were found for FD, indicating low functional diversity and also a possible redundancy between them. Therefore, the dry and rising seasons in the Pantanal favor species with similar functional characteristics.

We expected the flood period corresponding to the wet season in the Pantanal to have similar effects as other environmental factors, such as drought and fire

in savannas, on the functional diversity. These environmental impacts may limit resource availability for certain groups of species, generating negative values for functional diversity and consequently functionally clustered communities (Weiher & Keddy 1995). However, we found a functionally overdispersed bird community essentially dominated by Cerrado (savanna) bird species and affected by the annual floods each year. This finding suggests that functional traits can play an important role in this avian community and shows that flooding is not equivalent to fire and droughts in terms of its effects on functional diversity. According to the limiting similarity theory for coexisting species, niche differentiation is required by the different functional characteristics of the species (MacArthur 1958; MacArthur & Levins 1967; Weiher & Keddy 1995). In the Pantanal, we found a wide spectrum of niches and species supposedly competing with each other. Therefore, instead of limiting species with similar functional traits, there is a high diversity of species with similar characteristics occurring in this environment, mainly because they are generalist species adapted to the environmental changes triggered by floods and droughts.

Overview

One of the main drivers of the avian species distribution across habitats and seasons in the Pantanal is the turnover pattern (De Deus et al. 2020). Thus, the fluctuation in bird species diversity across the seasons may also be responsible for the observed functional groups. These groups may remain stable over time, but the species composing these groups may change while maintaining the functional traits of the replaced species. Such replacement has been considered to be one of the factors responsible for changes in functional diversity (Srivastava & Vellend 2005; Mayfield et al. 2010), and in fact, the changes in species diversity led by this replacement can also promote the stable diversity of functional groups (Fukami et al. 2005; De Bello et al. 2009). Therefore, turnover and competition serve as environmental filters as a response to resource availability, affecting the occurrence and functional characteristics of the species (Silvertown 2004; Stubbs & Wilson 2004; Leclerc & DesGranges 2005; Mason et al. 2007). The presence of generalist species adapted to flooding and able to use food resources according to their availability allows the permanence and co-occurrence of the species in the Pantanal across seasons. In this study, the main functional differences in bird communities were related to habitat type. We observed a functionally overdispersed bird community

according to the FR across all seasons (96.6% of the areas) and according to the FD during the wet and receding seasons (86.6% of the areas). Therefore, the bird species in these communities may become established in the environment independent of their niche or functional characteristics. According to neutral theory through dispersion, species have the same chances of establishing themselves in an environment (MacArthur 1963; MacArthur & Wilson 1967), and environmental conditions do not necessarily structure the functional groups in the community (Hubbel 2001; Jung et al. 2010; Cianciaruso et al. 2012). For the dry and rising seasons, a functionally clustered bird community was observed in regard to the FD when all habitats were considered together. Most of the areas displayed negative values (86.6%), with such values predominating in the areas with high numbers of species. The functional traits varied less than expected according to the richness among the functional attributes observed in these sites, indicating possible functional redundancy in these communities, which is a novel finding for the Pantanal wetlands. Species with a similar function could replace the roles of others in the case of species loss (Walker 1992, 1995; Lawton & Brown 1993), and for the Pantanal, we observed the high replacement of species across seasons and habitats, but the functional groups remained the same.

Conclusions

In our Pantanal avian community study, we observed that even the niches, the competition, and the dispersal ability of the species can strongly affect the functional structure of these communities. The generalist species of the Pantanal and their dispersal ability were the main determinants to explain the functional structure in this study. Therefore, the structure of the habitats, the environmental conditions, and the evolutionary history of the species are important in regard to the definition of functional groups, indicating that different patterns of bird functional community composition may be observed when comparing different seasons and habitats of different ecosystems. The seasonality affected the guild trophic structure, species richness, abundance and distribution of the species over the seasons in Pantanal. Functionally overdispersed bird communities predominate over the seasons to most part of the areas of forest and savanna in the Pantanal. Two patterns of functional divergence were found: bird communities functionally overdispersed during wet and receding, and functionally clustered during dry and rising season. Studies considering environmental changes over time provide important information about ecosystem

functioning and the distribution of species under adverse conditions and environmental impacts (Magurran & Dornelas 2010; Mouillot et al. 2012).

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Disclosure statement

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ORCID

Filipe Ferreira de Deus  <http://orcid.org/0000-0002-2936-8074>
Karl-L. Schuchmann  <http://orcid.org/0000-0002-3233-8917>
Marinêz Isaac Marques  <http://orcid.org/0000-0002-9890-8505>

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