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Review article

Knowledge gaps and biases in the Pantanal indicate future directions for ornithological research in large wetlands

GILBERTO J. FERNÁNDEZ-ARELLANO,*[1] ALBERTO L. TEIXIDO,[2] BIANCA BERNARDON,[1] ELAINE R. BUENO,[1] TIAGO V. FERREIRA,[1] STELA R. A. GONÇALVES,[1] MOISÉS JESUS,[1] KAMILA P. C. S. THOMAS,[1] MAYARA ZUCCHETTO,[1] VÍTOR Q. PIACENTINI[3] & JOÃO B. PINHO[1,3]

[1]*Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Universidade Federal de Mato Grosso, Cuiabá, Brazil*

[2]*Departamento de Botânica e Ecologia, Universidade Federal de Mato Grosso, Cuiabá, Brazil*

[3]*Programa de Pós-Graduação em Zoologia, Departamento de Biologia e Zoologia, Universidade Federal de Mato Grosso, Cuiabá, Brazil*

While taxonomic and biogeographical biases are often acknowledged, those for certain biological responses and species traits are routinely overlooked, generating major gaps in knowledge and conservation of biodiversity. Biases in research on birds – an over-sampled, diverse vertebrate class – may be readily detectable, and wetlands are important species-rich ecosystems in which to identify biases and research gaps for birds. The Pantanal, one of the world's largest wetlands, is globally relevant for bird conservation. In this wetland, we determined spatial, temporal, taxonomic and biological response-related biases in ornithological studies to guide future research in this ecosystem and, ultimately, in major global wetlands. Avian research was geographically biased, with 61 studies conducted in the Brazilian Pantanal and only one in Bolivia. Most studies were concentrated near urban centres, with poorly explored areas in the central Pantanal. Research was also over-represented during the dry season when field conditions are more favourable, but such temporal bias may hamper migration studies. Considering their richness, some families were studied disproportionately more (e.g. Jacanidae) or less (e.g. Tyrannidae). Some species (e.g. Wood Stork *Mycteria americana* and Yellow-billed Cardinal *Paroaria capitata*) were included in > 25% of studies, whereas a relatively low number of threatened bird species were studied. Behaviour was the most studied response, followed by abundance and reproduction, which were considered for > 65% of species studied. We conclude that further research needs to be focused on unexplored areas and periods, less detectable species, and ecological processes (e.g. interspecific interactions). Additionally, our results can provide useful information to better address future work and bird conservation actions in other large wetlands. For example, major gaps detected here constitute a primary roadmap to guide research in under-sampled regions, such as the Canadian peatlands and Tonlé Sap Lake. Specifically, more studies on waterbirds in highly diverse wetlands from low-income countries (e.g. Okavango and Sundarban Delta) may help to disentangle the essential functional role provided for these species and to prioritize conservation actions in regions with limited research capacity.

Keywords: biological response bias, bird conservation, Brazil, spatial and seasonal bias, taxonomic bias, threatened species.

*Corresponding author.
Email: giliusfernandez1@gmail.com

Research biases and resulting knowledge gaps are important and prevalent topics in biological and ecological studies. These biases are frequently geographical, with oversampled sites near research centres and major urban areas, while remote areas remain poorly explored (Nelson *et al.* 1990, Moerman & Estabrook 2006, Ribeiro *et al.* 2016). Likewise, taxonomic biases result in disproportionate surveys of few biological groups, often neglecting megadiverse clades (Clark & May 2002, Bini *et al.* 2006, Mokany & Ferrier 2011). In addition, further biological and ecological research biases that result in knowledge shortfalls for some species traits, biotic interactions, evolutionary patterns and species- or assemblage-level responses (e.g. richness, abundance, diversity) have received little attention (Cardoso *et al.* 2011, Schmidt-Lebuhn *et al.* 2013, Deikumah *et al.* 2014, Hortal *et al.* 2015). This uneven distribution of research across geographical areas, biological groups, traits and responses, and the knowledge gaps that result, ultimately have key consequences for biodiversity conservation, such as ineffective management strategies (Nelson *et al.* 1990, Clark & May 2002, Bini *et al.* 2006, Hortal *et al.* 2015, Lees *et al.* 2020). Identifying and filling knowledge gaps is therefore of paramount importance to direct future research to provide unbiased databases that can ultimately lead to improved decision-making and efficient conservation policies (e.g. responses of species to global change, conservation of priority areas or suitable reintroduction actions).

Birds are among the most diverse groups of vertebrates, ranging from small- to large-sized species and comprising both generalists and specialists (Gill 2007, Barrowclough *et al.* 2016). Richness patterns show an increase in bird species number from temperate to tropical zones (Orme *et al.* 2006). However, ecological studies of birds are clearly biased to less diverse temperate regions (Stutchbury & Morton 2001, McRae *et al.* 2017). Notably, the Neotropics is the most bird-rich realm of the world (Stotz *et al.* 1996, Smith *et al.* 2014), but more research is still required to better understand the ecology, evolution and distribution patterns of biodiversity in this biogeographical region (Antonelli *et al.* 2018). For example, major gaps in natural history knowledge of Neotropical birds limit understanding of the response by species to environmental changes (Lees *et al.* 2020).

A particularly important ecosystem for bird study and assessment of related sampling biases are wetlands. Wetlands provide food resources, breeding grounds and suitable habitat to a high diversity of resident and migratory bird species (Webb *et al.* 2010, Xia *et al.* 2017, Elliott *et al.* 2020). However, major knowledge gaps about the conservation value of wetlands for birds remain, especially under the existing rates of degradation (Ma *et al.* 2010, Xia *et al.* 2017, Giosa *et al.* 2018) and given the mandatory international conservation agenda for these ecosystems (e.g. goals 6.6 and 15.1 of the Agenda 2030: UN General Assembly 2015). The Pantanal is the world's largest tropical wetland (Fig. 1), covering *c.* 200 000 km^2 of seasonally flooded grasslands, savannas and evergreen and semi-deciduous forests through Brazil, Bolivia and Paraguay (Junk *et al.* 2006a, Overbeck *et al.* 2015). This wetland is especially important for breeding and feeding of both resident and migratory birds, and harbours one of the most species-rich bird faunas in the world (Tubelis & Tomas 2003). In the Pantanal, seasonality coupled with the proximity of three major ecoregions (i.e. Amazonia, Cerrado and Chaco) supplies diverse habitat and food resources, which ultimately determine the breeding season, abundance and diversity of birds (Pinho & Marini 2012, Pinho *et al.* 2017, Thomas *et al.* 2020). However, few studies have described the spatial and temporal dynamics of Pantanal bird communities (Figueira *et al.* 2006, Donatelli *et al.* 2017) or aspects related to behaviour, reproduction and conservation of species (Yabe 2009, Yabe *et al.* 2011, Pinho & Marini 2012, 2014, Pinho *et al.* 2017, Thomas *et al.* 2020). In recent decades, the spread of pastures for cattle, soy production and the introduction of exotic species have increased the rates of fragmentation and native habitat loss in the Pantanal by about 11% (MapBiomas 2017, Tomas *et al.* 2019). Despite this pervasive landscape conversion, the Pantanal still has the fewest protected areas among Brazilian biomes and is neglected in terms of ecological restoration (Guerra *et al.* 2020). Identifying gaps in ornithological research is crucial to guide future studies and thus conservation actions in this internationally important wetland. Ultimately, identification of knowledge gaps in the Pantanal can also serve as a foundation to outline research priorities and provide suitable conservation actions based on bird ecology research across wetlands worldwide.

To better understand the extent and limitations of our current knowledge about Pantanal bird

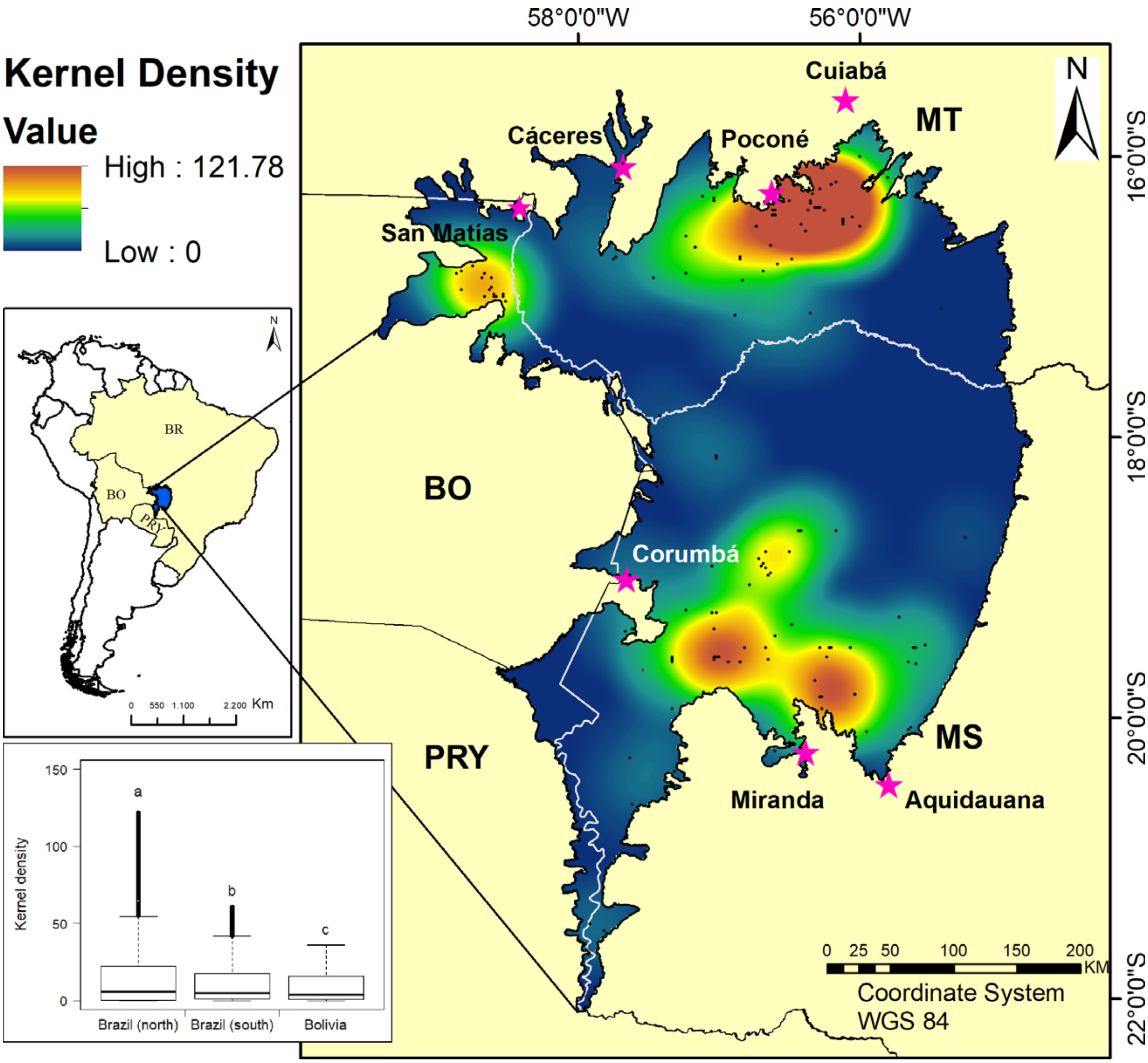

Figure 1. Mean kernel density (studies/km^2) for cases (each point refers to a single case) of ornithological publications in the Pantanal biome. Areas from higher to lower density of studies are depicted by a red-to-blue (i.e. high-to-low) colour gradient. Major cities (purple stars) in which most of the studies were concentrated (i.e. highest mean kernel density by concentrating the highest numbers of sampling points, shown as black dots) are indicated. The boxplot shows significant differences in the mean kernel density across regions. Different letters indicate significant differences ($P < 0.001$).

species and communities, we investigated spatial, temporal, taxonomic and biological response-related biases in this region. Specifically, our goals were to determine distribution among regions and sites across the Pantanal, and between seasons and periods following the flood regimen changes, among bird species and families, including threatened species, and representation of traits related to population and community dynamics, biotic interactions, genetics and functional traits. By assessing biases and identifying key gaps in ornithological research in the Pantanal, we can provide useful information to better address future work and bird conservation actions.

METHODS

Data source

We surveyed articles on 31 December 2018 in the Scielo (www.scielo.br) and the Web of Science (hereafter, WOS; www.webofkowledge.com) databases. Scielo is an electronic database covering a selected collection of Ibero-American scientific journals comprising articles in English, Portuguese and Spanish. We searched for 'bird' or 'birds' and 'Pantanal' in the title, abstract and keywords of articles from 1990 to 2018. We also searched for 'ave' or 'aves' and 'Pantanal' to complete our survey for articles in Portuguese or Spanish. We focused exclusively on bird species native to the Pantanal biome, including Brazil, Bolivia and Paraguay. After the literature survey, we selected articles specifically focused on birds based on the title and abstract. The database ultimately comprised the following items: year of study, geographical coordinates of the survey location(s), studied families and species, period(s) and month(s) of study, species threat category following both the IUCN Red List (www.iucnredlist.org) and the Brazilian Red List (MMA 2014), and studied biological responses (see 'Biological response biases' section). Studies frequently reported data from multiple species and families and several species responses. Therefore, each relationship studied between a given species and a specific response within an article was called a case, with the exception of diversity and richness, which were considered only once in each article, since they include all studied species. The taxonomy of all species reported was updated according to Piacentini *et al.* (2015). Species known to occur only outside the Pantanal (e.g. in neighbouring ecosystems, such as the Amazon forest) and some clear misidentifications or incomplete identifications were discarded; this was based on the revised species list for the Pantanal (cf. Tubelis & Tomas 2003, Nunes 2011).

Spatio-seasonal biases

To determine geographical research bias, we obtained the geographical coordinates included in the articles. When coordinates were missing, they were obtained by locating study sites in Google EARTH satellite imagery. Due to conservation concerns, coordinates from one of the articles (Pinto-Ledezma *et al.* 2014) were originally not disclosed, but they were made available to us upon request to the main author. These coordinates remain undisclosed in our available data (Fernández-Arellano *et al.* 2021). We followed Assine *et al.* (2015) to delimit the Pantanal area, which was subsequently divided into four sub-regions: Bolivian, Paraguayan, northern Brazilian and southern Brazilian. We used ARCGIS 10.5 software (ESRI, Redlands, CA, USA) to assess the density of studies by elaborating density raster layers by kernel interpolation (Yang *et al.* 2013, Ribeiro *et al.* 2016) with a resolution of 0.0083° (~ 1 km). To do this, we used the geographical coordinates described in the articles together with the coordinates that we obtained from the study sites as explained above. Overall, the density analysis contained 228 sites from 197 studies.

The kernel interpolation method is based on the definition of circular areas of influence around occurrence points (i.e. sampling points) of a phenomenon. Within the area of influence, the occurrence of the phenomenon decreases from the point to the limits according to a Gaussian function (Silverman 1986). Thus, the kernel density estimates the density of points, representing the number of studies per square kilometre. To determine differences in density among sub-regions, we generated 10 000 uniformly random points within the Pantanal, following the real distribution of the studies and the relative size of the four sub-regions (no points were generated in Paraguay, as no studies were conducted there; see Results), and subsequently calculated the mean kernel density values for each sub-region (Ribeiro *et al.* 2016, Teixido *et al.* 2020). To test for differences in mean kernel density values among sub-regions, we conducted an analysis of variance (ANOVA) with subsequent Tukey *post-hoc* test to compare significant differences between sub-region pairs in R (R Development Core Team 2018).

To determine temporal research bias, we included both the period(s) and the month(s) of study included in the articles. The Pantanal is characterized not only by a seasonal climate with a dry and a wet season, but also by a flood-pulse dynamic defined by a dry period, a flood period shortly following the rains, and a runoff period (Junk *et al.* 2006a, Pott & Silva 2015). We therefore categorized the articles into dry, wet, flood and runoff periods, or any combination of these when an article included two or more periods. We used the same method to classify articles into different months of study (July–September corresponds to the dry period, October–December to the wet period, January–April to the flood period, May–June to the runoff period: Junk *et al.* 2006a, Pott & Silva 2015).

Taxonomic biases

To determine taxonomic bias, we recorded both the families and the number of species per richness of the family recorded in the Pantanal using data from Tubelis and Tomas (2003) and Nunes (2011). For each family (i), we calculated the percentage of total species richness which it contributed (b_i) and the percentage of all articles in our database that included that family (a_i). Then, we calculated a relative bias rate (BR_i; Nemésio *et al.* 2013, Ribeiro *et al.* 2016) for each family with the formulae:

$$\mathrm{BR}_i = a_i / b_i \quad (1)$$

$$\mathrm{BR}_i = (b_i / a_i) \times (-1) \quad (2)$$

When the values of a_i were higher than the values of b_i, we used Equation 1, and when the values of b_i were higher than the value of a_i, we used Equation 2 (Nemésio *et al.* 2013, Ribeiro *et al.* 2016). Positive values indicate over-representation and negative values under-representation of family i in the literature than expected from its contribution to total species richness, and we tested the statistical significance of this bias using linear regression. Both percentages were square-root transformed to standardize the differences of the units of measure. Subsequently, we tested for significant departures of the slope from 1 (i.e. the expected relationship: $\beta \pm \mathrm{se} = 1 \pm 0$) in the observed relationships with t-tests (Ribeiro *et al.* 2016). When the observed slope is significantly > 1 the bias is positive and when < 1 the bias is negative. The analyses were conducted in R 3.5.1 (R Development Core Team 2018).

Biological response biases

We explored research biases and consequent knowledge gaps related to the set of different aspects of biodiversity beyond taxonomy and geographical distribution, including population and community dynamics, distributional data, evolutionary patterns, responses to abiotic conditions and ecological interactions (i.e. biological responses; reviewed in Hortal *et al.* 2015). To classify biological responses, we followed Teixido *et al.* (2020). Specifically, we distinguished the conventional assemblage-level species responses: abundance (single-species and multispecies abundance), diversity (alpha and beta, divergence and evenness) and richness of species. We also included responses related to ecological interactions, specific and individual conditions and genetic diversity: behaviour (e.g. moving, foraging, diet), distribution, functional traits (e.g. body mass, wing size), genetics (e.g. heterozygosity, allelic richness), interspecific interactions (antagonism, commensalism, competition, mutualism), and reproduction (e.g. clutch size). Distinctions among behavioural and interspecific interactions were useful to distinguish between intraspecific co-operation or aggression, and interspecific mutualisms (e.g. seed dispersal), antagonisms (e.g. parasitism) or competition (e.g. for nesting sites), respectively.

RESULTS

Spatio-seasonal biases

We found 75 ornithological studies that had been conducted in the Pantanal wetland and 2161 cases (each one a relationship between a given species and a specific response within an article), mostly between 2001 and 2018, but with a single study in 1990 (Fig. 2). Overall, 13 studies were conducted in several northern and southern sites simultaneously, but these were mostly checklists providing information on many species. Of these, 39 were carried out in the northern Pantanal in Brazil, 22 in the southern part and one in the Bolivian Pantanal. Accordingly, the northern Pantanal of Brazil showed the highest mean kernel density and most of the studies were concentrated around the town of Poconé (Fig. 1). The studies conducted in the southern Pantanal were mostly concentrated near Corumbá and Miranda (Fig. 1). We found that there were neglected and poorly explored areas in the central Pantanal. In relation to study period, most articles (about 40%) did not report any specific period (Fig. 3). For those studies that showed the sampling period, a relatively higher percentage of studies were conducted year-round, but the dry season was the most studied period, especially between August and September (Fig. 3).

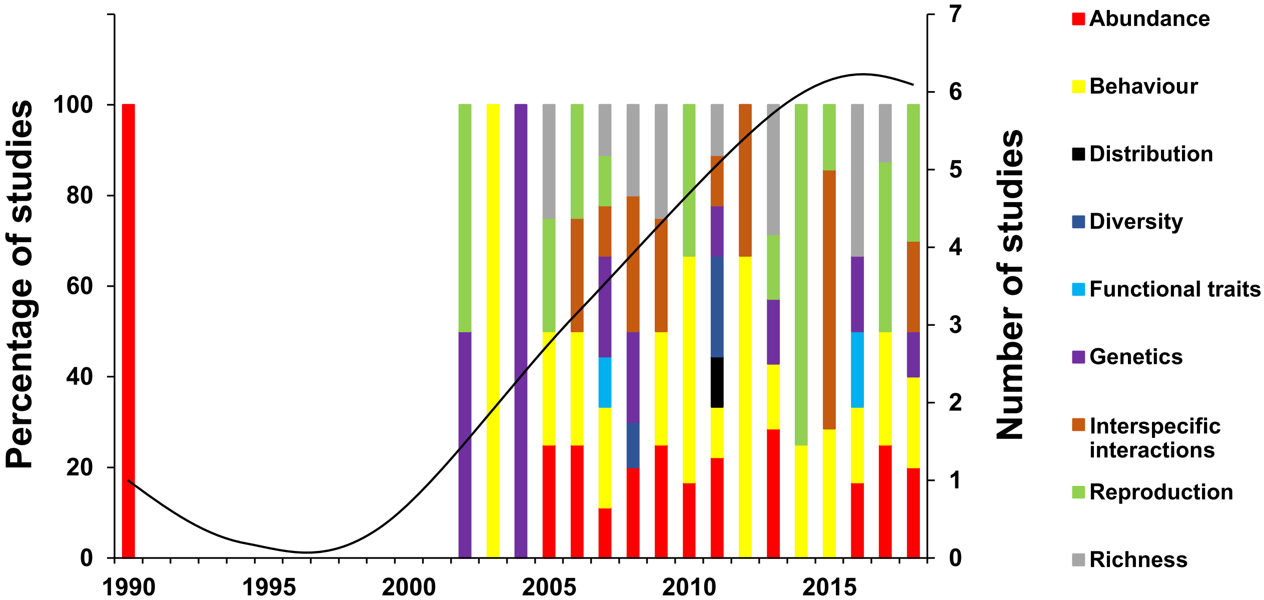

Figure 2. Temporal variation in the number of articles published on birds in the Pantanal biome. Data were retrieved from Scielo and Web of Science platforms between 1990 and 2018. Stacks show the percentage of studies for each biological response and the black line the total number of articles published per year, representing the best fit (third-degree polynomial response) regressions: $R^2 = 0.81$, $P < 0.001$.

Taxonomic biases

We found that ornithological research in the Pantanal was taxonomically biased. Overall, 70 families and 493 species (85% of 582 species occurring in the Pantanal; Nunes 2011) were reported in the studies, but some were only part of studies quantifying species diversity or richness. A few families (e.g. Psittacidae and Ciconiidae) were included in > 30% of studies, and a few species (e.g. Wood Stork *Mycteria americana* and Yellow-billed Cardinal *Paroaria capitata*) were present in > 20% of studies (Table 1). Likewise, families and species that were over-sampled generally also showed the greatest number of biological responses considered (Table 1). The relative bias rates showed that some families are positively or negatively biased in relation to their contribution to overall species richness. Thus, the Jacanidae (11 studies but only one species) was the most over-sampled family, whereas the Tyrannidae (23 studies of 71 species) was the most under-sampled (Fig. 4a). Overall, research effort was negatively biased, as the increase in the number of studies was disproportionately lower than the increase of richness for each family (Fig. 4b). Lastly, about a half of threatened species were studied (Fig. 5), with the possibly extinct Eskimo Curlew *Numenius borealis*, included as Critically Endangered in both the Brazilian and the IUCN Red Lists, being absent from all studies. The number of studied threatened species was proportionally similar between both Red Lists (Fig. 5).

Biological response biases

Ornithological research in the Pantanal was also biased in relation to studied responses, and the proportion of biological responses considered

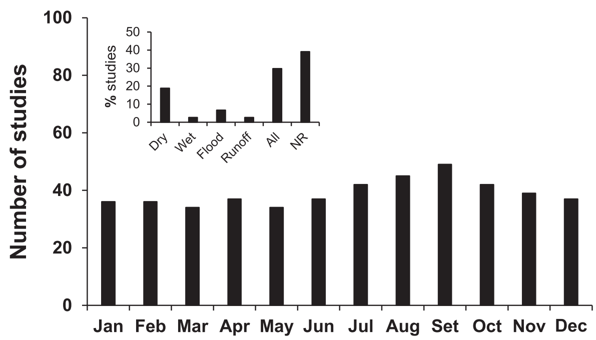

Figure 3. Number of articles published on birds in the Pantanal biome in relation to the study period (i.e. month). The inserted chart shows the percentage of studies for each study season, including studies comprising all seasons. NR means no season reported.

Table 1. Most-studied families and species based on the number of articles (% indicates percentage of the total number of articles) and studied responses (% indicates percentage of the total number of responses reported).

	Articles		Responses	
Taxonomic rank	*n*	%	*n*	%
Family				
Psittacidae	31	40.8	7	63.6
Ciconiidae	25	32.9	–	–
Thraupidae	23	30.3	7	63.6
Tyrannidae	23	30.3	7	63.6
Columbidae	–	–	7	63.6
Species				
Amazona aestiva	19	25.0	4[a]	36.4
Anodorhynchus hyacinthinus	–	–	4[b]	36.4
Cercomacra melanaria	–	–	4[c]	36.4
Galbula ruficauda	–	–	4[c]	36.4
Jabiru mycteria	–	–	4[a]	36.4
Mycteria americana	20	26.3	4[a]	36.4
Paroaria capitata	20	26.3	5[d]	45.4
Cacicus solitarius	16	21.1	–	–
Ramphocelus carbo	–	–	4[a]	36.4
Taraba major	–	–	5[d]	45.4

[a]Abundance, behaviour, genetics and reproduction. [b]Abundance, behaviour, genetics and interspecific interactions. [c]Abundance, behaviour, genetics and interspecific interactions. [d]Abundance, behaviour, genetics, interspecific interactions and reproduction.

varied over time (Fig. 2). Among all studies, behaviour was the most studied response, followed by abundance and reproduction (Table 2). These three responses made up about 85% of the studies. Abundance and behaviour were also studied for most families and species (Table 2). Species richness, genetics and interspecific interactions were investigated in approximately 53% of studies, whereas functional traits and distribution were poorly explored.

DISCUSSION

Our review shows that ornithological research in the Pantanal is spatially, temporally, taxonomically and functionally biased, leading to major knowledge gaps in the biology of birds in the world's largest tropical wetland. Most of the studies were conducted near cities (Fig. 1), and vast and inaccessible areas remained unexplored. Only a few species and families were reported in most articles, whereas some families were over- or under-sampled when considering their species richness. Lastly, a few biological responses (e.g. abundance) were also more commonly considered.

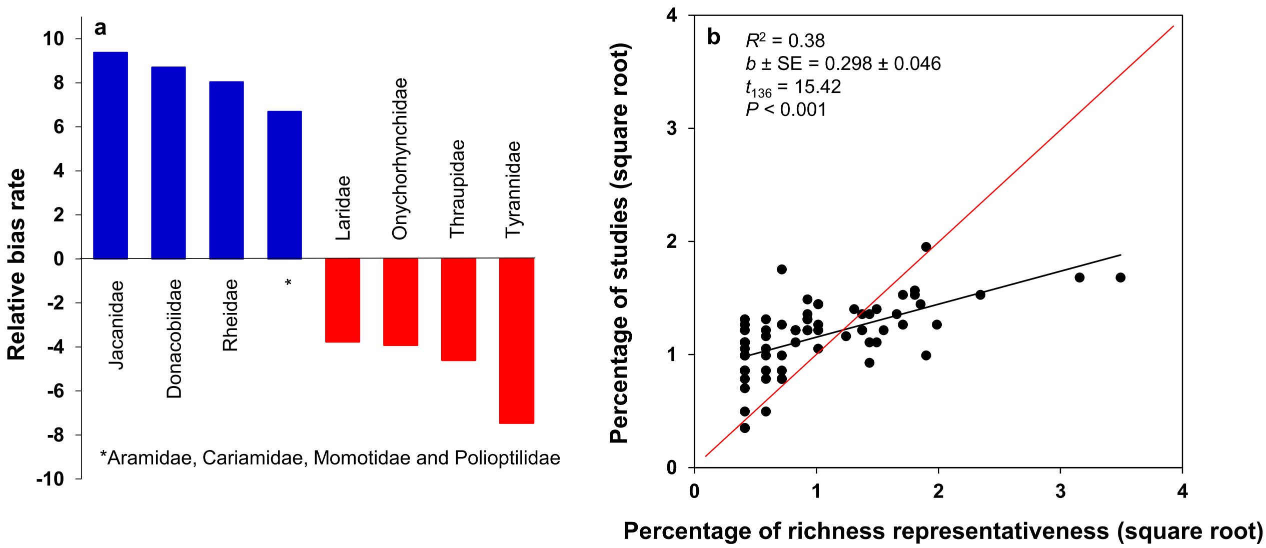

Figure 4. (a) Relative bias rates for bird families showing those families that were either over- or under-represented in published studies relative to their contribution to overall species richness in the Pantanal biome. (b) Relationship between percentage contribution to published studies and percentage contribution to overall species richness in the Pantanal biome. Each point represents a bird family. The red line represents the expected slope (i.e. =1) and the black line represents the observed slope.

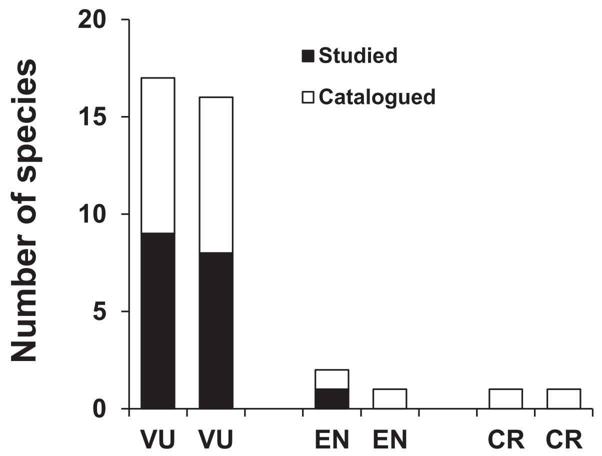

Figure 5. Number of studied bird species nationally (left column of each pair) and globally threatened (right column of each pair) that occur in the Pantanal biome.

Table 2. Number of articles, families and species (% indicates the percentage of the total articles, families and species, respectively) for which each of the studied responses was reported.

	Articles		Families		Species	
Response	*n*	%	*n*	%	*n*	%
Abundance	20	26.7	68	97.1	430	87.2
Behaviour	26	34.7	65	92.9	356	72.2
Distribution	1	1.3	1	1.4	1	0.2
Diversity	3	4.0	47	67.1	–	–
Functional traits	2	2.7	2	2.9	2	0.4
Genetics	11	14.7	23	32.9	39	7.9
Interspecific interactions	16	21.3	23	32.3	42	8.5
Reproduction	17	22.7	25	35.7	54	11.0
Richness	13	17.3	70	100.0	493	100.0

Assessment of research bias

Knowledge of Pantanal birds has advanced in the last two decades (Fig. 2). Nevertheless, there were relatively few studies in this ecoregion, considering the high number of publications about birds worldwide (Bonnet *et al.* 2002, Troudet *et al.* 2017) and the number of species occurring in the Pantanal in relation to total species richness in Brazil. This megadiverse country harbours 1919 bird species, 582 occurring, although not exclusively, in the Pantanal (Tubelis & Tomas 2003, Nunes 2011, Piacentini *et al.* 2015). Nevertheless, this wetland includes a disproportionately small number of studies for birds compared with other species-rich biomes such as the Amazon and the Atlantic Forest (Jenkins *et al.* 2015). Our results reveal that ornithological research in the Pantanal has traditionally been an overlooked topic that deserves further attention.

Most of the Pantanal (88%) lies in Brazil (Junk *et al.* 2006a) and, accordingly, most Pantanal research has been conducted in this country. Despite a concentration of sampling points in Bolivia, they all came from a single work on a single threatened species, the Hyacinth Macaw *Anodorhynchus hyacinthinus*. The almost complete lack of published research from Bolivia and Paraguay in the studied databases may also reflect distinct policies and funding opportunities compared with Brazil, which leads in the number of research articles in Neotropical ornithology as a whole (Freile *et al.* 2014). Regardless, this geopolitical bias rises to an important level, as the western Pantanal, particularly in Bolivia and Paraguay, harbours most of the areas influenced by the Chaco region, and hence this biogeographical relationship has been largely neglected (Straube *et al.* 2006, Vasconcelos & Hoffmann 2006).

Most of the bird studies in Brazil and the one study in Bolivia were carried out in areas close to medium-sized cities that facilitate the logistics and data collection in those areas. Major sampling gaps detected in the central Pantanal may result from limited access to remote areas (e.g. unpaved roads or exclusive access by river, which is mostly restricted to local people; Alho 2011). Road systems, however, may permanently alter the environments and the animal communities by facilitating the access and spread of more human activities such as farming, cattle-ranching and mining (Fearnside 2005, Alho 2008, 2011). Likewise, accessibility via a major river (i.e. Paraguay River) is restricted to large boats transporting cargo among distant cities (Alho 2011). Simultaneously, seasonal changes of the environment in the Pantanal may also constrain access to remote areas. About 80% of the Pantanal area is covered by water during the flood season (Junk *et al.* 2006a). Our results show that the dry season is the predominant period of study, being more favourable to field campaigns.

Seasonal bias of field studies also hampers the study of bird migration. Even though the Pantanal is a key wintering area for birds (Nunes & Tomas 2004), the gathering of basic data on the use of the Pantanal by migratory bird species is still in its infancy. The least-sampled seasonal periods in the Pantanal (i.e. wet and flood seasons) overlap with spring migration of Nearctic species, as well as the spring and autumn migration of several Austral migrants. It is therefore no surprise that it has been only recently reported that the Pantanal may hold flocks of hundreds of Mississippi Kite *Ictinia mississippiensis* during their flight back to North America (Whittaker *et al.* 2008). Similarly, Cestari (2006) recorded six migratory seedeaters (*Sporophila* spp.), some of them threatened, that were previously unknown to occur in the Pantanal. Overall, spatial and seasonal biases reported here may compromise our inferences about responses of Pantanal bird species and communities (e.g. composition or relative abundance of species). Therefore, considering both spatial and seasonal biases may be particularly important in designing future collection of data on the natural history of bird species in the Pantanal, which may subsequently provide a better basis for decision-making and conservation policies.

A few species (e.g. Wood Stork and Yellow-billed Cardinal) and families (e.g. Psittacidae and Ciconiidae) were also reported in most of the studies. However, the relative bias results showed that some families were either under-sampled (e.g. Tyrannidae) or over-sampled (e.g. Jacanidae). Some of these results may be due to the general abundance of some species and families. Indeed, Donatelli *et al.* (2017) found Psittacidae to be the most abundant bird family in their sampling area in the southern Pantanal, also reporting a species of a monotypic family (Recurvirostridae) as a dominant species in some common habitats. Nevertheless, the lack of abundance data in most studies and regions of the Pantanal precludes us from understanding whether detectability confounds our results (i.e. gregarious species commonly found in large flocks, such as parrots, may be over-sampled). Moreover, each habitat in the Pantanal harbours a distinct community (Donatelli *et al.* 2017) and, therefore, any sampling bias towards a given habitat may also account for the taxonomic bias we report. In summary, we suggest that taxonomic bias on bird-related research in the Pantanal results from both the characteristics of species (e.g. abundance, body size) and researcher experience (e.g. aural detection), which may limit our knowledge of less detectable species.

We also found relatively few studies of nationally and globally threatened bird species. Global reviews provide evidence that threatened species are under-sampled in biodiversity research when compared with non-threatened species (Clark & May 2002, Donaldson *et al.* 2016), a recurrent pattern also reported for avifauna (Marsden & Royle, 2015, Roberts *et al.* 2016). Overall, an interplay of low detectability of individuals, low accessibility to remote, unexplored and/or protected areas, and logistical constraints related to licences and permits largely explains the uneven sampling between threatened and non-threatened species. Ultimately, taxonomic bias, including major gaps in knowledge of threatened species, may compromise conservation actions and our understanding of the responses and vulnerability of the species to human-induced environmental changes.

Behaviour and abundance were included in the highest number of studies and most of families and species. Behaviour-based responses such as foraging, movement or habitat use, and assemblage-level responses (i.e. species richness, abundance and diversity) are common in the literature (Ellis *et al.* 2011, Teixido *et al.* 2020) and are relatively practicable to measure to evaluate the effects of environmental changes on biodiversity (Ewers & Didham 2006). Thus, abundance and behaviour may better capture some important characteristics of bird populations and communities facing seasonality in the Pantanal. Indeed, abundance is a well-documented measure to determine differences in bird populations between the dry and the flooding season in this biome (Pinho & Marini 2012, Thomas *et al.* 2020). By contrast, process-related responses such as interspecific interactions (e.g. predation), individual conditions (e.g. reproduction) and components of functional diversity (i.e. functional traits such as body mass or wing size) are more difficult and time-consuming to document and quantify (Ewers & Didham 2006, Cianciaruso *et al.* 2009). Knowledge of the species responses to flooding-related environmental changes in the Pantanal is crucial to understand the relationship between biodiversity and ecosystem services and for improvement of cost-effective management strategies and conservation.

Future research on bird species in wetlands

The world's large wetlands present high habitat heterogeneity and other difficulties that pose challenges for field research (Junk 2002, Keddy *et al.* 2009, Xia *et al.* 2017). Major gaps in ornithological research, even for basic data such as the beta diversity and the structure of bird communities, as we report here, prevent a better understanding of the environmental dynamics of large wetlands, including its resilience and ecosystem services, as well as energy and matter exchange within the wetland habitats and with surrounding regions. Specifically, we recommend a better sampling across the Pantanal that could also be applied to other large and particularly under-sampled wetlands around the world (e.g. the seasonally inundated Tonlé Sap Lake and the Sundarban Delta; Junk *et al.* 2006b), including better geographical and seasonal coverage and incorporating easy-to-gather data, such as species abundance, diet, interspecific interactions and presence of potentially harmful human activities. Our review also found several problems with the reliability of the identification of some species, beyond what has already been reported for the Pantanal (Tubelis & Tomas 2003). Thus, we recommend that bird inventories and research in the Pantanal and other large wetlands seek a higher standard in species identification and occurrence documentation, applying as much as possible the guidelines already recommended for other ecosystems (Lees *et al.* 2014). All those recommendations should also be fostered within citizen science initiatives, given their potential to fill several of the gaps (e.g. data on species abundance and seasonality) but also some of the pitfalls associated with such data (Lepczyk 2005, Kamp *et al.* 2016). Citizen science may also help to study some threatened species from under-sampled families (e.g. Tyrannidae and Thraupidae) by accessing specific remote areas and/or detecting species (Tulloch & Szabo 2012, Lees *et al.* 2020). The collaboration of local volunteers and birdwatching tourism may therefore be essential to fill these knowledge gaps and inform conservation policy.

Future research should cross international and continental borders. As mentioned above, a full understanding of the role of the Pantanal for migratory species, including several Neartic and threatened species, remains to be clarified. The Pantanal may be both the wintering ground and a stopover site for migrant birds (Nunes & Tomas 2004). As such, the spatial and seasonal biases and consequent knowledge gaps need to be overcome, perhaps with closer integration and collaboration of Brazilian researchers with partners in Bolivia and Paraguay. The position of the Pantanal in the centre of South America, the most bird species-rich continent, and in an ecotonal region that connects the Chaco, Amazon and Cerrado ecoregions, requires this collaboration across borders. The ecotonal and habitat heterogeneity of the Pantanal certainly affects the geographical distribution and location of contact zones of many species and pairs of taxa neglected in this wetland (e.g. the Northern Slaty Antshrike *Thamnophilus puntactus* complex), a sampling gap key to understanding species limits and speciation within these birds (Isler *et al.* 1997). Yet, we are at present far from having a solid knowledge even in basic fields, such as taxonomy and distribution of birds from the Pantanal.

In conclusion, our study suggests that future research needs to be orientated to unexplored places and flood periods, small-sized, less abundant or detectable, and threatened species, and process-related biological responses. By filling those knowledge gaps, we may be able to reach more robust conclusions on the dynamics, ecology, natural history and structure of bird communities in the Pantanal, which may ultimately be essential to fully understanding how species respond to human-induced environmental changes (Lees *et al.* 2020). We call future studies to take into account the current sampling biases and to consider them an opportunity to better direct our efforts to fill major information gaps. Specifically, we outline some key recommendations in more detail to steer future bird-related research in the Pantanal:

- precise geographical coordinates, study period and type of environment (e.g. forest, grassland, body of water) wherein the study was conducted, should be recorded to obtain comprehensive datasets;
- studies should be conducted in poorly explored areas and during the flood period for at least 1 month;
- more research on under-sampled and threatened species is required to ensure protection and inform conservation policy;

- future studies should consider biological responses beyond abundance and behaviour, such as functional traits, genetics and inter-specific interactions;
- ornithologists, birdwatchers and non-profit organizations are encouraged to provide data through online checklists and databases.

These issues may also be applicable as primary steps towards better bird monitoring and sampling in other wetlands, particularly for those where major gaps exist, such as the Canadian peatlands and the Tonlé Sap Lake (Junk *et al.* 2006b). A specific example of practicability of our recommendations where more research is required is to determine how aquatic environments provide food resources and subsequently influence the behaviour, distribution and reproduction of waterbirds in the floodplains of Kakadu National Park (Hamilton & Gehrke 2005). Further research on waterbirds is also particularly important in major global wetlands, where they play key functional roles such as nutrient cycling, pest control and seed dispersal (Green & Elmberg 2014). Despite their importance, research of waterbirds is still biased towards most common species in high-income countries (Roberts *et al.* 2016). Therefore, significant gaps in knowledge of waterbirds remain in bird species-rich wetlands from developing countries (e.g. the Okavango and Sundarban Delta).

New studies could address the above issues by implementing methods such as rapid biological inventories and automatic acoustic monitoring (Shonfield & Bayne 2017). Using citizen science, volunteer surveys from non-scientists might assist in detecting less abundant and threatened species in under-sampled habitats (Tulloch & Szabo 2012, Lees *et al.* 2020). Additionally, implementation of new technologies such as computational modelling, radiotracking and advanced genetic procedures may promptly fill knowledge gaps (Lees *et al.* 2020). By adapting these methods to particular situations (e.g. flood period), researchers may obtain quick and reliable data about overlooked and threatened bird species. Last, studies may also bring theoretical development and compelling empirical evidence (e.g. functional diversity, multi-specific interactions, responses to seasonality and environmental changes) to increase our knowledge, suggest new research lines and steer suitable conservation policies and recovery networks, especially under the pervasive reduction of native habitat.

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AUTHOR CONTRIBUTIONS

Gilberto J. Fernández-Arellano: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Project administration (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing-original draft (equal); Writing-review & editing (equal). **Alberto L. Teixido:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Project administration (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing-original draft (equal); Writing-review & editing (equal). **Bianca Bernardon:** Data curation (equal); Methodology (equal); Writing-review & editing (equal). **Elaine Bueno:** Data curation (equal); Methodology (equal); Writing-review & editing (equal). **Tiago Ferreira:** Data curation (equal); Methodology (equal); Writing-review & editing (equal). **Stela Gonçalves:** Methodology (equal); Writing-review & editing (equal). **Moisés Jesus:** Data curation (equal); Methodology (equal); Writing-review & editing (equal). **Kamila Thomas:** Data curation (equal); Methodology (equal); Writing-review & editing (equal). **Mayara Zucchetto:** Data curation (equal); Methodology (equal); Writing-review & editing (equal). **Vitor de Q. Piacentini:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Project administration (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing-original draft (equal); Writing-review & editing (equal). **João Pinho:** Conceptualization (equal); Data curation (equal);

Formal analysis (equal); Investigation (equal); Methodology (equal); Project administration (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing-original draft (equal); Writing-review & editing (equal).

DATA AVAILABILITY STATEMENT

Our data will be available online once the article is accepted.

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