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ARTICLE

Waterbirds in a floodplain: influence of spatial and environmental factors through time

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ABSTRACT: Wetlands are rapidly being lost and fragmented around the world, making it imperative to seek an understanding of the drivers of their diversity. Among aquatic assemblages, birds constitute a conspicuous group that provides many ecosystem services. Here, we use a metacommunity approach to understand the influence of spatial (distance among patches) and environmental factors (local characteristics) in wading bird (Pelecaniformes and Ciconiiformes) assemblages in a river-floodplain system through time. We tested the hypothesis that, due to the small scale of our study, spatial factors have no determinant role in waterbird assemblages, and, due to the annual occurrence of flood pulses, the importance of environmental factors varies through time, according to the hydrological cycle. We tested this hypothesis using Partial Redundancy Analysis (pRDA). We used abundance data for the birds in 20 lagoons, sampled quarterly during two years. The spatial factors did not explain variation in community structure in any sampled month, whereas environmental factors explained variation in the assemblages only in two months. Due to high waterbird mobility, the non-significance of the spatial factor is expected among lagoons in the same floodplain. Environmental factors are important in determining the community structure only in two sampled months, evidencing that their importance varies through time in the floodplain, partially agreeing with our hypothesis. The non-conformity between the influence of environmental factors on assemblages and the hydrological cycle may be due to human impacts caused by the operation of upstream reservoirs, which alter the natural flood events, and caused a long drought period previous to this study. A multiscale approach is fundamental to the understanding on how anthropogenic impacts on wetlands affect waterbird assemblages. Thus, this study contributes to the understanding of how seasonality, environmental conditions of lakes, and a local spatial scale act in structuring waterbird assemblages.

KEY-WORDS: Ciconiiformes, metacommunity, Paraná River, Pelecaniformes, variance partitioning.

INTRODUCTION

Wetlands are mosaic-like environments, which generally comprise patches of different types, sizes and distances from other patches (Whited *et al.* 2000). Additionally, wetlands have suffered continuous loss and fragmentation, which has negatively affected the ecosystem services they provide and biodiversity they harbor, including waterbirds (Ma *et al.* 2009). Waterbirds (*e.g.* Pelecaniformes, Ciconiiformes, Charadriiformes, Anseriformes) are highly dispersive birds, moving between favorable areas in search of resources and are dependent on wetlands during most or all of their life cycle (Haig *et al.* 1998). The inherent patchiness and rapid loss of wetlands around the world makes it important to integrate spatial components into analyses of waterbird diversity and distribution (Paracuellos & Tellería 2004, Luis *et al.* 2005). However, few studies have considered space as a structuring factor for local waterbird communities (Pagel *et al.* 2014, Sebastián-González & Green 2014). Here, we used metacommunity theory to better understand the distribution of waterbirds in their patchy environment.

Metacommunity theory is a theoretical and mechanistic framework that serves to explain the interdependence of local and regional processes in structuring communities (Logue *et al.* 2011). As viewed through the lens of this concept, two general types of forces affect community structure: local (biotic interactions and environmental conditions) and regional (spatial dynamics, linked to the dispersal of organisms). These processes interact to produce a local species assemblage (Leibold *et al.* 2004).

Depending on the degree of influence of local and regional processes in structuring the local communities, four perspectives were defined concerning the organization of metacommunities: neutral model, patch dynamics, species sorting and mass effects. The neutral model assumes environmental homogeneity and species with similar competitive capacities, so that their distribution is influenced only by dispersive capacity. Patch dynamics considers patches also to be homogeneous, but species differ among them, in what constitutes a trade-off between colonization and competition capacities. Species sorting assumes environmental heterogeneity associated with differences among species and with a dispersive capacity that is sufficient for the species to reach different patches, but which does not influence their distribution. Finally, mass effects considers that there is a high dispersive capacity in a heterogeneous environment, which brings to communities affected by source-sink relations, with a greater influence of dispersal than environmental heterogeneity in the structure of communities (Leibold *et al.* 2004). However, the complex dynamics of communities suggests that these models are not discrete or mutually exclusive (Logue *et al.* 2011). Winegardner *et al.* (2012) reviewed the terminology used by Leibold and proposed that the mechanisms underlying these paradigms interact. Thus, they reorganized the models according to the relative importance of dispersal, suggesting that metacommunities can be classified as follows: neutral, species-sorting with limited dispersal (which would be equivalent to patch dynamics, *sensu* Leibold *et al.* 2004), species-sorting with efficient dispersal (equivalent to species sorting), or species-sorting with high dispersal (equivalent to mass effects).

The metacommunity approach contributes to a better understanding of how spatial dynamics and local interactions influence community ecology (Logue *et al.* 2011). Studying metacommunities of waterbirds at different scales is necessary to understand how local communities are structured within and among wetlands. Considering the importance of waterbirds as suppliers of ecological services such as dispersal of seeds and eggs, ecosystem engineering, population control and scavenging, understanding their metacommunity dynamics is essential for wetland management (Green & Elmberg 2013). Knowledge on spatial dynamics for waterbird assemblages enables one to answer questions such as how distances between wetland patches influence assemblages.

As an example of how the metacommunity approach can be used to better explore the mechanisms that shape communities of waterbirds, we evaluated the local and regional drivers of assemblages of wading birds (Pelecaniformes and Ciconiiformes) in a Neotropical floodplain. Floodplains are heterogeneous environments with high biological diversity and are influenced by cyclical variation in river discharge, or flood pulses (Junk *et al.* 1989). Flood pulses act by connecting and homogenizing the patches of aquatic environments in a floodplain and are a major driver of biodiversity in these ecosystems (Junk *et al.* 1989, Thomaz *et al.* 2007).

Pelecaniformes and Ciconiiformes are medium-to-large waders that occur in most floodplains, and many aspects of their ecology are affected by the hydrologic regime (Kushlan 1986, Dimalexis & Pyrovetsi 1997, Russell *et al.* 2002). The density and vulnerability of prey vary seasonally and spatially (Fernandes *et al.* 2009, Gimenes & Anjos 2011), and depend on the frequency, duration and magnitude of the flooding (Petry *et al.* 2003). Because wading birds forage in shallow waters, prey availability is highest when water is shallower during dry seasons (Gawlik 2002). The seasonal variation in the environment therefore makes it necessary to consider the influence of the hydrological cycle on the local communities of waders.

The goal of this study was to assess the relative importance of regional (spatial) and local (environmental) factors in structuring the wading bird communities in the upper Paraná River floodplain throughout the hydrological cycle. Due to the small scale of our study (a single floodplain spanning *c.* 50 km) and to the vagility and habitat selection capacity of birds (tending to an ideal free distribution, see Fretwell & Lucas-Jr. 1970), we expect that dispersal limitation and mass effects will not play important roles in structuring wader communities in this floodplain. At the same time, due to the cyclic alterations of the water level, we expect that the importance of environmental variables is not equivalent throughout the year. Therefore, we hypothesize that the wader metacommunity of the upper Paraná River floodplain is shaped by species sorting with efficient dispersal (Winegardner *et al.* 2012), and that the role of environmental characteristics in structuring the local communities of waders changes seasonally. Thus, we predict that the regional component will not impact metacommunity structure and that the local component (environmental conditions) will be more important during drier periods, when there is more heterogeneity among the water bodies in the floodplain.

METHODS

Study area

The Paraná River stretches for 4695 km from the Brazilian central plateau southward to the Plate River between Argentina and Uruguay. In Brazil, the Paraná River is affected by dams along most of its length, and only a stretch of 230 km between the Porto Primavera and Itaipu reservoirs remains as a floodplain (22°40'S to

22°52'S and 53°12'W to 53°38'W). The dams installed along the hydrographic basin have modified the natural pattern of magnitude, duration, periodicity and discharge frequency of the Paraná River, increasing the control on the discharge regime, eliminating the highest water level values and causing variability between night and day discharges (Thomaz *et al.* 2004). Thus, the seasonal water level fluctuation in the upper Paraná River floodplain is not continuously sinusoidal, as uninterrupted periods of falling and rising water are rarely observed (Agostinho *et al.* 2000).

The climate of the area is classified as Tropical Subtropical, with an annual average temperature of 22°C (average of 26°C in summer and 19°C in winter). The pluvial regime is marked by a wet summer, with monthly average precipitation greater than 125 mm, and a dry winter, with averages under 80 mm. The high-water period in the Paraná River usually occurs from November/December to April/May and is characterized by an increase in the water level averaging 2.5 m and reaching 7.5 m in years of extreme flood events, with almost no variation observed in years in which the characteristic flood period does not occur. It is quite common for two or three annual flood pulses to be observed during high water levels, while smaller pulses (< 0.5 m) occur weekly in the dry season, caused by the operation of upstream reservoirs.

The study area, located between the mouths of the Paranapanema and Ivinhema Rivers, encompasses environments with very different characteristics. At this point, the Paraná River has an extensive alluvial plain on its west margin. This floodplain consists of a mosaic of habitats, including rivers, streams, channels, and marginal lagoons with different degrees of hydrological connectivity. Two types of lagoons are used in this study: permanently connected lagoons, which have an above-ground connection with the river all year long, and isolated lagoons, which are disconnected from the river during most of the year and have an above-ground connection only during flooding events.

Data collection

The birds were sampled in 2002 and 2003 (both years on February, May, August and November) in connected (permanently connected to rivers or canals, n = 10) and isolated perennial lagoons (not connected to rivers, except during the flood, n = 10) (Figure 1). The areas

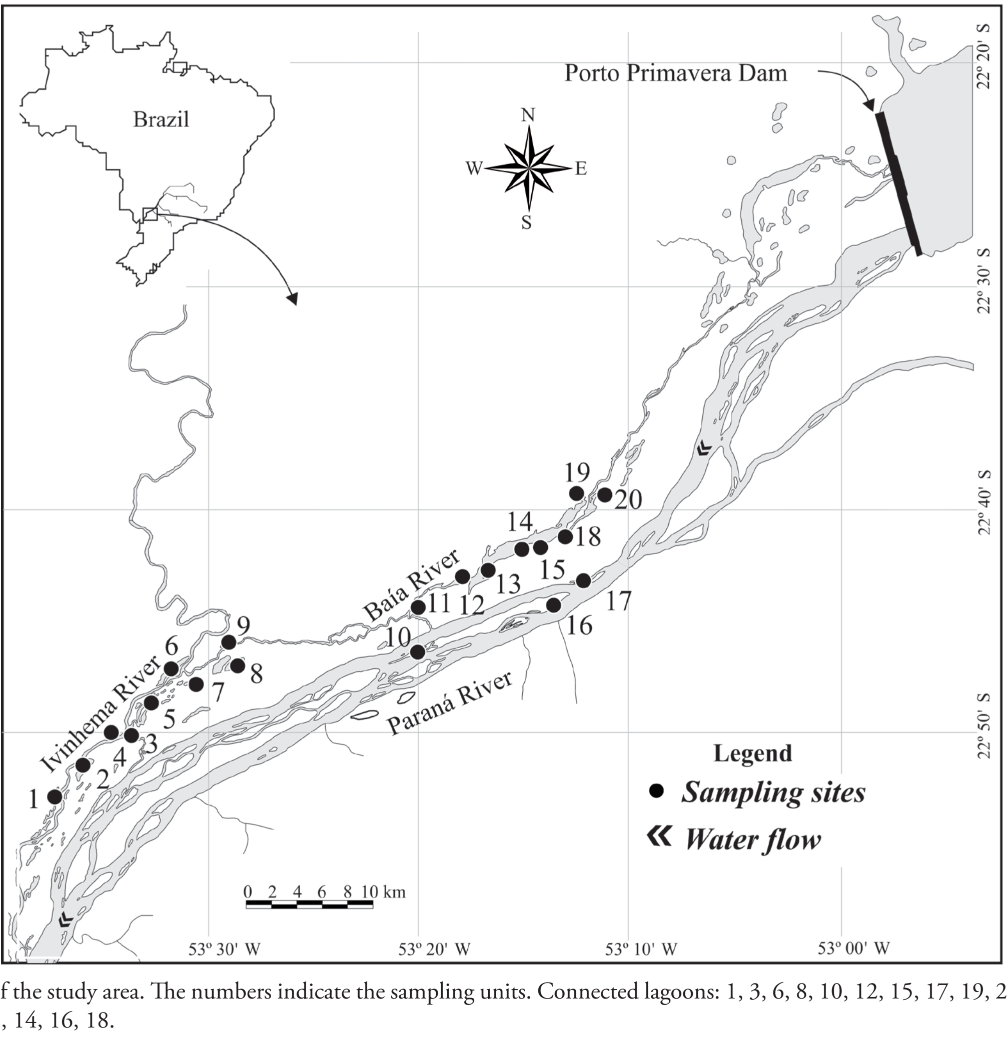

FIGURE 1. Map of the study area. The numbers indicate the sampling units. Connected lagoons: 1, 3, 6, 8, 10, 12, 15, 17, 19, 20; isolated lagoons: 2, 4, 5, 7, 9, 11, 13, 14, 16, 18.

of the sampled lagoons varied from 0.43 to 89.8 ha, and their perimeters from 251.4 to 7151.2 m. These months were chosen in order to sample all the phases of the hydrological cycle. In each month, two visits lasting for 1 h were conducted in each sampling unit, always beginning 1 h after sunrise. In each sampling, a circular transect was performed around the lagoon, through the whole perimeter, either by boat in a constant speed of 30 $km.h^{-1}$ (connected lagoons) or on foot (isolated lagoons), with identification and registration of each individual sighted (Bibby *et al.* 1992). The entire lagoon was fully visible along transects. Birds observed within a range of up to 5 m from the water were included, but individuals in flight were not recorded, unless they were observed leaving or arriving at the lagoons. In all sampled lagoons only the margins of the water bodies are shallow enough to allow the presence of waders. Birds were identified to species according to Sigrist (2009).

To characterize the environmental component, environmental variables considered important for the distribution of species of Pelecaniformes and Ciconiiformes and possibly related to the vulnerability of prey capture were selected. The recorded environmental variables were: perimeter (in m), average depth (in m), type of dominant vegetation in the surrounding area (forest, grasslands, macrophyte or *Polygonum*), and type of lagoon (connected or isolated). Measurements of water bodies were performed through aerial images. All datasets were obtained from the PELD Technical Report, site 6 (Souza *et al.* 2001, Souza-Filho & Stevaux 2002).

Data analyses

To determine the relative contributions of local (environmental characteristics – E) and regional factors (spatial determinants, or distances between patches – S) to the community structure of Pelecaniformes and Ciconiiformes, we used a variance partitioning technique: partial redundancy analysis (pRDA) (Borcard *et al.* 1992, Cottenie 2005). This method of analysis can be characterized as a multiple regression with multiple response variables. In this case, we used a dependent matrix (species abundance) and two explanatory matrices (spatial and environmental variables) (Legendre & Legendre 1998, Beisner *et al.* 2006). The variation in community structure was decomposed into the following components: E+S - the total variation explained by the analyses; E - environmental variation; S - spatial variation; E|S - the variation explained by the environmental variables, independent of spatial variables, or the pure environmental component; S|E - the variation explained by spatial variables, independent of environmental variables, or the pure spatial component; E∩S - the explained variation shared by environmental and spatial variables; and the residue, or the variation not explained by any of the above components (Borcard *et al.* 1992) (Figure 2). We considered the adjusted R^2 values as the results of the variance partitioning procedure (Peres-Neto *et al.* 2006). The significance of each component ($P < 0.05$) was tested by Monte Carlo randomization tests (9999 runs) (Legendre & Legendre 1998).

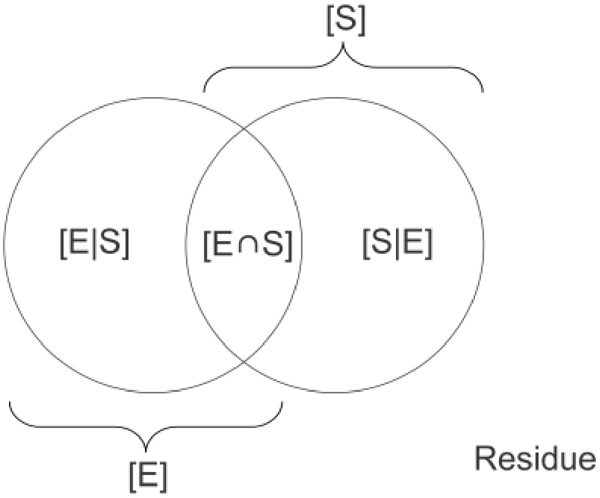

FIGURE 2. Venn diagram representing the decomposition of the community structure into: E = environmental variation or local factor, S = spatial variation or regional factor, E|S = variation explained by environmental variables independent of spatial variables, or pure environmental component, S|E = variation explained by spatial variables independent of environmental variables, or pure spatial component, E∩S = variation explained together by environmental and spatial variables; and residue, variation not explained by any of the previous components.

To construct the spatial matrix, a Euclidean distance matrix was generated between the sampled sites based on their geographic coordinates, measured from the center of each lagoon. From the distance matrix, Moran (MEM) eigenvector maps were created to quantify the spatial arrangement of the sampling points (Dray *et al.* 2006). The eigenvectors (spatial variables) allow one to represent the spatial relationships among the sampling units at different spatial scales. Small eigenvalues indicate the absence of spatial autocorrelation and, therefore, are not suitable for defining spatial structures. We included all eigenvectors with a Moran's I coefficient greater than 0.1 in the spatial predictor matrix (Nabout *et al.* 2009). Variance partitioning was carried out using total abundance data (number of birds recorded per lagoon), which were previously transformed into Hellinger values. The Hellinger distance is a measure recommended for the clustering or ordination of species abundance data (Legendre & Gallagher 2001). We performed eight pRDAs, one for each sampled month, in both years. All analyses were conducted in R software (R Development Core Team 2012) using the packages *vegan* (Oksanen *et al.* 2013) and PCNM (Legendre *et al.* 2013).

RESULTS

The water level of the Paraná River was higher between January and April in both the 2002 and 2003 annual monitoring periods. However, it is noticeable that the water levels varied more in the last half of 2003 than in the same period of 2002. In fact, the water levels reached as high as 3.5 m in November 2003, the level that begins to provide connections between the river and isolated lagoons. The year 2001, which preceded our sampling activities, was markedly dry, showing minimum water level values close to 1 m and maximum values not reaching 4 m (Figure 3).

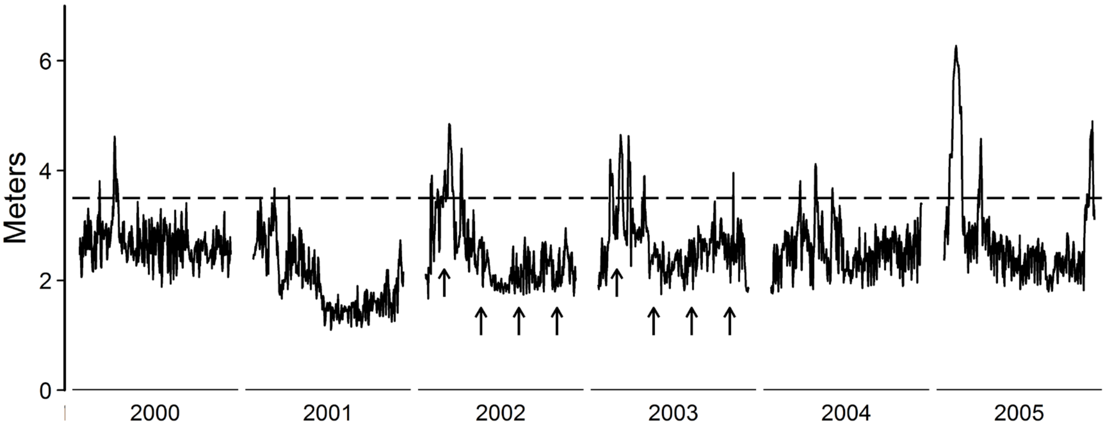

FIGURE 3. Daily fluviometric levels for years 2000–2005. Black arrows represent the sampling months. The line indicates the level at which a connection begins to be established between the environments.

A total of 2028 individuals belonging to 13 species of the orders Pelecaniformes and Ciconiiformes were recorded (Table 1). Six species were common (*Ardea cocoi*, *Butorides striata*, *Egretta thula*, *Ardea alba*, *Tigrisoma lineatum* and *Nycticorax nycticorax*), occurring in almost all sampling months (only in one month, one of the species was absent), with presence in a maximum of 22 sites each month. Other species (*Platalea ajaja*, *Bubulcus ibis*, *Syrigma sibilatrix*, *Mycteria americana*, *Ciconia maguari*, *Jabiru mycteria*, *Mesembrinibis cayennensis* and *Theristicus caudatus*) were less abundant, occurring in only a few months and sites, mostly in connected lagoons, and present in a maximum of six sites each month. The peak of bird abundance occurred in November 2002. February 2002 and February and August 2003, in turn, were the months with the lowest abundances (Figure 4).

TABLE 1. Species registered in the study area for all the sampled months and according to sampling sites (lagoons). Lagoons are numbered according to the map (Fig. 1). Classification of the species is according to the American Ornithologists' Union (AOU).

	Connected										**Isolated**									
Lagoons No.	**16**	**2**	**8**	**13**	**12**	**7**	**10**	**11**	**17**	**6**	**1**	**14**	**18**	**20**	**15**	**9**	**3**	**5**	**4**	**19**
Ciconiiformes																				
Ciconiidae																				
Ciconia maguari					x		x		x											
Jabiru mycteria			x				x	x	x											
Mycteria americana			x				x	x										x		
Pelecaniformes																				
Ardeidae																				
Ardea alba	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x
Ardea cocoi	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Bubulcus ibis				x													x			
Butorides striata	x	x	x	x	x	x	x	x	x	x	x	x			x	x	x	x		x
Egretta thula	x	x	x	x	x	x	x	x	x	x	x	x			x	x	x	x		
Nycticorax nycticorax	x	x		x		x	x	x	x	x								x		x
Syrigma sibilatrix								x												
Tigrisoma lineatum	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	
Threskiornithidae																				
Mesembrinibis cayennensis	x								x											
Platalea ajaja			x				x	x	x											

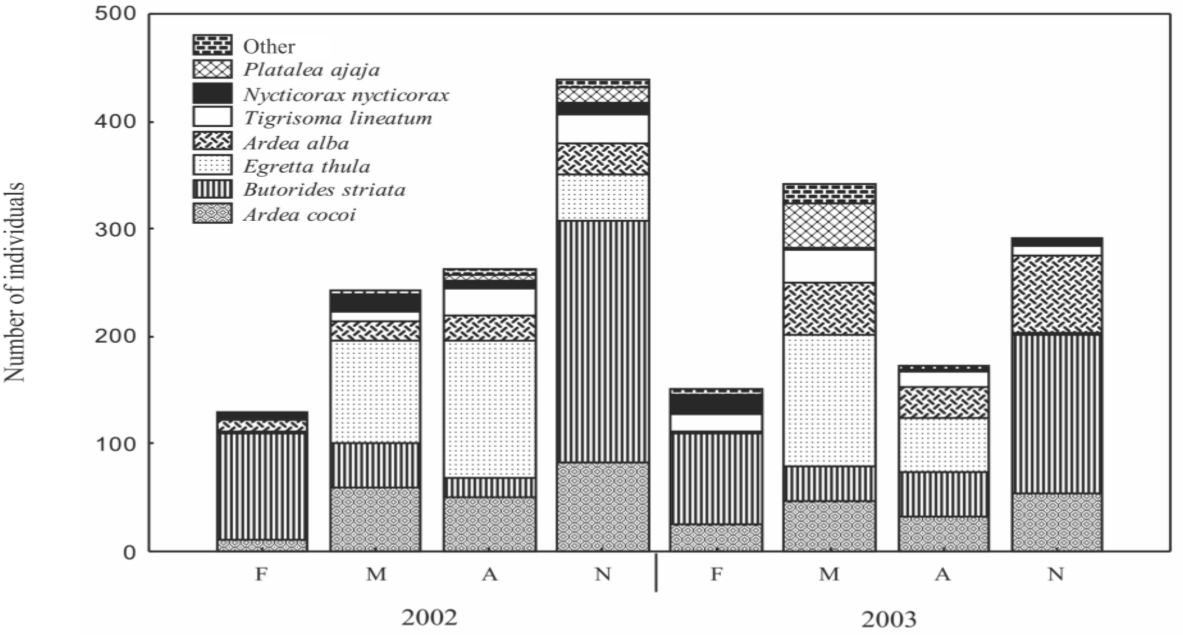

FIGURE 4. Number of individuals of the species of Ciconiiformes and Pelecaniformes recorded in the perennial lagoons of the upper Paraná River floodplain. The letters F, M, A and N stand for the months February, May, August and November, respectively.

The results of the RDA variance partitioning differed between months. In 2002, the environmental factor - E - explained the structure of the bird communities in February (R^2 = 0.15; P = 0.0430), May (R^2 = 0.14; P = 0.0149) and November (R^2 = 0.28; P = 0.0001), whereas the pure environmental factor E|S explained the variability of the communities of birds only in February (R^2 = 0.22; P = 0.0257) and November (R^2 = 0.25; P = 0.0011). In 2003, the environmental factor E explained the structure of the communities in February (R^2 = 0.14; P = 0.0215) and November (R^2 = 0.13; P = 0.0468), and the spatial factor S was also important in February (R^2 = 0.13; P = 0.0060). The pure environmental factor - E|S - did not explain the variation of community structure observed in any month of 2003, and the pure spatial factor S|E showed no importance for the communities in any month of this study (Table 2).

TABLE 2. Variance partitioning of the community structure of Ciconiiformes and Pelecaniformes in different months during the two years of sampling in the 20 lagoons of the upper Paraná River floodplain. E = environmental variation, S = spatial variation, E|S = pure environmental component, S|E = pure spatial component, E∩S = shared variation explained by environmental and spatial variables; residue, or unexplained variation; significance level at $P < 0.05$, Adj. R^2 = adjusted coefficient of determination. Significant values are underlined.

	February		**May**		**August**		**November**	
	Adj. R^2	**P**	**Adj. R^2**	**P**	**Adj. R^2**	**P**	**Adj. R^2**	**P**
2002								
E	0.15	0.0430	0.14	0.0149	0.03	0.2951	0.28	<0.0001
S	0.06	0.7305	0.01	0.3256	0.01	0.3322	0.05	0.0958
E|S	0.22	0.0257	0.10	0.0748	0.00	0.7105	0.25	0.0011
S|E	0.02	0.3161	0.00	0.6917	0.00	0.8977	0.02	0.2471
E∩S	0.00		0.04		0.07		0.04	
Residue	0.82		0.89		1.00		0.69	
2003								
E	0.14	0.0215	0.06	0.1681	0.00	0.4450	0.13	0.0468
S	0.13	0.0060	0.04	0.1824	0.00	0.5351	0.09	0.0521
E|S	0.04	0.2288	0.03	0.3188	0.00	0.6269	0.06	0.1864
S|E	0.04	0.1753	0.01	0.3996	0.00	0.7578	0.02	0.2976
E∩S	0.10		0.03		0.03		0.07	
Residue	0.83		0.93		1.00		0.85	

DISCUSSION

Although we have used the metacommunity concept to analyze local communities of waders in a single floodplain, we should emphasize that this approach can be a useful tool, especially to determine the pattern of waterbird communities at larger scales, *e.g.* among different wetlands. Given that human activities often change the spatial structure within and among wetlands, a multiscale approach is essential for understanding how these changes may affect waterbird communities. Therefore, our approach should be viewed as a first step in understanding the importance of the metacommunity concept in structuring local communities of waterbirds.

As we hypothesized, the pure spatial factor S|E did not play an important role in shaping the local communities of waders. Wading birds are highly vagile, which allows them to keep up with the seasonally fluctuating mosaic of suitable habitat (Fretwell & Lucas-Jr. 1968, Haig *et al.* 1998). For this reason, distances between sites may not be important in shaping communities at small spatial scales. Meynard & Quinn (2008) suggested that for bird communities studied on a scale of 1000 km or less, environmental factors will predominate, whereas dispersion will become more important for the structure of local communities at larger scales. Thus, it is expected that space does not play an important role for wader communities within patches of a single floodplain (see Figure 5).

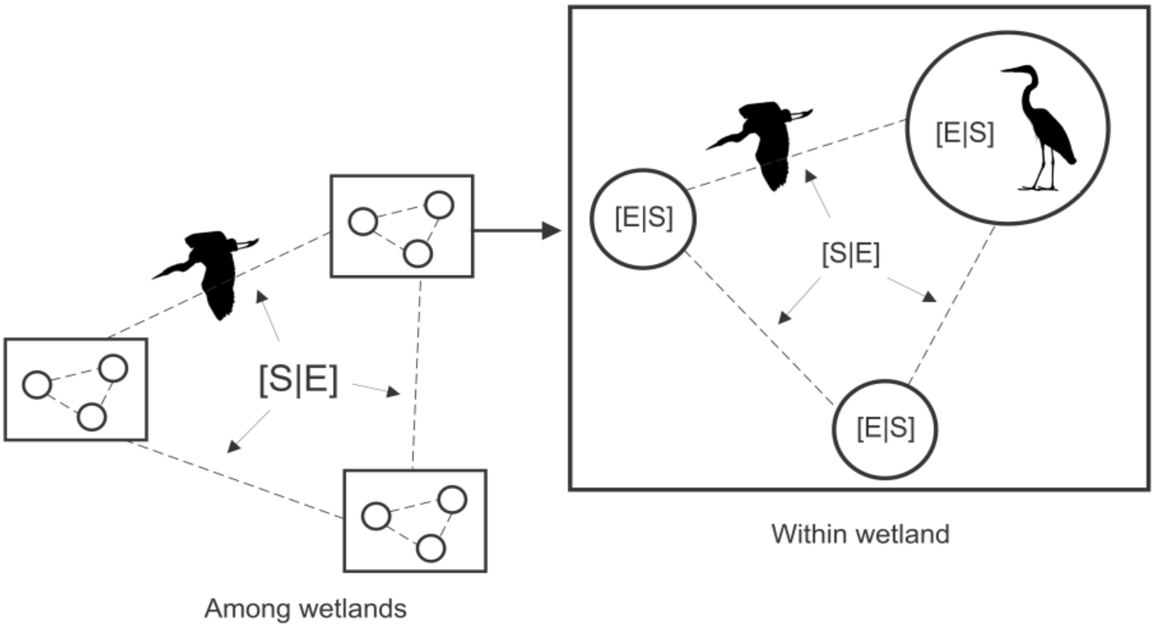

FIGURE 5. Schematic representation of how Local (environmental - LF) and Regional (spatial – RF) factors may influence waterbird assemblages within and among wetlands. Larger distances between sites may imply a more important role of the regional factor in structuring communities.

The significance of the pure environmental component E|S in February and November 2002 shows that these waterbird communities are influenced by local factors and also that the importance of the purely environmental factors varies according to time in the floodplain, partly corroborating our hypothesis. Although we hypothesized that there would be temporal variation in the importance of E|S, we also predicted that the pure environmental factor would be important in most months, being more important during drought. This prediction was not confirmed by data. The pure environmental component was significant only in two months, February and November 2002, the first of which falls within the beginning of the flood period.

The contrasting results found in 2002 and 2003 may be the outcome of human impacts in the Paraná River floodplain. As the Paraná River and its tributaries are affected by dams, one of the main downstream impacts of the reservoirs is to change the natural water level fluctuations. This change affects the water exchange between the river main channel and the floodplain, and, in extreme years, even the absence of floods is observed. This alteration in the hydrological regime directly impacts wading birds whose life cycles depend on water fluctuation (Agostinho *et al.* 2004). During the two sampled years of this study, the water regime was not consistent. The first year (2002) was typical, with floods occurring from January to April and lower water levels characterizing all other months. The second year of sampling (2003) also had a typical flood period in its first months, but the expected dry period had a higher water level than the same period of 2002, with several flood pulses reaching the level at which the river starts to overflow. Additionally, 2002 was preceded by a dry year, in which the supposed flood period was characterized by a water level closer to the levels observed in the last months of 2003 (Figure 3).

The variation in the importance of the environmental factor to the local communities of waders is linked to the flood regime of the floodplain. The pure environmental component was important in shaping the community in February 2002, the beginning of the flood, and in November 2002, the end of the dry period. This result might be explained by the differences in water fluctuation among 2001, 2002 and 2003. Wading birds seek optimal foraging habitats given their morphological and behavioral restrictions. They then select habitat based on local conditions. To reflect this, the environmental variables selected for this study are related to the availability of prey to waders, the majority of which are piscivores (Bancroft *et al.* 2002, Gawlik 2002). Previous studies performed in the same floodplain showed that differences among the density of fish in different lagoons increase during the year, becoming more apparent at the end of the dry period (Fernandes *et al.* 2009, Gimenes & Anjos 2011). Additionally, according to Thomaz *et al.* (2007), a time lag is expected after the flood period until the effects of environmental heterogeneity become apparent. Thus, we suggest that there is a tendency for the environmental factor to become more important in shaping communities at the end of the dry period (represented by November in our samples). As we see, 2003 was an atypical year, in which higher water levels caused an interruption in the dynamics of the dry period and thus altered the role of the environment in structuring waterbird communities. In the same way, the significance of the pure environmental factor in February 2002 may be a consequence of the dry year that preceded it. Specifically, as the flood period was still at its beginning in February, it is possible that the effects of the flood pulse were delayed by the long 2001 drought.

The lack of signal from our explanatory variables may be in part due to limitations of our study. The lack of importance of the spatial factor may be associated with the small scale of the floodplain. As wading birds are vagile organisms, the size of the floodplain may be too small for distances between sites to influence the structure of the community. At the same time, environmental characteristics other than those considered in this study are known to influence waterbird assemblages, such as water transparency, productivity, aquatic vegetation and marginal vegetation (Bancroft *et al.* 2002, Guadagnin & Maltchik 2007, Cintra 2015). The addition of such variables could increase the importance of environmental factors or change its seasonal variation. Furthermore, sampling along only two years could not be enough to determine a seasonal variation pattern of the importance of environmental or spatial factors for wading bird community structure. More years of study could bring better information on the influence of the hydrological cycle for these organisms.

This study is an example of the use of the metacommunity concept as an important tool to better understand the drivers of waterbird diversity in space and time. Knowing the factors driving waterbird distribution in space, as well as the variation in the importance of these factors seasonally is essential to understand waterbird community dynamics. Here, we showed that space is not a strong driver of wading bird assemblages at small scales, considering the area of a floodplain. Furthermore, we showed that there is seasonal variation in the importance of the environmental variables used in this study for this group of waterbirds. Indeed, environmental variables other than those used in this study could be important for these birds in different phases of the flood regime. These additional variables, such as water transparency and aquatic vegetation, could be the focus of future investigations. This approach can be explored to recognize important factors for the maintenance of waterbird communities in recognition of the continuous loss, alteration and fragmentation of wetlands around the world.

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