

Temporal variation of bird assemblages in a wetland: influence of spatial heterogeneity

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ABSTRACT

The temporal variation of bird assemblages at three sites within a wetland of the Parana River was examined. The aim was to obtain an overview of the influence of spatial heterogeneity on communities in such a variable environment as the wetlands. We recorded 1,662 individuals belonging to 139 species from 40 families. There were no significant differences between sites in richness, abundance nor diversity. Species richness in the first year was greater than during the second year. Number of resident and migrant species decreased in the second year. Community composition differed between the two years of study and was significantly different among seasons. Species were grouped into 19 trophic guilds. In this study, number of species and their abundances were not significantly different among sites; there were differences in the composition of birds among sites. Thus, the structure of the environments influenced the composition of assemblages in different areas. Guild composition remained fairly constant between years and among seasons. Geomorphological and hydrological dynamics of the river produce a heterogeneous availability of habitats and resources that affect the composition of bird assemblages. Annual and seasonal changes in meteorological variables can lead to changes in the structure and/or composition of those assemblages.

Keywords: birds, wetlands, temporal variation, spatial heterogeneity

1 INTRODUCTION

Wetlands are among the most productive and ecologically important ecosystems in the world (Mitsch and Gosselink, 1986). Their high productivity and the important functional roles in many natural phenomena and processes (IUCN, 1990) derives in part from the fact that much of their surface area is temporarily or permanently flooded throughout the year. Wetlands are also very important because of the rich biodiversity they support, as well as the cycling and filtering of nutrients and the hydrological and ecological processes that occur in them (Cantero, 1993; Page *et al.*, 1997; Mengui, 2000). The biota present in wetlands is particularly rich and abundant in both plant and animal species, many of which are essential resources for humans. The need to conserve these environments as biogenetic reserves has been widely recognized and forms the goal of many current conservation programs worldwide (Williams and Koenig, 1980; Withers and Chapman, 1993; Page *et al.*, 1999).

One of the largest wetlands of Argentina is the floodplain of the Paraná River, which harbors a particularly rich

diversity of birds (Bo *et al.*, 2002; Chatellenaz, 2005, Giraudo, 2008) with aquatic species among the best represented components of the fauna (Martínez, 1993). From the limnological perspective, this vertebrate group is directly and indirectly involved in the overall functioning of aquatic ecosystems (Hurlbert and Chang, 1983). Knowledge of the structure and composition of bird communities in wetlands can provide basic information on the status of a water body and productivity at different trophic levels.

Understanding the factors that contribute to the diversity of assemblages within a habitat requires consideration of spatial and temporal heterogeneity, *i.e.*, the horizontal, vertical and qualitative variation of the physical and biotic elements (De Angelo, 2003). In the wetlands of the Paraná River floodplain, spatial heterogeneity in the habitat helps sustain a wide range of bird species.

At a local spatial scale, structure and composition of bird communities depend on such factors as habitat characteristics (*e.g.*, size and depth of the water body for aquatic birds), food availability, and availability of suitable breeding or resting sites (Wiens, 1989). The environmental

characteristics that influence bird assemblages within wetlands are spatially variable because patches of vegetation are interspersed with patches of open water, increasing the overall suitability of the system for use by aquatic birds (e.g., Weller, 1978; Kaminski and Prince, 1981; Ball and Nudds, 1989). On the other hand, at a temporal scale, the structure and composition of bird assemblages may vary throughout the year in response to different factors, such as fluctuations in available trophic resources (Stiles, 1980; Levey, 1988; Poulin et al., 1993; Jaquemet et al., 2004), arrival and departure of migratory species (Herrera, 1978; Cueto and Lopez de Casenave, 2000; Greenberg and Marra, 2005) and the local presence and absence of resident species (Filipello and López de Casenave, 1993). Seasonal and annual variation in bird assemblages are highly dependent on events such as rainfall and hydrological variation, whereas interannual variation also may depend on macroclimatic events that operate at regional or global scales.

This study compared the temporal variation of bird assemblages at three sites within a wetland of the Parana River, with the aim of evaluating spatial and temporal variations in diversity, abundance and trophic guild structure. The objective was to obtain an overview of the influence of spatial heterogeneity on communities in such a variable environment as the wetlands.

2 MATERIALS AND METHODS

2.1 Study area

The study was conducted in Pre Delta National Park located southwest of Entre Rios Province, Diamante Department, Argentina (32 ° 03 '43''S 60 ° 38' 39''W). The park is included in the landscape unit referred to as "Forests, prairies, and lagoons of meander floodplains" based on the subdivision of the region of the Parana River Delta produced by Malvárez (1999). The park covers 2,458 ha that have been protected since the park was established in 1992. The climate is generally temperate to warm and humid. Average annual temperature is 19 °C and there is approximately 900 mm rain per year with precipitation occurring mainly in the period from October to April (73%). The hydrologic regime is characterized by an annual flood, which occurs in late summer, and a winter low-water period that occurs in August–September (Rojas and Saluso, 1987).

Spatial heterogeneity in geomorphology allows us to differentiate environmental units according to their height and distance to the main river bed and by the composition of the vegetation, which is related to the topographical gradient. Here, we studied aquatic environments formed by swamps and lagoons that experience temporary or permanent floods, including

the associated herbaceous vegetation communities. Firmly-rooted or floating aquatic vegetation includes species that temporally dynamic in occurrence as they are highly dependent on the water level. *Myriophyllum* sp., *Hidrocotyle bonariensis*, *Enhydra anagallis*, *Salvinia berzoguii*, *Victoria cruziana*, *Eichhornia carssipes* and *E. azurea*, cover both temporary and permanent bodies of water. *Sagittaria montevidensis* and *Ludwigia peploides* and abundant herbaceous vegetation such as *Panicum prionitis*, *Poligonum* spp., *Panicum elephantipes*, *Typha latifolia*, *Solanum glaucophyllum*, *Sellaginella* spp., *Azolla* sp., *Eichhornia* spp. and *Pistia stratiotes* are also found in such areas. Adjacent to these aquatic habitats are island forests that occur on the higher strip of land that follows the watercourse (Burkart, 1957; Aceñolaza et al., 2005; Ronchi-Virgolini et al., 2008). These forests includes species such as *Salix humboldtiana*, *Tessaria integrifolia*, *Albizia inundata*, *Sapium haemospermum*, *Erythrina crista-galli*, *Sapium haemospermum* and *Teucrium vesicarium* (Aceñolaza et al., 2005).

2.2 Bird sampling

Birds were sampled along three sites in wetlands of Pre Delta National Park from March 2006 until March 2008. Sites within were 750 m apart to ensure independence. Five points were established along each transect (sites) with points separated by 250 m to avoid counting the same individual at more than one point (Ralph et al., 1996; Huff et al., 2000). All birds seen or heard within a radius of 100 m of the point were recorded during periods of 10 min at each point (Morrison et al., 1981; Hutto et al., 1986; Blake, 1992). Points along each transect were treated as subsamples with data averaged across the five points (i.e., sites were considered replicates). This may underestimate the local abundance of some uncommon species but avoids potential problems associated with the use of maximum numbers, such as overestimating abundance of very audible species [e.g., saltators (*Saltator* spp.), Rufous Hornero (*Furnarius rufus*), some pigeons].

Bird counts began at sunrise and continued for 4 hours, a period of greater stability in terms of detecting birds (Ralph et al., 1996; Huff et al., 2000). Observers were rotated among the samples with the goal of reducing the influence of observer variation. Each transect was sampled twice during each season, with 45 days between samples. The order of sampling was rotated among sites to overcome biases associated with activity of birds and time of day (Verner and Milne, 1989).

Identification of species and assignment of species to trophic groups followed Narosky and Yzurieta (2010). Nomenclature and migrant status follows Mazar Barnett and Pearman (2001). Migrant categories followed Alonso and Ronchi (2008).

2.3 Trophic guilds

Species were grouped into trophic guilds according to the concept of “functional guild”, a group of species that use similar resources in a similar way (Gitay and Noble, 1997). This term fits the original definition of Root (1967) as a group of species that use similar types of resources, defined subjectively by the researcher (Wilson, 1999). We defined bird guilds based on their main diet, the main substrate used for foraging and, for some species, the method of obtaining food, based on literature accounts (Marone, 1992; Lopez de Casenave *et al.*, 1998) and personal observations.

2.4 Statistical analyses

We compared assemblages of birds between sites in several different ways. We used repeated-measures ANOVA to compare species richness and abundance by site, season and year; comparisons were based on total numbers of species and mean number per point on a given site (*i.e.*, taking the mean across the five sample points per site).

We used several approaches to compare community composition. First, we used analysis of similarity (ANOSIM; Clarke and Warwick, 2001) to compare the level of similarity in species composition among a set of related samples to the level of the similarity across all samples, to determine if species composition of samples within a season were more similar than expected by chance. Significance of the ANOSIM test statistic is determined by comparison with values obtained by a Monte Carlo randomization procedure. Next, we used Indicator Species Analysis (ISA) (Dufrêne and Legendre, 1997; McCune and Grace, 2002) to determine which species were particularly characteristic (indicative) of each season and year. Indicator values were tested for significance with a Monte Carlo randomization procedure (McCune and Mefford, 1999). Finally we used rarefaction analyses to compare total numbers of species based on similar numbers of detections (*i.e.*, to remove the effect of total numbers of birds detected); analyses were based on a Monte Carlo simulation procedure implemented with Ecosim Version 7 (Gotelli and Entsminger, 2006). During a count, not all birds will be detected and, as a consequence, some species will be missed. Thus, we also calculated interpolated Bootstrap estimates of number of species present during a given sample using program Primer Version 5.2.9 (Clarke and Gorley, 2002). Analyses were based on mean numbers per point when sites were considered separately.

We also compared sites on the basis of the most important guilds through a repeated-measures ANOVA, as described above (*i.e.*, using means per point). Statistical tests were performed using StatView 5.0 (SAS INSTITUTE, 1998). All tests were two-tailed, and differences were

considered significant at $P < 0.05$. Reported values are means \pm SD.

3 RESULTS

3.1 Species richness and abundance

We recorded 1662 individuals belonging to 139 species from 40 families. Number of species per transect was relatively highly correlated with abundance during the first year of sampling ($r = 0.65$, $P < 0.01$) but not during the second year ($r = 0.11$, $P = 0.5$). Of all species detected, 74 (53.23%) were present at all three sites, 39 (28.5%) at two sites and 26 species (18.7%) were recorded at only one site (a list of all species and numbers of detections, per site and season, can be requested from the senior author). There were no significant differences between sites in richness ($F = 2.23$, $df = 2$, $P = 0.19$), abundance ($F = 2.34$, $df = 2$, $P = 0.18$), or diversity ($F = 0.72$, $df = 2$, $P = 0.52$).

Species richness in the first year (124 species) was greater than during the second year (107) when comparisons were based on the same number of individuals (768 individuals). Similarly mean richness differed between samples (mean 2006/07 = 30.79 ± 7.10 , mean 2007/08 = 24.87 ± 4.57 , $F = 14.04$, $df = 1$, $P < 0.01$). Mean richness did not differ among seasons (mean autumn = 26.42 ± 4.96 , mean winter = 28.42 ± 5.37 , mean spring = 30.17 ± 10.30 , mean summer = 26.33 ± 4.12 ; $F = 0.87$, $df = 3$, $P = 0.48$), nor did it show different seasonal variation between years and between sites (season-year interaction: $F = 0.36$, $df = 3$, $P = 0.78$; season-site interaction: $F = 0.47$, $df = 6$, $P = 0.82$). Number of resident and migrant species decreased in the second year, consistent with results for the general assemblages and the results of ANOVA.

We recorded a total of 4470 individuals in the first year and 3840 in the second. Mean abundance per transect did not differ between years (average 2006/07 = 37.07 ± 16.44 , average 2007/08 = 31.69 ± 17.51 ; $F = 0.850$, $df = 1$, $P = 0.39$).

Diversity was highest in the spring of the first year ($H' = 3.31$) and lowest during summer of the second year ($H' = 1.54$). Diversity did not differ between years ($F = 2.79$, $df = 1$, $P = 0.15$) or between seasons ($F = 1.30$, $df = 3$, $P = 0.31$). Seasonal variation did not differ between years or between sites (season-year: $F = 0.44$, $df = 3$, $P = 0.73$; season-site: $F = 0.32$, $df = 6$, $P = 0.92$).

3.2 Assemblage composition

The overall assemblage was composed of 97 permanent resident species, five probable permanent residents, 11 summer residents, one probable summer resident, eight summer visitors, seven winter visitors, two probable winter visitors, three occasional species, and five species whose residence in the study area could not be determined. We

recorded 64 species of birds belonging to aquatic habitats and 75 from terrestrial habitats. The most abundant species were *Agelaius* spp., *Plegadis chihi*, *Vanellus chilensis*, and *Jacana jacana*. The best represented families were Tyrannidae with 17 species, Emberizidae with 10 species and Anatidae with 11 species.

Community composition differed somewhat between the two years of study (ANOSIM: Global $R = 0.037$, $P < 0.082$) and was significantly different among seasons (Global $R = 0.109$, $P < 0.004$). Pairwise comparisons indicated significant differences between autumn–winter ($P < 0.012$), autumn–spring ($P < 0.021$), autumn–summer ($P < 0.04$) and winter–summer ($P < 0.009$).

No differences were found between winter–spring ($P = 0.101$) or spring–summer ($P = 0.212$). Seven species were identified as indicators for autumn with six indicator species for each of the other seasons (Table 1).

3.3 Trophic guilds

Species were grouped into 19 trophic guilds. Guilds with highest species richness were aquatic carnivores, carnivores–insectivores and filter feeders. In terms of abundance, granivores–insectivores, aquatic carnivores and carnivores–insectivores were dominant (Table 2). Aquatic carnivores, herbivores–granivores, soil–

Table 1 Species selected as indicators for the different seasons and years for wetlands found in Pre Delta National Park, Argentina, based on indicator-species analysis (Dufrêne and Legendre, 1997).

Species	Season/2006–07	Species	Season/2007–08
<i>Pitangus sulphuratus</i>	Autumn	<i>Laterallus melanophaius</i>	Autumn
<i>Poospiza melanoleuca</i>	Autumn	<i>Taraba major</i>	Autumn
<i>Dendrocygna viduata</i>	Winter	<i>Satrappa icterophrys</i>	Autumn
<i>Tigrisoma lineatum</i>	Winter	<i>Vireo olivaceus</i>	Autumn
<i>Himantopus melanurus</i>	Winter	<i>Saltator caeruleus</i>	Autumn
<i>Turdus amaurochalinus</i>	Winter	<i>Gallinago paraguayae</i>	Winter
<i>Calidris melanotos</i>	Spring	<i>Agelaioides badius</i>	Winter
<i>Tyrannus melancholicus</i>	Spring	<i>Tachycineta meyeni</i>	Spring
<i>Geothlypis aequinoctialis</i>	Spring	<i>Sturnella supercilialis</i>	Spring
<i>Sicalis luteola</i>	Spring	<i>Anas cyanoptera</i>	Summer
<i>Bubulcus ibis</i>	Summer	<i>Sicalis flaveola</i>	Summer
<i>Chlorostilbon aureoventris</i>	Summer	<i>Sporophila collaris</i>	Summer
<i>Progne tapera</i>	Summer		

Only species showing a significant ($P \leq 0.05$) association with a season are shown.

Table 2 Numbers of species and individuals (totals and by year of sample) for guilds recorded during studies at Pre-Delta National Park, Argentina

Trophic guild	Richness			Abundance		
	Total	2006–07	2007–08	Total	2006–07	2007–08
Carnivores–omnivores	4	2	4	76.2	42.2	34
Aquatic carnivores	13	12	10	148.8	108.8	40
Carnivores–scavengers	11	9	8	53.2	32.8	20.4
Carnivores–insectivores	12	10	9	134.4	76.8	57.6
Filter-feeders	12	11	8	90	54.2	35.8
Phytophagous	4	4	2	25.4	20.8	4.6
Granivores	5	4	5	18.6	10.6	8
Herbivores–granivores	10	9	10	85.2	37.8	47.4
Soil-granivores	4	3	4	39.4	10.4	29
Granivores–insectivores	6	6	6	585	266.2	318.8
Frugivores–insectivores	9	9	6	98.8	55	43.8
Foliage–insectivores	11	10	9	80.6	41	39.6
Soil-insectivores	7	7	6	69.2	41.4	27.8
Bark-insectivores	3	3	3	3.6	2.4	1.2
Short-or-long-flight insectivores	11	10	8	22.4	13.4	9
Aereal insectivores	5	4	3	52.6	32.6	20
Nectarivores	2	2	0	2	2	0
Omnivores	7	7	3	58	37	21
Piscivores	3	3	3	19	9.2	9.8

insectivores, and omnivores all varied significantly in abundance between years (ANOVA, $P < 0.05$ in all cases). Seasonal variation was noted for carnivores–insectivores, filter-feeders, herbivores–granivores, and aerial insectivores (ANOVA, $P < 0.05$ in all cases).

4 DISCUSSION

Floodplains of lowland rivers, such as those of the Parana River, represent only one type of wetland within the wide range of wetlands present in Argentina. Each type of wetland can be described in terms of characteristic birds, whose composition largely depends on the environmental attributes of the site (Blanco, 1999). The number of species recorded in this study (139 species) is very similar to that found in other types of wetlands, such as Lagoons of Mar Chiquita, with 138 species (Canevari et al., 1998) and Lagoons La Felipa Natural Reserve, with 127 species (Brandolin et al., 2007).

The diversity of vegetation structures, that provide food, shelter, or substrates for the nest, largely determines the potential richness of water birds inhabiting a wetland (Blanco, 1999). Variation in landscape structure among floodplain sites may cause changes in the attributes that characterise bird assemblages, either in terms of structural characteristics (richness, abundance, diversity) or in composition. In this study, structural aspects of the bird assemblages showed little variation either among sites (transects) or over time (season, year), with the exception that species richness differed between years. In contrast, species composition did show significant variation both spatially and temporally. There are many elements that can explain these changes, perhaps the most important being the hydrologic regime, size and heterogeneity of the site and vegetation structure (Blanco, 1999).

4.1 Species richness and abundance

Wetlands show great horizontal variability in occurrence of water bodies with or without floating vegetation, marsh vegetation, grasslands, shrubs and woody patches that extend out from the forests. Accordingly, richness and abundance of birds might be expected to vary among samples from different sites. Weller and Fredrickson (1974) found that richness and abundance of aquatic birds in a wetland with marsh vegetation and dominance of *Typha* sp. Increased with the number of gaps and areas of open water. In the present study, however, no significant differences in species richness or abundance were observed between, despite the occurrence of spatial variability in the vegetation; lack of significant differences may indicate that a similar range of microhabitats was present in each site. Temporal variation in bird assemblages may have masked differences among sites, as suggested by the significant interactions (i.e., richness

and abundance varied in different ways among sites). Overall species richness was higher in the first year of this study; several different factors may have contributed to this difference. For example, a higher water level may result in a smaller range of habitats and microhabitats (i.e., because vegetation is covered by higher water levels) and, therefore, a lower the number of species present at a given moment (Beltzer and Neiff, 1992). Average river water level in the first year of study (2.98 ± 0.73) was lower than in the second year (3.37 ± 1.07), which would indicate a wider range of habitats throughout the first year, in agreement with the larger number of species detected. Species that were present only in the first year were primarily aquatic birds (41%) and passerines (33%). Many of these species, especially those of the aquatic group, display region movements (Capllonch, 2004), which may have contributed to these differences. *Netta peposaca*, for example, had a high relative abundance during the first year but was absent the following year.

Variation in the number of passerines, particularly insectivorous species, also contributed to the variation in species richness between years. Previous studies have found that the distribution and abundance of insectivorous birds in wetland habitats was related to the availability of aquatic insects in habitats peripheral to a watercourse. Similarly, Nakano and Murakami (2001) noted that aquatic insects were a crucial food resource for adjacent forest bird communities. Abundance of these insect preys may vary between years, reflecting changes in the flood-pulse regime and the corresponding supply of water. This could explain the difference in the number of passerines recorded between the first and second year of sampling.

Although species richness differed between years, there was no significant variation among seasons. Lack of variation reflects the fact that only a few species (16%) were present in only one season (see composition). The absence of seasonal differences in abundance may be related to mild winters (Romano, 2005) that characterize the the region, in contrast to wetlands located at high latitudes (De la Balze and Blanco, 2002) or altitudes (Caziani et al., 2001). The buffering effect of the great rivers on regional climate (Menalled and Adamoli, 1995) might have some effect on this seasonality, reducing environmental differences among seasons.

4.2 Assemblage composition

Of the 139 species recorded, only 46% were aquatic birds, i.e., species completely or partially dependent on wetlands. According to Martínez (1993), about 253 species of birds in Argentina have some relationship with inland aquatic environments, so the number of water bird species recorded in this study represents 25% of that total. The remaining 54% of species recorded in this study were terrestrial birds, representing a large percentage of birds typical of wetlands. This is consistent with findings reported by Nores (1996) and Brandolin et al. (2007), who

recorded a large number of terrestrial species that are part of the avifauna characteristic of other types of wetlands.

Although number of species and their abundances were not significantly different among sites, there were differences in the composition of birds among transects (sites). Such differences likely reflect species-specific differences in habitat requirements. For example, *Columbina talpacoti* and *Myiarchus swansoni* were only recorded in the transect where non-flooded riparian forests were contiguous to wetlands. In contrast, the second site had the largest number of ducks, including *Anas platalea* and *A. sibilatrix* being related to the ponds present in this site. The third transect, which included more non-vegetated lake edges than the other sites, was the only site where several species of plovers and sandpipers, such as *Tringa flavipes*, *Calidris fuscicollis* and *Pluvialis dominica*, were found. *Ixobrychus involucris* was also observed only at this site, in an area with *Typha* sp. and *Schoenoplectus* spp., which were not well represented in the other two sites. *Schoeniophylax phryganophila*, *Suiriri suiriri* and *Camptostoma obsoletum* were also observed only at this site and were associated with woody plants. Thus, variation in the structure of the environments exerted a substantial influence on the composition of assemblages in different areas.

Arrival and departure of migrants (approximately 22% of species) accounted for some of the seasonal variation in assemblage composition; 10 of the species 23 species (44%) recorded in only one season and six of the species selected as indicators of a season (24%) exhibit some form of migratory movement. Among these migratory species were many plovers, such as *Calidris melanotos*, *Tringa melanoleuca*, *T. flavipes* and *T. solitaria*, which are found present in significant numbers during the summer when the river is at a low water level, as noted by Chatellenaz (2005). Variation in resource availability in wetlands may also have had an influence on the seasonal composition of the avifauna. Of the total number of exclusive and indicator species, of a particular season of the year were especially characteristic of forest-based diets in whole or in part, in invertebrates. Invertebrate abundance is known to vary seasonally in relation to hydrological changes (e.g., Iwata et al., 2003, Chan et al., 2008) and could, therefore, influence the distribution and abundance of birds that rely on invertebrates for food. Variation in the use of wetlands by forest species could have influenced the variation in species composition throughout the study period.

4.3 Trophic guilds

Guild composition remained fairly constant between years and among seasons, with some exceptions. Aquatic carnivores, for example, comprised the most abundant guild in the first year but not the second. This guild is composed terrestrial species which feed on the borders of bodies of water. The greater abundance during the

first year could be related to the state of the lakes and other water bodies. According to Beltzer and Neiff (1992), guilds composed of terrestrial species benefit when river water levels fall, as this provides access to feeding sites and allows higher local concentrations of these species. However, water levels in pools and lagoons also depend on local rainfall. The comparison of rivers levels and rainfall between years shows that rainfall was higher in the first year of sampling (annual monthly average of 46.7 mm during the period 2006/07, versus 26.1 mm during the period 2007/08); hence, this element would not be in agreement with that proposed by Beltzer and Neiff (1996). However, the river levels were lower during the first year (annual average of 2.98 m per month during the period 2006/07, versus 3.37 mm for the period 2007/08); hence, this factor would agree with predictions of these authors. The prediction that terrestrial species would benefit from lower water levels is based on the anatomical limitations of the species that compose the guild; shorter-legged species would not have access to feeding sites if water bodies are too deep.

At this point, however, it is necessary to consider the depths of the river at which each particular site is flooded. Soil insectivores, whose feeding substrates also are affected by water levels, were recorded in higher numbers in the first year, in agreement with the pattern discussed above. Filter feeders, by contrast, would benefit from a greater area and / or depth of bodies of water; hence, they would show abundance patterns opposite to those of guilds composed of terrestrial species, as reported by Giraudo (1992) and Beltzer and Neiff (1992). However, filter feeders showed no interannual variation in abundance during the current study. Given that abundance of aquatic invertebrates may be positively related to wet periods (Chan et al., 2008), the greater abundance of these guilds in the first year could be, in turn, related to the greater availability of food. Omnivores also showed this trend; the only exception was herbivores- arboreal granivores, which varied significantly between years, but, unlike the others, were better represented in the second year. The fact that their diet is based on resources very different from those of the other guilds that showed annual changes in abundance may indicate the existence of other processes that explain these differences.

Seasonal variation in the abundance of trophic guilds may have been related to migration patterns, food availability and/or reproductive behavior. For example, carnivore- insectivores, filter feeders and aerial-insectivores include many migratory species (Narosky and Yzurieta, 2010; Capllonch, 2004; Alonso, 2008) that display seasonal variation in abundance. In the case of filter feeders, the migratory behavior of its component species might in turn explain the absence of interannual variation mentioned in previous paragraphs.

Geomorphological and hydrological dynamics of the river produce a heterogeneous availability of habitats and resources that affect the composition of bird assemblages.

Annual and seasonal changes in meteorological variables, such as temperature and rainfall, can lead to changes in the structure and/ or composition of those assemblages. The greater rainfall during the first year of study, for example, likely helped produce the higher species richness seen in the first year and also the greatest abundances of guilds that showed significant annual changes. The flood pulse, which is determined by factors other than local rainfall, would in turn influence those changes; however, to assess the influence of the flood pulse it is necessary to consider the overflow level of each site (i.e., at what river level do different bodies of water fill). Seasonality of the river and climatic variables also influence local and migratory movements of birds, further affecting the taxonomic composition of the assemblage.

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