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BIRD ASSEMBLAGES IN TWO TYPES OF FORESTS IN THE FLOODPLAIN OF THE LOWER PARANÁ RIVER (ARGENTINA)

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Resumen. – Ensambles de aves en dos tipos de bosques en la planicie de inundación del río Paraná Inferior (Argentina). – La heterogeneidad de las planicies de inundación afecta en muchos aspectos la biodiversidad, incluidas las comunidades de aves. En el río Paraná Inferior, el paisaje está compuesto principalmente por dos tipos de bosques: "Albardón" y "Barranca". El objetivo del presente estudio fue describir y comparar los ensambles de aves de ambos bosques en términos de composición de especies y estructura, a través de puntos de conteo realizados desde marzo de 2006 hasta marzo de 2007. Un total de 76 especies fueron registradas entre ambos hábitats, incluyendo 68 en Albardón (2482 detecciones) y 59 en Barranca (2269 detecciones). La variación estacional en la riqueza de especies mostró un patrón similar en ambos bosques: con valores más altos en primavera y los más bajos en invierno. La variación estacional en la riqueza de especies en ambos tipos de bosques se refleja, al menos en parte, por las especies migrantes. La composición a nivel de familia, en general, fue similar en ambos bosques. Las diferencias entre los bosques fueron más evidentes a nivel de especie, como lo demuestra el análisis de especies indicadoras. Gran parte de la diferencia en la composición de especies entre los tipos de bosque estuvo relacionada con la presencia o ausencia de especies asociadas con hábitats acuáticos. La composición por gremios fue muy similar en ambos tipos de bosque, difiriendo principalmente en la importancia relativa de especies asociadas a hábitats acuáticos o áreas abiertas, más que con respecto a la dieta o el sustrato. El gremio insectívoros de follaje con picoteo y espigueo, fue el mejor representado en cuanto a número de especies en ambos bosques, seguido por los insectívoros-frugívoros por espigueo. La mayoría de los gremios aparentemente mostraron una marcada variación estacional en la abundancia, pero los patrones de variación generalmente difirieron entre los dos hábitats.

Abstract. – Heterogeneity in floodplains affects many aspects of biodiversity, including bird communities. In the Lower Paraná River, the landscape is primarily made up of two types of forests: "Albardón" and "Barranca." The goal of the present study was to describe and compare the bird assemblages of both forest types in terms of species composition and structure, based on points counts conducted from March 2006 until March 2007. A total of 76 species was recorded across both habitats, including 68 in Albardón (2482 detections) and 59 in Barranca (2269 detections). Seasonal variation in species richness followed a similar pattern in both forests, highest in spring and lowest in winter, reflecting, at least in part, arrival and departure of migrant species. Family composition generally was similar in both forests. Differences were more evident at the species level as demonstrated by indicator-species analysis. Much of the difference in species composition between forest types was related to the presence or absence of species associated with aquatic habitats. Guild composition was very similar in both forests, differing primarily in the relative importance of species associated with aquatic habitats or more open areas, more than with respect to diet or substrate. Foliage-gleaning insectivores were represented by the most species in both forests, followed by arboreal frugivore-insectivores and terrestrial granivores. Most guilds appeared to show marked seasonal variation in abundance but patterns of variation generally differed between the two habitats. *Accepted 26 July 2011.*

Key words: Albardón, Argentina, avian diversity, Barranca, Lower Paraná, riparian forest, seasonal floods, spatial variation, temporal variation.

INTRODUCTION

The specific composition of bird communities depends on factors that act at different spatial and temporal scales (Wiens 1989). Among the factors that determine spatial variation in bird species richness, environmental heterogeneity, primarily determined by the structure of vegetation, has long been recognized to have its greatest impact at a local scale (Willson 1974, Roth 1976, Rotenberry 1985). Temporal variation in bird communities is manifested through seasonal and annual changes in species distributions and their abundances (Herrera 1981). Such variation may be particularly noticeable in bird communities associated with floodplains (see later). The often close relationship that exists between bird species and habitats suggests that composition of bird communities of floodplains should vary not only over time (i.e., in response to changes in habitat associated with flood pulses) but also should differ from nearby communities in upland forests.

The heterogeneity characteristic of floodplains affects various aspects of biodiversity that these environments sustain. For example, the variety of habitats can increase beta diversity, the replacement of species from one area to another (Vellend 2001), which can contribute substantially to the overall species richness of a region. Similarly, the temporal dynamics of floodplain systems, determined primarily by the seasonal flood, which can cause marked increases in the extent of flooded areas (Tockner *et al.* 2000), can have substantial, concomitant effects on the distribution of terrestrial and aquatic organisms (e.g., Beltzer & Neiff 1992, Knuston &Klaas 1997, Kohler *et al.* 1999). Several studies have compared bird communities among floodplain habitats or between floodplains and adjacent areas to examine how birds respond to the spatial variability of the floodplains (Remsen & Parker 1983, Rosenberg 1990, Reynaud 1998, Warkentin & Reed 1999). Temporal dynamics of such bird communities have also been addressed in studies that have examined the responses of birds to flooding (Knuston & Klaas 1997).

The Paraná River system is the second largest in South America (Burkart 1957), extending from tropical to temperate latitudes (Bonetto 1986). It is characterized by an extensive and complex floodplain with a wide diversity of habitats and a highly productive system that favors the existence of many different biotic communities that are adapted to the fluctuating water regime (Neiff & Malvárez 2004). Di Giacomo & Contreras (2002) found that bird diversity within the lower part of Paraná was higher within the floodplain than in adjacent uplands. In the Middle Paraná, overall bird diversity fluctuated and the responses of different functional groups varied in relation to the hydrological regime of the river (e.g., terrestrial species and species that forage on or close to the ground were more likely to be affected by floods than aquatic species or species that forage in the air or in higher strata in the forest) (Beltzer & Neiff 1992, Bosisio & Beltzer 2003/2004).

In the Lower Paraná River, the landscape is primarily made up of two types of forests: "Albardón" forests that are located within the floodplain and "Barranca" forests that are located on the edge of the floodplain but outside the flood zone. Their floristic and structural differences primarily reflect their susceptibility to floods, which is determined by their respective topographical positions (Aceñolaza *et al.* 2004). The major goal of the present study was to describe and compare the bird assemblages of both forest types in terms of species composition and structure. Thus, we analyzed their similarities and differences both in space and over time, comparing community dynamics both within and between forest types. Analyses were conducted at family, species, and guild levels, with guilds defined *a priori* (Wiens 1989) based on differences in use of resources and space. Our overall objective was to obtain an overview of how these forests contribute to bird diversity across the entire landscape based on their degree of complementarity and to assess the dynamics of assemblages in relation to the seasonal flooding that affects Albardón but not Barranca.

METHODS

Study area. The study was conducted in Pre Delta National Park (32°03'43"S, 60°38'39"W, 18 m a.s.l.). Located in southwestern Entre Rios Province, Diamante Department, 6 km south of Diamante city, the park covers 2458 ha that have been protected since the park was established in 1992. In accordance with the subdivision of the region of the Paraná River Delta produced by Malvárez (1999), the park is included in the landscape unit referred to as "Forests, prairies, and lagoons of meander floodplains." Situated in the alluvial floodplain of the Paraná River, it is comprised of a zone of islands characteristic of the northern region of the delta, or superior delta. In addition, there is a smaller sector of riparian forest environment (Barranca). 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 & Saluso 1987). From a biogeographic perspective, Pre Delta National Park is located in a region influenced by diverse floristic components, with input of species primarily drawn from the Paranaense Province (Dominio Amazónico), and from Chaqueña and Espinal provinces (Dominio Chaqueño) (Cabrera & Willink 1973, Cabrera 1994).

Following Aceñolaza *et al.* (2004, 2005), we delineated two distinct habitats that either do not flood (Barranca) or that experience different frequencies of flooding (Albardón). Albardón is a wide area within the highest elevations of the floodplain formed by the Paraná River. Originally, Albardón supported a more diverse and extensive forest that has now been reduced to isolated remnants in some sectors of the floodplain system. Vegetation consists primarily of *Salix humboldtiana* and *Tessaria integrifolia* with additional species such as *Croton urucurana*, *Sapium haematospermum*, *Albizia inundata*, *Erythrina crista-galli*, and *Enterolobium contortisiliquum*. Swamps and lagoons in Albardón, either temporary or permanent, are characterized by short and sparse vegetation with remaining patches of *Acacia caven*, *Albizia inundata*, and *Sapium haematospermum*. The herbaceous layer is abundant and includes *Panicum prionitis*, *Panicum elephantipes*, *Polygonum* sp., *Sagittaria montevidensis*, *Typha latifolia*, *Solanum glaucophyllum*, *Selaginella* spp., *Azolla* sp., *Eichhornia* spp., and *Pistia stratiotes*, among others. Barranca, in contrast, has steep slopes and is not subject to flooding. Forest cover is relatively dense, with many tree species, including *Ruprechtia laxiflora*, *Myrsine laetevirens*, and *Phytolacca dioica*. Undergrowth is sparse, principally *Fagara hyemalis* and *Coccoloba argentinensis*; the herbaceous layer is comprised of such species as *Dicliptera tweediana*, *Sida* *rhombifolia*, *Teucrium vesicarium*, *Rivina humilis*, and *Melica sarmentosa*.

Bird sampling. Birds were sampled along three transects in each habitat (Albardón and Barranca) from March 2006 until March 2007; transects within a habitat were 750 m apart to ensure independence. Five points were established along each transect with points separated by 250 m to avoid counting the same individual at more than one point (Ralph *et al.* 1996). All birds seen or heard within a radius of 100 m of the point were recorded during periods of 10 min at each point (Hutto *et al.* 1986, Blake 1992). Points along each transect were treated as subsamples with data averaged across the five points (i.e., transects 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 h, a period of greater stability in terms of detecting birds (Robbins 1981, Ralph *et al.* 1996). Observations were conducted by Ronchi-Virgolini, Lorenzón and Alonso; observers were rotated among samples to reduce the influence of observer variation. Each transect was sampled twice during each season, with 45 days between samples; all three transects in a habitat were sampled on the same day. Order of sampling was rotated among transects to overcome biases associated with activity of birds and time of day (Verner & Milne 1989). Thus, there was a total of 48 samples during the entire study (2 habitats, 3 transects per habitat, 4 seasons, transects sampled twice during each season).

Identification of species and assignment of species to trophic groups followed Narosky & Yzurieta (2003), Beltzer (2003) and de la Peña (2006). Nomenclature and migrant status follows Mazar Barnett & Pearman (2001). Migrant categories included partial Austral migrants (species whose populations disperse after breeding to more northern latitudes in autumn, and winter mostly within Argentina) and Austral migrants (species that move north after breeding, departing Argentina in the southern autumn and wintering outside the country).

Statistical analyses. We compared species richness between habitats in several different ways. First, 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 & 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 & Gorley 2002). We used repeated-measures ANOVA to compare species richness and mean number of detections (all species) by habitat and season; comparisons were based on total numbers of species and mean number of detections per point on a given transect (i.e., taking the mean across the five sample points per transect).

We used several approaches to compare community composition. First, nonmetric multidimensional scaling (NMS), implemented with PC-ORD Version 4.0 (McCune & Mefford 1999), was used to graphically represent similarities (and differences) in species composition between habitats and among samples (Clarke & Warwick 2001, McCune & Grace 2002). Then, we used analysis of similarity (ANOSIM; Clarke & Warwick 2001) to compare the level of similarity in species composition among a set of related samples (e.g., Barranca vs Albardón) to the level of the similarity across all samples, to determine if species composition of samples within a habitat was 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 & Legendre 1997, McCune & Grace 2002) to determine which species were particularly characteristic (indicative) of each forest. Indicator values were tested for significance with a Monte Carlo randomization procedure (McCune & Mefford 1999). Analyses were based on mean numbers per point when transects were considered separately.

We followed the methods of Pitman *et al.* (2001) to compare the relative importance of different families (based on number of detections or number of species by family) and different species (number of detections by species) in the two habitats, with data combined across all samples. We arbitrarily selected Albardón as the x-axis and calculated the slope of the line between Barranca and Albardón to test the null hypothesis that the two habitats were equivalent in terms of species or family composition. If the numbers of detections or species per family, or detections per species, were the same in the two plots, the slopes of the lines should be equal to one (Pitman *et al.* 2001; see also Blake 2007, Blake & Loiselle 2009). We also compared habitats on the basis of guild structure. Comparisons between habitats and across seasons in abundance of the most important guilds were based on 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 ± SD.

RESULTS

Species richness and abundance. A total of 76 species was recorded across both habitats, including 68 in Albardón with 2482 detections and 59 in Barranca with 2269 detections; 51 species occurred in both habitats, 17 were restricted to Albardón, and 8 were found only in Barranca (a total list of species and numbers of detections, by habitat and season, is available by contacting the senior author). Rarefaction analysis confirmed that species richness was greater in Albardón than in Barranca (Fig. 1). Species-accumulation curves suggested that most but not all species were recorded in each habitat after 24 samples (i.e., the curves are close to an asymptote in each habitat). Similarly, estimated species totals were only slightly higher than observed (Fig. 2) further indicating that additional samples likely would yield few additional species in each habitat. When species-accumulation curves were examined by season, however, an asymptote was not approached except for Albardón in summer; thus, additional samples per season likely would have recorded more species in each habitat. Abundance-rank curves were similar for both habitats and indicated that most species were represented by relatively few detections.

The number of species per transect was correlated with the number of detections in Albardón ($r = 0.77$, $P < 0.01$) and Barranca ($r = 0.73$, $P < 0.01$). Mean number of species per transect did not differ between habitats (Albardón 24.7 ± 7.6, Barranca 21.8 ± 5.9; $F = 2.63$, df = 1, $P = 0.16$) but did vary among seasons (autumn 22.1 ± 7.7, winter 19.2 ± 6.3, spring 27.6 ± 6.5, summer 24.1 ± 4.7; $F = 4.79$, df = 3, $P = 0.013$); interaction between habitat and season was not significant ($F = 0.71$, df = 3, $P = 0.56$; repeated-measures ANOVA). Mean number of detections per point in each transect (all species) did not differ between habitats (Albardón 20.7 ± 7.7,

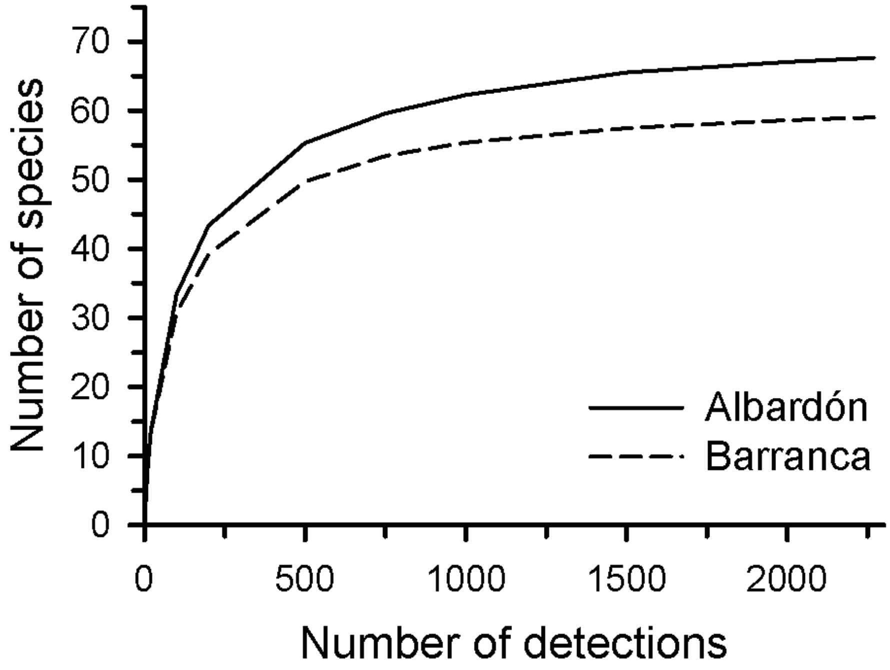

FIG. 1. Rarefaction analyses to compare rates of species accumulation in the two distinct habitats that do not flood (Barranca) or that experience different frequencies of flooding (Albardón), Pre Delta National Park, Argentina, based on numbers of detections from March 2006 through March 2007.

Barranca 18.9 ± 6.2; $F = 0.49$, df = 1, $P = 0.51$) or across seasons (autumn 20.7 ± 7.8, winter 17.3 ± 7.1, spring 22.9 ± 7.3, summer 18.3 ± 4.6; $F = 1.84$, df = 3, $P = 0.18$); the interaction between habitat and season was not significant ($F = 0.57$, df = 3, $P = 0.64$).

Across both habitats, there were 21 partial Austral migrants [e.g., Lesser Canastero (*Asthenes pyrrholeuca*), White-tipped Plantcutter (*Phytotoma rutila*), Tawny-crowned Pygmy-Tyrant (*Euscarthmus meloryphus*), Black-backed Water-Tyrant (*Fluvicola albiventer*)] and 7 Austral migrants [e.g., Dark-billed Cuckoo (*Coccyzus melacoryphus*), Large Elaenia (*Elaenia spectabilis*), Tropical Kingbird (*Tyrannus melancholicus*)]. More migrants were recorded in autumn in Albardón (22 spp.) but in spring in Barranca (13 spp.); migrants were least common in winter in Albardón (6 spp.) and in autumn and winter in Barranca (7 spp. in each season). For residents, more species were recorded in spring in Albardón (39 spp.) whereas in Barranca the greatest number of species was in autumn (36 spp.); residents were less common in autumn in Albardón (31 spp.) and in winter in Barranca (31 ssp.) (Fig. 3).

Community composition. Results of the NMS indicated a clear separation of the two forest types, with Barranca dominated more by Southern Beardless-Tyrannulet (*Camptostoma obsoletum*) and White-browed Warbler (*Basileuterus leucoblepharus*), and Albardón by Red-eyed Vireo (*Vireo olivaceus*) and Masked Yellowthroat (*Geothlypis aequinoctialis*) (Fig. 4).

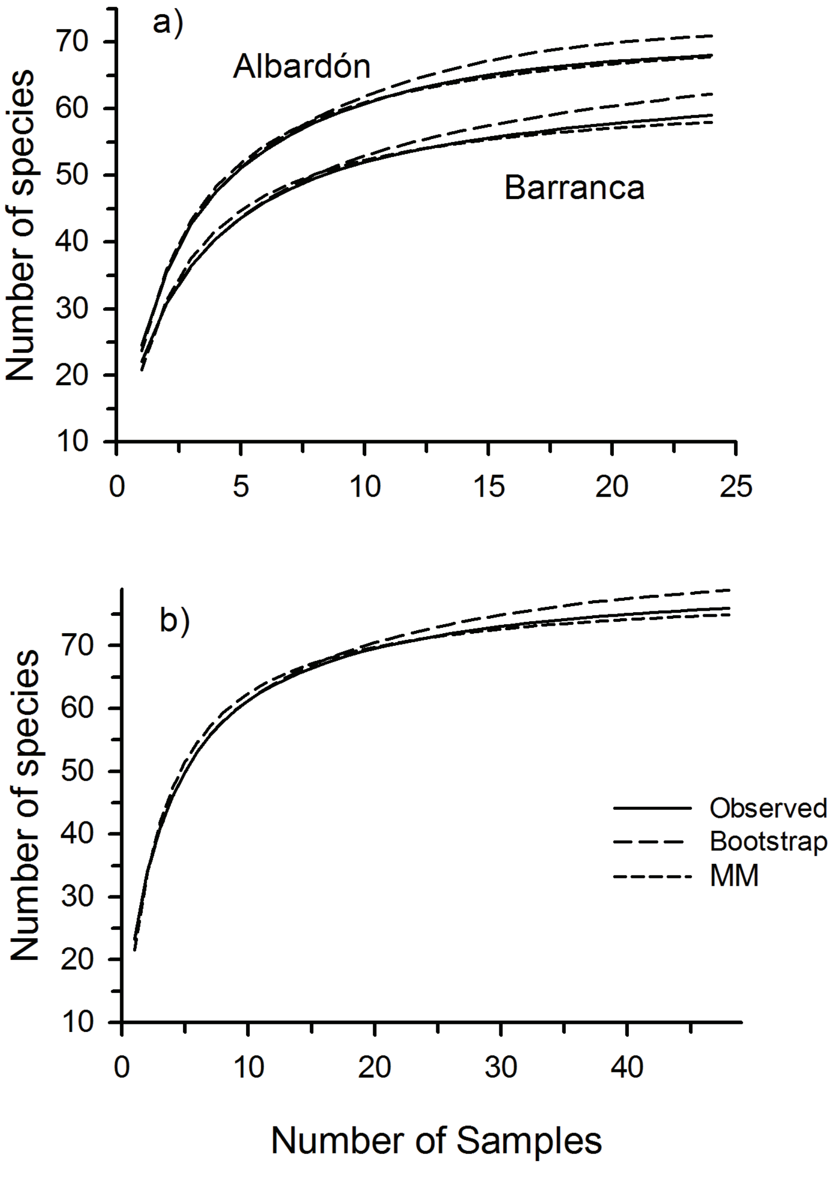

FIG. 2. Species-accumulation curves in (a) Albardón and Barranca, and (b) both habitats combined, Pre Delta National Park, Argentina, based on numbers of samples from March 2006 through March 2007.

Results of the ANOSIM supported ordination results and indicated a significant difference in species composition between the two forest types (Global R = 0.54, *P* < 0.01). Seasonal samples did not show as clear a separation in the NMS (Fig. 4) but, nonetheless, ANOSIM indicated a significant effect for season (Global R = 0.29, *P* < 0.01). Indicator-

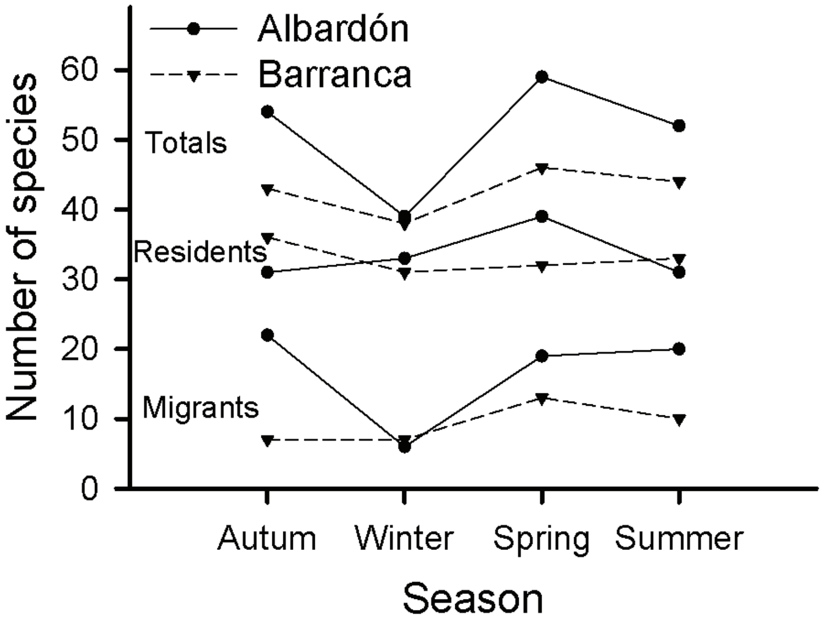

FIG. 3. Species richness by season based on number of migrant species, number of resident species and total number of species in Albardón and Barranca, Pre Delta National Park, Argentina.

species analysis selected 11 spp. as indicators for Albardón and 9 spp. for Barranca, supporting the results of the ordination and ANOSIM (Table 1).

There were 24 families represented among all birds detected. Families with the most species included Tyrannidae (18 spp.), Emberizidae, Columbidae, and Icteridae (6 spp. each). Albardón had more species of Tyrannidae and Icteridae (and *Schiffornis*), whereas Columbidae, Emberizidae, and Coccyzidae were represented by more species in Barranca. The remaining families had the same number of species in both forests. Columbidae and Furnaridae had the most number of detections (898 and 816, respectively) and were the most common families in both forest types.

To further compare composition between habitats, we plotted number of species per family, number of detections per family, and number of detections per species for the two habitats. The slope of the regression between Barranca and Albardón based on species per family was 0.73 (Fig. 5a) and largely reflected the influence of Tyrannidae, which were more important in Albardón. In contrast, the slope of the regression based on average detections per family was 1.07, reflecting the higher overall similarity between forest types in number of detections per family (Fig. 5b). When comparisons between forests were based on number of detections by species, the slope of the regression (0.75) was lower than that based on detections by family and similar to that for species per family (Fig. 5c). The lower slope largely reflected the influence of Rufous-bellied Thrush (*Turdus rufiventris*), Greyish Saltator (*Saltator caerulescens*), and Greater Thornbird (*Phacellodomus ruber*) with higher detections in Albardón and

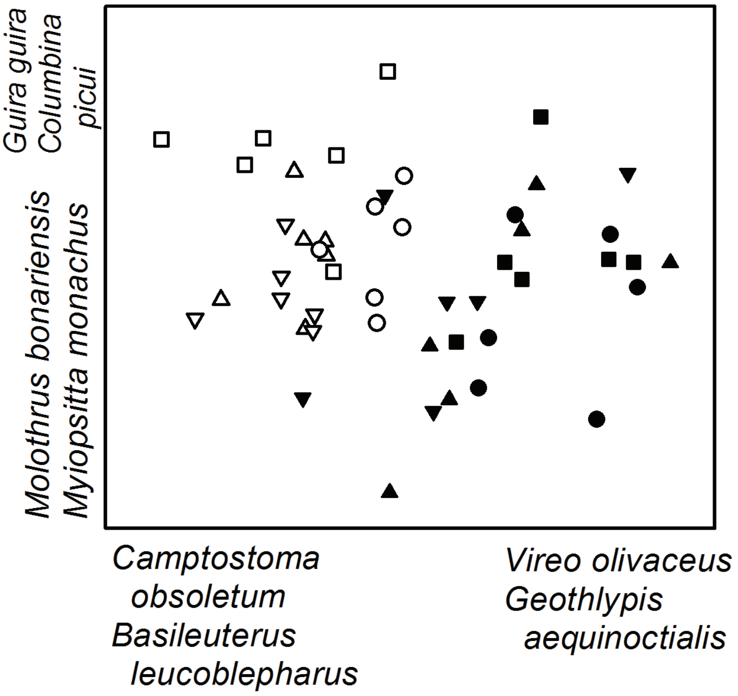

FIG. 4. Nonmetric multidimensional scaling ordination (Axis 1 – x-axis; Axis 2 – y-axis) based on number of detections per sample for Albardón and Barranca habitats in the Pre Delta National Park, Argentina. Axes reflect differences in composition between two forest types. The two species most highly correlated with each axis are indicated. Solid symbols – Albardón; open symbols – Barranca; up-triangle – fall; down-triangle – winter; circle – spring; square – summer.

White-tipped Dove (*Leptotila verreauxi)* and Rufous Hornero (*Furnarius rufus*) in Barranca. Of these species, only the Greyish Saltator was selected as an indicator species (Table 1).

Guild structure. Twelve guilds were recorded in Albardón and 11 in Barranca (Table 2); aerial insectivores were not recorded in Barranca. Foliage-gleaning insectivores were represented by the most species in both Albardón (21 spp.) and Barranca (20 spp.), followed by arboreal frugivore-insectivores (16 and 14 spp., respectively). Based on total number of detections, foliage insectivores were the most important guild in both forests, followed by arboreal frugivore-insectivores in Albardón and terrestrial granivores in Barranca (Table 2).

Most guilds varied in abundance across seasons in both forest types but there were no significant differences among seasons for any guild in either habitat ($P > 0.05$, all cases) and no significant interactions. Some guilds (e.g., foliage-gleaning insectivore, arboreal frugivore-insectivore) showed similar seasonal fluctuations in abundance in both forest types, whereas others (e.g., terrestrial insectivore, terrestrial granivore, terrestrial frugivore-insectivore) showed complementary seasonal fluctuations in abundance between forests in two or more seasons (i.e., fluctua-

TABLE 1. Species indicators of Albardón and Barranca forests, Pre Delta National Park, Argentina, based on indicator-species analysis (Dufrêne & Legendre 1997). Lower *P*-value indicates higher degree of association with that plot.

Albardón		Barranca	
Species	*P* <	Species	*P* <
Tachycineta leucorrhoa	0.0002	*Basileuterus leucoblepharus*	0.0002
Vireo olivaceus	0.0002	*Columbina picui*	0.0002
Paroaria coronata	0.0002	*Synallaxis frontalis*	0.0002
Geothlypis aequinoctialis	0.0004	*Saltator aurantiirostris*	0.0034
Saltator coerulescens	0.0034	*Camptostoma obsoletum*	0.0038
Progne tapera	0.0098	*Saltator similis*	0.0428
Myiopsitta monachus	0.0128	*Coryphospingus cucullatus*	0.0446
Agelaius cyanopus	0.0204	*Thamnophilus caerulescens*	0.0464
Coccyzus melacoryphus	0.0330		
Suiriri suiriri	0.0494		

tions in abundance were in opposite directions between forests). However, only terrestrial insectivores varied significantly in abundance between habitats ($F = 9.91$, df = 1, $P = 0.02$, repeated-measures ANOVA).

DISCUSSION

Albardón and Barranca, the two major forest types found in the Lower Paraná, support a diverse array of bird species, including both migrants and residents. These two forest types differ in a number of important characteristics associated with topography and vegetation but nonetheless share a substantial number of bird species. At the same time, each habitat also supports a number of species that are not found in the other habitat or that are found in very different numbers. As a consequence of these differences, the overall composition of bird communities differs between the two habitats. This complementarity in species composition contributes to the region's overall diversity. As in other riparian systems (Remsen & Parker 1983, Rosenberg 1990, Knuston & Klaas 1997, Reynaud 1998, Warkentin & Reed 1999), spatial and temporal variation in species richness and composition, seen in both habitats, likely were related both to differences in vegetation and to seasonal effects of floods and their impacts on availability and abundance of resources, primarily insects (see Beja *et al.* 2010). Arrival and departure of migrants further contributed to the dynamic nature of the entire system and of the two habitats separately, especially with respect to temporal variation in species richness. On a smaller scale, movement of individuals between habitats in response to changes associated with seasonal floods further contributed to both spatial and temporal variability. Results of this study illustrate the dynamic nature of floodplain ecosystems and the complex relationships between species and habitats.

The Paraná is one of the largest rivers of the Neotropics, in terms of volume, and as a result, has developed an extensive floodplain with a great variety of habitats. In fact, the floodplain of the Paraná presents great similarities with that of the larger Amazon (Iriondo & Paira 2007) and differences in composition encountered between assemblages in this study are similar to those found

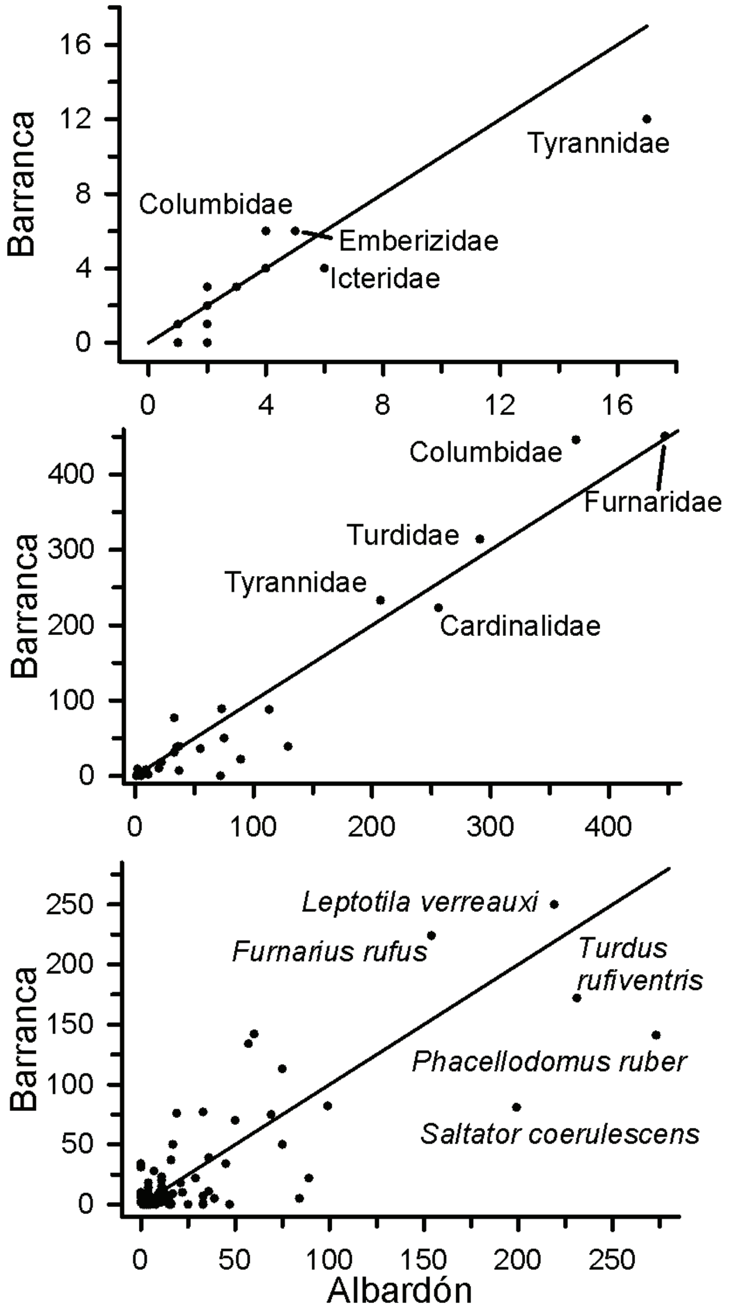

FIG. 5. Number of (a) species per family, (b) detections per family, and (c) detections by species in two forest types (Albardón and Barranca) in the Pre Delta National Park, Argentina. Straight lines indicate a 1:1 relationship between values for the two forests. Actual slopes of the regressions are: a) 0.73 ± 0.06, r^2 = 0.86; b) 1.07 ± 0.06, r^2 = 0.94; c) 0.75 ± 0.06, r^2 = 0.64.

TABLE 2. Guild structure, number of species, and number of detections per guild in all seasons on Albardón (Alb) and Barranca (Bar) forests, Pre Delta National Park, Argentina.

Guild	Nº species		Nº detections		Nº detections for seasons							
					Autumn		Winter		Spring		Summer	
	Alb	Bar	Alb	Bar	Alb	Bar	Alb	Bar	Alb	Bar	Alb	Bar
Carnivore	2	1	14	8	5	1	5	3	2	3	2	1
Scavenger	1	1	2	9	0	4	1	4	1	0	0	1
Arboreal frugivore-insectivore	16	14	489	394	113	93	83	76	177	138	116	87
Nectarivore-insectivore	2	2	33	31	3	1	0	2	6	15	24	13
Terrestrial insectivore	1	1	154	224	29	58	39	44	58	56	28	66
Foliage-gleaning insectivore	21	20	728	611	184	208	147	141	226	145	171	117
Insectivore-omnivore	9	3	114	122	33	40	29	21	18	30	34	31
Aerial insectivore	2	0	72	0	18	0	22	0	19	0	13	0
Bark insectivore	4	4	71	77	21	15	13	15	18	33	19	14
Terrestrial granivore	5	7	461	468	97	144	126	94	153	93	85	137
Omnivore	2	3	20	10	11	0	0	0	4	3	5	7
Terrestrial frugivore-insectivore	3	3	324	315	92	69	67	105	93	86	72	55
Totals	68	59	2158	1954	514	564	465	400	682	516	497	474

in studies of birds of Amazonian riparian forests (Remsen & Parker 1983, Rosenberg 1990). In both systems, riparian habitats contribute substantially to regional bird diversity. Similarly, although dos Anjos *et al.* (2007) studied riparian forests of a much smaller river in the Atlantic Forest of Brazil, they found that riparian forests contributed greatly to diversity in adjacent tall forests. The present study provides further evidence that riparian areas contribute to regional biodiversity and, if remnants from adjacent upland forest (Espinal Province) were included in the present comparison, the importance of riparian forest would be even more pronounced.

Species richness and abundance. In landscapes where water is not a limiting factor, such as in the Paraná River, the higher ground vegetation does not differ as markedly from that in riparian areas as it does in more arid regions. The relative importance of these two environments, as habitat for birds, is not, however, well known and studies conducted to date have generated mixed conclusions, with some reporting more species and or greater abundance in riparian forests (e.g., Stauffer & Best 1980, Gates & Giffen 1991, LaRue *et al.* 1995), others in high ground forests (McGarigal & McComb 1992), and others that found no differences in species richness or abundance (Murray & Stauffer 1995, Whitaker & Montevecchi 1997). Results were equivocal with respect to the relative importance of structural versus floristic complexity as factors influencing bird species richness.

In terms of the number of species per transect, Albardón, despite being structurally more complex, was only somewhat more speciose than Barranca. Barranca is more floristically complex but, unlike other studies (Bersier & Meyer 1995, Rodríguez-Estrella *et* *al.* 1996, Bojorges-Baños & Lopez-Mata 2006), this complexity apparently did not affect species richness or, alternatively, may have diminished the effect of structural complexity on differences in number of species between habitats. Thus, there was no evidence of a clear pattern as to whether structural or floristic diversity was more important with respect to avian diversity. Nonetheless, if the total number of species found in the two forests is considered, the nine more species found in Albardón represent an important difference that suggests a greater influence of structural complexity, in terms of its effect on avian diversity, than the floristic complexity of Barranca. As with species richness, there was no clear difference between habitats in numbers of birds detected. Lack of substantial differences in habitat complexity, combined with the availability of water in Barranca as well as in Albardón, likely contributed to similarity in overall abundance.

Seasonal variation in many bird communities, particularly those in temperate regions (although tropical regions also experience seasonal variation related to migration), largely is related to patterns of migration. Migrants were a major component of bird communities in the Paraná River system and contributed to the temporal variation in species richness and composition seen in both forests. In agreement with the great similarity between seasonal variation of migrants and seasonal variation of the entire assemblage, and given that the same pattern was not seen with the assemblage of residents, it is apparent that seasonal variation in species richness and abundance were more strongly related to patterns of migration, rather than to the variability in resources and habitats produced by seasonal floods.

Community composition. In contrast to total richness and abundance, we observed more pronounced differences in species composition between the two forest types. Much of the difference in species composition was related to the presence or absence of species associated with aquatic habitats. In general, differences in the abundance of individual species may reflect ecological processes operating at a relatively small scale (i.e., differences in habitats between forests and differences in the habitat-selection patterns by species), given that both forest types are close to each other. Indicator species acted as a complement to the species that were exclusive to one forest or the other in terms of distinguishing between forests on the basis of species composition. In the case of *Saltator* species, for example, one member of the genus was an indicator of each forest type. Given their morphological and behavioral similarities, this separation could indicate some degree of habitat segregation. Most indicator species, as well as those species exclusive to one forest type or the other, are prominent and relatively easy to identify so it is unlikely that they were under-sampled in one habitat versus the other.

At a larger scale, the association of species with different phytogeographic provinces influenced the composition of bird assemblages. For example, some of the species exclusive to Barranca are associated with forests characteristic of the Espinal province, forests that have a vegetation structure very distinct from Barranca forests per se and from Albardón (e.g., *Synallaxis albescens*, *Euscarthmus meloryphus*). In the same way, some of the species exclusive to Albardón are associated with Provincia Paranaense (e.g., *Thlypopsis sordida*).

Differences in species distribution patterns within forests were not examined in the present study but such differences likely occur and relate to small-scale variation in habitat and habitat preferences of different species (Karr & Freemark 1983). For example, Palmer & Bennett (2006) found that tree cover of intermediate strata and height of the canopy, as well as cover and presence of certain plant life forms (e.g., trees, ferns, vines), were related to riparian bird community composition. Rosseti & Giraudo (2003), on the other hand, compared bird assemblages within two types of Albardón (heterogeneous and willow forests) in the Middle Paraná, but did not find differences in species richness, abundance, composition or diversity. Anderson *et al.* (1983) found that attributes of bird communities were related with parameters of the vegetation at the habitat scale in the flood-plains of the Colorado River. In the Paraná, species of open areas [Fork-tailed Flycatcher (*Tyrannus savanna*), Cattle Tyrant (*Machetornis rixosus*), White-rumped Swallow (*Tachycineta leucorrhoa*)], for example, were found in the areas of Albardón with a simpler vegetation structure (i.e., monospecific forests dominated, generally, by *Salix humboldtiana*, and with few shrubs or herbaceous vegetation in the lower strata). In this way, studies at the habitat scale (i.e., Barranca vs Albardón) may obscure important within-habitat differences that influence patterns of species distribution.

Guild structure. In this study, guild composition was very similar in Albardón and Barranca forests, differing primarily in the relative importance of species associated with different habitats, more than with respect to the diet or substrate. Insectivorous guilds were more important in this study, particularly those associated with tree and shrub foliage, and typically are the most species rich in bird communities found in most tropical and subtropical forests (e.g., Blake *et al.* 1990, Cueto & López de Casenave 2000, Blake & Loiselle 2001, Codesido & Bilenca 2004, Piratelli & Blake 2006).

Other studies have encountered differences in guild composition between inundated and non-inundated forests. Willis (1979) and dos Anjos *et al.* (2007), for example, found that edge omnivores and mid-story insectivores were better represented in riparian forests; gaps in those forests benefitted such guilds. In contrast, in our study, only terrestrial insectivores showed a significant difference between forests but were better represented in Barranca (see later), despite the existence of well-marked gaps in riparian forests. Nevertheless, number of detections of foliage-gleaning insectivores and arboreal frugivore-insectivores were greater in inundated forest, in agreement with the results of Willis (1979) and dos Anjos *et al.* (2007).

Flooding can influence the supply of resources and, thus, can be related to variation in guild composition. Soil invertebrates, for example, might benefit from the increased humidity and thereby favor guilds associated with soil (Volpato *et al.* 2006). dos Anjos *et al.* (2007) found this pattern in the Atlantic forest of Brasil, where terrestrial omnivores were better represented in riparian forests than in high-ground forests. This pattern was not, however, found in the present study where none of the guilds associated with soil were better represented in inundated forests. This lack of difference could be because Barranca is a generally wet or humid forest type (although without flooding) so that differences in soil moisture between forest types may not be strongly developed.

The effect of floods, apart from the influence on availability of microhabitats in a given moment, also could be a factor related to the contrasting patterns between forests in the seasonal variation of some guilds. Terrestrial insectivores and terrestrial granivores showed this pattern most strongly. Abundance of both guilds was high in Albardón and low in Barranca during spring but the reverse was true in the summer and fall. Floods typically occur in the summer–fall period and, during this study, an exceptional flood-tide occurred in summer–fall 2007. This flood directly affected the feeding substratum of terrestrial guilds in Albardón, with the result that many individuals likely retreated to the unflooded uplands (i.e., Barranca). Knuston & Klass (1997) found a similar pattern when comparing birds between flooded and unflooded plots in the Mississippi River floodplain. This could help explain the greater representation of terrestrial insectivores in Barranca. Variation in resource abundance (e.g., insects, seeds) in the herbaceous stratum could be an additional factor contributing to variation in abundance of these guilds (Aceñolaza pers. com.). The flood pulse in Albardón could directly affect birds given that it inundates the foraging stratum and makes it unavailable for those species and/or could affect sources of food. Reynaud (1998) was unable to find granivores in riparian forests and associated this to the fact that wet and inundated soil does not provide sufficient seeds. In the case of insectivorous species, it has been suggested that they could move to riparian forests when the productivity of aquatic insects is greater than the productivity of terrestrial insects, or to upland forests when the opposite pattern occurs (Nakano & Murakami 2001, Uesugi & Murakami 2007). Terrestrial frugivore-insectivores did not show the same response to flooding as did terrestrial insectivores, likely because the former guild was chiefly represented by *Turdus* species, which feed on fruits of trees and shrubs as well as on soil invertebrates.

The absence of seasonal variation in guilds is surely related to various factors that involve alternative approaches for study. In the first place, the classification of seasonal patterns in terms of climate is somewhat arbitrary and perhaps alternative classifications could reveal other patterns (e.g., reproductive versus non-reproductive periods, periods of inundation versus periods without inundation). In the same way, grouping species on the basis of other criteria could bring a better perspective for the study of guild structure and temporal variation. The general tendency of a guild (e.g., food type consumed) does not necessarily reflect the tendencies of all the component species (Faaborg *et al.* 1984), so that species-specific studies of temporal variation surely would improve our knowledge of temporal variation in bird assemblages.

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