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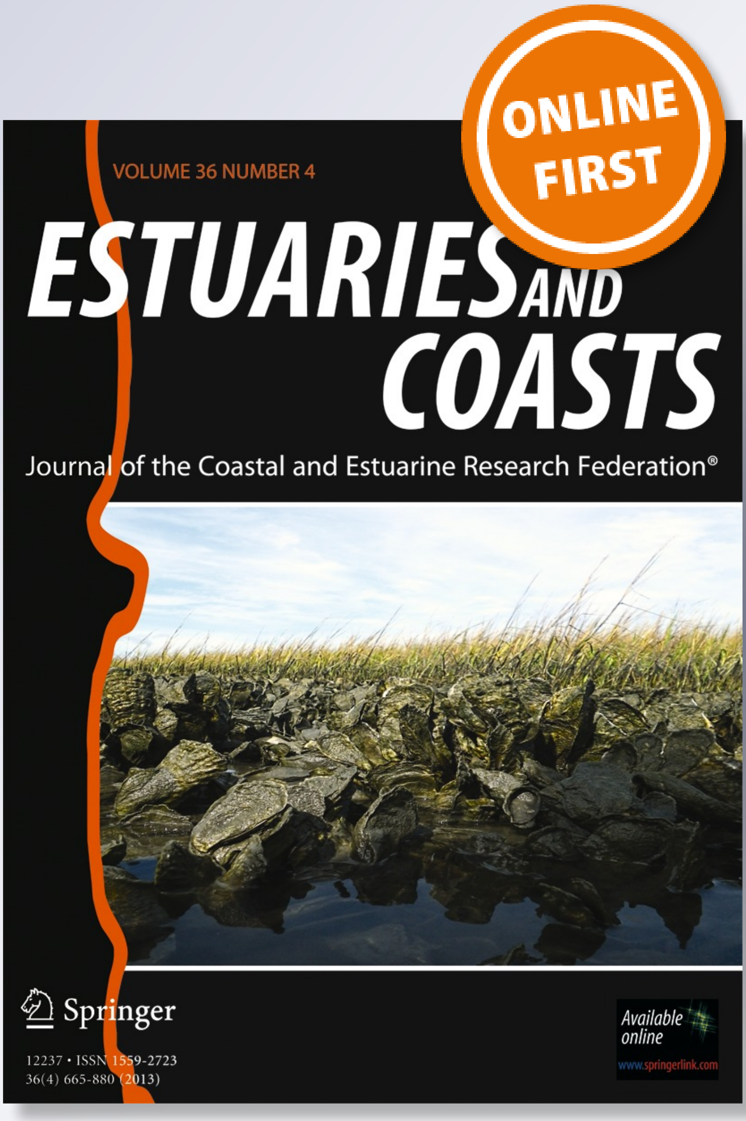

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Abstract We studied variation in bird assemblages with plant associations for three different coastal marshes from Southeastern South America (SESA) and assessed how marsh bird assemblages related to nearby upland bird assemblages. We surveyed bird species and plant structure along the tidal gradient of each locality from the low tide level to the upper habitats bordering coastal marshes. Twenty species frequently used coastal marshes, including relatively few migratory species. We found that birds occurring in SESA coastal marshes do not have distributions constrained to coastal marshes. Nonetheless, four bird assemblages were recognized in association with vegetation types and/or sites. Among the recorded coastal marsh species, the bay-capped wren-spinetail (*Spartonoica maluroides*) is both the most frequent and the most habitat constrained. Bird richness increases steadily along the tidal gradient associated with the increase in vegetation structure, suggesting that bird richness is directly explained by vegetation and indirectly by the physical conditions influencing vegetation structure. Results highlight the importance of SESA middle marshes as habitat for conservation of some threatened SESA grassland birds.

Keywords Argentina · Bay-capped wren-spinetail · Bird diversity · Emberizid · Furnarid · Fresh marsh · Grasslands · South America

Introduction

Coastal marshes shape the ecotone between land and sea along the sheltered, temperate shorelines of all the major continents (Chapman 1960). The steep gradient of physical conditions in intertidal habitats, ranging from entirely marine to entirely terrestrial over only a few meters, makes the zonation of intertidal organisms more compact and conspicuous than in most other physical gradients (Bertness and Hacker 1994). The physical flux of tidal cycles and the chemical influence of salt combine to create a wetland ecosystem where the benthic environment has strong marine characteristics, yet the vegetative structure resembles that of terrestrial marsh habitats (Greenberg and Maldonado 2006). This pattern determines a typical zonation pattern along the salt marsh with harsh conditions for terrestrial vertebrates in the lower marsh and relatively better conditions in the upper marsh.

It is well known that the tidal gradients generate zonation patterns of plants and benthic invertebrates (e.g., Bertness and Ellison 1987; Kneib 1984; Wang et al. 2010). However, outside North America, with its high level of salt marsh endemism (Greenberg and Maldonado 2006), it is unknown whether these gradients affect bird composition and abundance. Although coastal marshes support a relatively low diversity of non-aquatic bird species, a high proportion of these inhabitants, at least along Northeastern North American (NENA) coasts (one of the largest coastal marsh systems of the world; Isacch et al. 2006), are restricted to or have subspecies restricted to coastal marshes (Greenberg et al. 2006). The harsh conditions of salt marshes may generate an island-like process (i.e., low interspecific and high intraspecific competition) for colonizing bird species (Greenberg and Olsen 2010), which could increase even more due to the contrast in vegetation structure between salt marsh and upland habitats. In NENA coastal marshes, this effect may be increased by the large contrast between the structure of the salt marsh habitat, mostly composed of grasses (i.e., *Spartina* spp.), and the upper forested habitat, which is represented by the Mixed Forest Region in North America (Bailey 1995). Southeastern South America coastal

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marshes (distributed from southern Brazil to northern Patagonia in Argentina) are composed of two major habitat coverage groups which are separated geographically along the Southeastern South America (SESA) coast: brackish and marine waters dominate the northern and southern parts of the latitudinal gradient, respectively (Isacch et al. 2006). Brackish water marshes are dominated by the grass *Spartina densiflora* and are mostly distributed along the coast of the pampas region (Cabrera and Willink 1973), a large biome characterized by a flat topography and dominated by tall grasslands (Soriano et al. 1991). Marine-water salt marshes are dominated by *Spartina alterniflora* and *Sarcocornia perennis* with shrubby vegetation dominating upper lands (Cabrera and Willink 1973; Isacch et al. 2006). The relative similarity between coastal marsh habitats and upland habitats in the SESA coastal marshes contrasts with NENA coastal marshes that are surrounded by forests. The lower contrast between coastal marsh and upland habitats for the SESA may generate a less specialized bird assemblage than in the NENA.

Studies developed on SESA coastal marsh birds have primarily focused on assessing the effect of natural (crab bioturbation (Cardoni et al. 2007)) and anthropogenic (fire (Isacch et al. 2004), grazing-fire (Isacch and Cardoni 2011), sewage discharge (Cardoni et al. 2011)) disturbances on vegetation and birds. Evidence consistently supports the importance of vegetative structural characteristics (i.e., height and cover of tall grass) for salt marsh birds in *S. densiflora* and *S. alterniflora* marshes. When disturbances, such as fire and grazing, decrease salt marsh vegetation cover and height, the typical salt marsh bird species disappear or decrease in abundance (Isacch et al. 2004; Cardoni et al. 2007; Isacch and Cardoni 2011). However, sewage discharge may generate an increase in vegetation cover and height that results in an increase in salt marsh bird abundance and richness (Cardoni et al. 2011).

Despite the advances in knowledge of SESA coastal marsh bird ecology, patterns of bird diversity and composition on SESA coastal marshes remain poorly understood. We specifically studied the variation in bird "assemblages" (i.e., a group of animals that may or not interact directly or indirectly, and coincide in space and time; after Jaksic (1981)) along different plant associations for three different coastal marshes in SESA, and assessed how similar the marsh bird assemblages were to the upland habitat bird assemblages. Given the similarity of coastal marsh and upland habitats (dominated by grasslands and shrublands), we expected low differentiation of coastal marsh versus upland habitat bird assemblages in contrast with NENA coastal marshes. In addition, we evaluated the seasonal variation of coastal marsh bird assemblages, determined whether ecologically or taxonomically similar species segregate by habitat, and identified nesting species for different habitats.

Materials and Methods

Study Area

The study area included three main coastal marshes in Argentina: Bahía Samborombón (821 km^2; 35°13′–36°18′), Mar Chiquita Lagoon (116 km^2; 37°29′–37°46′) and Bahía Blanca (296 km^2; 38°41′–39°30′; Fig. 1). Bahía Samborombón (BS) and Mar Chiquita Lagoon (MCL) are brackish water marshes situated on the coast of the pampas region (dominated by grasslands; Cabrera and Willink 1973), have a mean tidal amplitude of 0.8 m, an annual rainfall of 930 mm, and are dominated by the influence of freshwater, by the Río de la Plata for BS and by a number of creeks and artificial channels for MCL (Isacch et al. 2006). Bahía Blanca (BB) is a salt marsh situated along the coast of Espinal and pampas regions (dominated by low trees, shrubs, and grasslands; Cabrera and Willink 1973), has a mean tide amplitude of 2.44 m, an annual rainfall of 645 mm, a negligible freshwater influence, and primarily seawater conditions (Isacch et al. 2006). Major anthropogenic disturbances on coastal marshes are the combined use of fire and cattle grazing for BS and MCL, and sewage discharges for BB (Isacch et al. 2004; Cardoni 2011; Cardoni et al. 2011; Isacch and Cardoni 2011). Surveyed plant associations were those most representative of the tidal marsh for each site (after Isacch et al. 2006). Along the tidal gradient vegetation grows in discrete bands, each dominated by a typical plant species (*S. alterniflora*, *S. perennis*, *S. densiflora*, *Scirpus maritimus*, *Juncus acutus*; Vervoost 1967; Isacch et al. 2006). We surveyed plant associations when they were disturbed, adding to the name of the plant association the type of the disturbance associated (i.e., cattle grazing/fire and sewage discharges). We also included in the surveys habitats bordering the upper marsh, such as fresh marshes, grasslands, and halophytic shrub lands, which represent diffuse limits to salt marsh habitats due to the tolerance of their dominant plants to low levels of salinity and the low slopes between marine and terrestrial habitats (Perelman et al. 2001; Vervoost 1967). These upland plant assemblages were considered to be outside the coastal marsh habitat limit. For details of plant assemblages surveyed and abbreviations used, see Table 1.

Bird and Vegetation Surveys

We conducted bird surveys in each habitat detailed in Table 1, using eight transects distributed to assure independence among them (>100 m apart). Surveys were made in fall–winter and spring–summer and each transect was surveyed twice in both periods (fall–winter, early July to early September 2009; spring–summer, early November to late December 2009). Bird data for each transect by season are the result of averaging both censuses. We sampled bird species

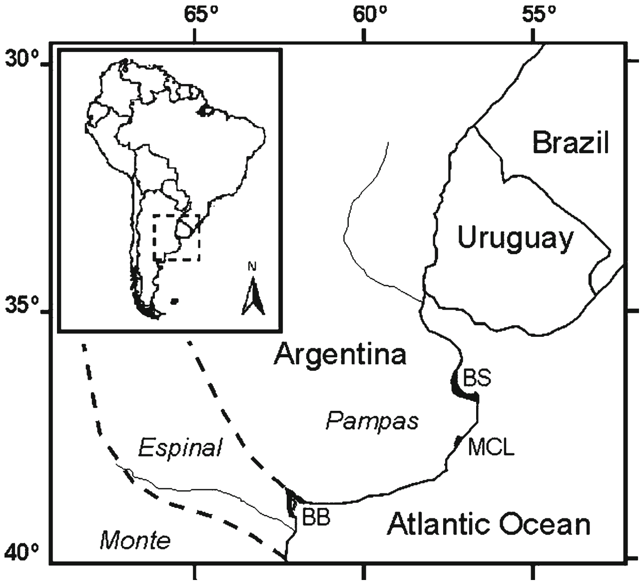


Fig. 1 Studied salt marshes (*black polygons*) of the Southeastern South America and phytogeographic regions influencing coastal habitats (adapted from Cabrera and Willink (1973)). The *inset* in the *upper left* shows the location of the area in Argentina. *BS* Bahía Samborombón, *MCL* Mar Chiquita Lagoon, *BB* Bahía Blanca

using a fixed-width strip-transect method, 100 m in length by 60 m wide, recording bird species and number of individuals (Conner and Dickson 1980). Within the fixed width of the transect (i.e., 30 m distance to each side) we assumed that species have the same detectability (after Isacch et al. 2004; Cardoni et al. 2011; Isacch and Cardoni 2011). We also surveyed bird nests during spring in 2 months (November and early December) into each sampling unit. We selected four transects and exhaustively searched for nests on a quadrate of 30×30 m randomly situated within each transect. Additionally, we searched for bibliographic and personal observations of birds nesting in coastal marshes. Finally, we developed a list of birds nesting in each vegetation type from both sources of data. Scientific and common names of bird species are listed in Table 2. Taxonomy and nomenclature of birds follow the classification of the South American Checklist Committee (Remsen et al. 2011).

Table 1 Habitats studied in three sites of the Southeastern South America coast with the abbreviations used in the text

Site habitat	Abbreviations
Bahía Blanca	
S. perennis (P. Mill.) A.J. Scott marsh	BB-SAR
S. alterniflora Loesel. marsh	BB-SAL
Eutrophized *S. alterniflora* marsh	BB-SALEU
S. densiflora Brong. marsh	BB-SDE
Halophytic shrubland	BB-SHR
Mar Chiquita Lagoon	
S. densiflora marsh	MC-SDE
Grazed *S. densiflora* marsh	MC-SDEGR
J. acutus L. marsh	MC-JUN
C. selloana (Schult.) Asch. et Graeb. grassland	MC-COR
S. californicus (C. A. Mey.) Steud. marsh	MC-SCH
Bahía Samborombón	
S. perennis marsh	BS-SAR
S. alterniflora marsh	BS-SAL
S. densiflora marsh	BS-SDE
Grazed *S. densiflora* marsh	BS-SDEGR
S. maritimus L. marsh	BS-SCI
C. selloana grassland	BS-COR

We measured the following vegetation variables: average height of tall vegetation, dominant plant species (i.e., plant species with highest cover and structure), and visual obstruction. We surveyed the vegetation in each bird sampling transect during winter and summer by using two squares (1×1 m) randomly located along the transect. We used a modification of the pole method described by Robel et al. (1970) to measure visual obstruction. We placed a 1-m pole (divided in twenty 5-cm segments) in the center of each sampling unit and made visual obstruction readings (VOR) from a distance of 4 m, always in the same direction, with the reader's eyes at a height of 1 m (Robel et al. 1970). We recorded the percentage not covered by vegetation for each square of 5×5 cm of the pole from zero to 1 m. These data were expressed as the percentage of each 5×5 cm square along the pole and by a single measure as the average value across all squares of each measure. All vegetation values shown in the results represent the average of the two squares within each transect.

Data Analysis

First, to understand how coastal marsh bird assemblages change among sites as well as between coastal marsh and upland habitats, we developed a cluster analysis with a Bray–Curtis Similarity Index and a single linkage (Bray and Curtis 1957) with data of relative abundance for species recorded in each habitat site. Analyses were concentrated on the most representative habitats in each area, where coastal marsh areas were dominated by *Spartina* spp. and *S. perennis* marshes, and upland was dominated by *Cortaderia* grasslands and shrublands. Because we assumed that salt marsh habitats represent a challenge for colonizing terrestrial birds, we predicted that similarity among salt marshes will be higher than between coastal marsh and upland habitats despite the relative similarity between tidal and upland habitats.

Second, we evaluated whether specific bird assemblages were associated with particular coastal marsh and upland habitats. We applied a nonmetric multidimensional scaling (Clarke and Gorley 2001) to the pairwise similarity matrix to order habitats in a two-dimensional plane. The relevant contribution of each species to habitat distribution in the two-dimensional

Table 2 Bird species recorded in coastal marsh habitats and adjacent habitats of three sites along the Southeastern South America during fall–winter (W) and spring–summer (S) seasons. Bird numbers represents the average of birds by transect for each season. Abbreviations for habitats are in Table 1. Taxonomy was based on Remsen et al. (2011)

	Bb-sar		Bs-sar		Bb-sal		Bs-sal		Bb-saleu		Bb-sde		Mc-sde		Bs-sde		Mc-sdegr		Bs-sdegr		Bs-sci		Mc-jun		Mc-cor		Bs-cor		Bb-shr		Mc-sch	
	W	S	W	S	W	S	W	S	W	S	W	S	W	S	W	S	W	S	W	S	W	S	W	S	W	S	W	S	W	S	W	S
Long-winged Harrier-*Circus buffoni*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.1	–	0.1	–	–	–	0.1	–	0.1	–	–	–	–	–
Cinereous Harrier-*Circus cinereus*	–	–	–	–	–	–	–	–	–	–	0.1	–	–	–	0.1	–	–	0.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chimango Caracara-*Milvago chimango*	0.3	0.1	–	–	0.6	0.7	0.1	–	1.3	1.7	0.6	0.7	0.2	–	–	–	–	–	0.1	0.1	–	–	–	–	0.1	–	0.2	0.5	1.3	1.5	0.1	–
Southern Lapwing-*Vanellus chilensis*	–	0.2	–	–	0.1	–	0.1	–	–	–	–	–	–	–	–	–	0.3	0.1	0.3	0.3	–	–	–	–	–	–	–	–	–	–	–	–
American Oysterctacher-Haematopus palliatus	0.4	0.1	–	–	–	–	0.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Dot-winged Crake-*Porzana spiloptera*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.2	0.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Bar-winged Cinclodes-*Cinclodes fuscus*	–	–	–	–	–	–	0.1	–	–	–	–	–	–	–	–	–	0.1	–	0.3	–	–	–	0.2	–	–	–	–	–	0.3	–	0.1	–
Bay-capped Wren-Spinetail-*Spartonoica maluroides*	–	–	–	–	–	–	–	–	–	0.3	–	–	0.1	0.5	0.5	0.7	–	1.1	–	0.8	–	–	–	–	–	–	–	–	–	–	–	0.3
Sulphur-bearded Spinetail-*Cranioleuca sulphuriphera*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.2	0.1	–	–	0.4	0.8	0.7	0.6	–	–	0.2	0.3
Short-billed Canastero-*Asthenes baeri*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.4	0.5	–	–
Hudson's Canastero-*Asthenes hudsoni*	–	–	–	–	–	–	–	–	–	–	–	–	0.1	–	–	–	–	0.1	0.3	0.1	–	–	0.1	0.1	–	–	–	–	–	–	–	–
Wren-like Rushbird-*Phleocriptes melanops*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.2	1.1	–	–	–	–	–	–	–	–	–	–
Spectacled Tyrant-*Hymenops perspicillata*	–	–	–	–	–	–	–	–	–	–	–	0.2	0.3	0.2	–	0.1	0.1	0.1	–	–	–	–	0.1	0.2	0.8	1.5	0.3	1.4	0.1	0.4	0.4	1.8
Austral Negrito-*Lessonia rufa*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.1	–	–	–
Tufted-tit Tyrant-*Anairetes parulus*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.2	0.1	–	–
Warbling Doradito-*Pseudocolopterix flaviventris*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.1	–	–	–	0.6	–	0.1	–	–	–	2.2
Great Kiskadee-*Pytangus sulphuratus*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.1	–	–	–	–	–	0.1	–	–	–	0.1	–
Correndera Pipit-*Anthus correndera*	–	–	0.1	0.1	–	0.1	–	–	0.1	–	–	–	–	–	–	–	0.6	1.5	0.9	1.1	–	–	–	0.1	–	1.5	–	–	–	–	–	–
Grass Wren-*Cistothorus platensis*	–	–	–	–	–	–	–	–	–	–	0.1	0.2	0.2	0.2	–	–	–	0.3	–	0.3	–	–	0.3	0.1	0.1	–	–	–	–	0.1	–	–
Long-tailed Reed Finch-*Donacospiza albifrons*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.4	0.2	–	–	0.1	–	–	0.2	–	–
Great Pampa-finch-*Embernagra platensis*	–	–	–	–	–	–	–	–	–	–	0.1	–	0.1	–	0.1	0.1	–	0.1	0.3	0.7	–	–	0.1	0.4	0.7	0.2	0.1	1.1	–	0.2	0.1	–
Black-and-White Warbling-finch-*Poospiza nigrorufa*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.2	–	–	–	–	–	–	–	–	0.4	–
Rufous-collared Sparrow-*Zonotrichia capensis*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.2	–	0.1	–	–	–	–	0.5	0.6	0.6	0.1	0.1	0.2	0.2	1.4	0.4	1
Grassland Yellow-finch-*Sicalis luteola*	–	–	–	–	–	–	–	–	–	–	–	0.3	–	0.5	–	0.9	0.1	0.6	0.3	1.3	–	0.3	0.2	1	0.2	3.3	–	0.1	–	–	–	0.8
Yellow-winged Blackbird-*Agelasticus thilius*	–	–	0.6	0.3	0.2	0.3	0.8	0.1	1	1.9	–	–	–	–	–	–	0.6	–	–	–	2.2	2.1	–	–	0.3	–	0.1	–	0.1	0.1	4.4	0.5
Brown-and-Yellow Marshbird-*Pseudoleistes virescens*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.1	–	–	–	–	–	0.1	–	–	0.2	–	–	–	–
Long-tailed Meadowlark-*Sturnela loyca*	–	0.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	−0.1	−0.9	–	–

plot was determined by an analysis of dissimilarity using the SIMPER routine (Clarke and Gorley 2001). Bird species with higher percentages of contribution to discriminate groups can be considered representative and/or diagnostic for each habitat group. Finally, we performed a one-way statistical analysis (ANOSIM routine, test R; Clarke and Gorley 2001) to test the null hypothesis of no differences among groups. *R* statistic values close to unity indicate a very different composition of species between groups, whereas values close to 0 indicate a strong similarity. All statistical analyses were performed using the PRIMER software package. We predicted that specific assemblages of birds would be associated with the different plant associations that occur along the gradient of physical conditions in coastal marshes.

Finally, because we expected that bird distribution is primarily determined by vegetation structure in these habitats (Isacch and Martínez 2001; Isacch et al. 2004; Cardoni et al. 2007, 2011; Isacch and Cardoni 2011), we assessed vegetation structure (VOR) and bird richness differences among habitats for all sites. We evaluated the null hypothesis of no difference among habitats for VOR and bird richness using a one-way ANOVA. We used an a posteriori LSD test to identify differences (Zar 1999).

Results

Summing all samplings, we recorded 51 bird species in coastal marshes and surrounding habitats. Twenty-four species had less than three records in all censuses (*N*=361) and they are excluded from the following descriptions. Twenty species were recorded in coastal marsh habitats (e.g., *Spartina* and *Sarcocornia*) with 18 species associated with brackish water-dominated marshes (MCL and BS) and 10 with seawater dominated marshes (BB; Table 2). Seven species were recorded only in one season, but only three are strictly migratory: two arrive in austral winter and one in summer (Table 2). Fourteen other species changed abundance by more than a factor of two between seasons (abundance was always higher in summer), which indicates seasonal movement despite a lack of strict migration (Table 2).

The northern sites, those dominated by brackish conditions (MCL and BS), had more similarities between each other than between salt marsh and upland habitats of the same localities (Fig. 2). The southern salt marsh (BB) showed few similarities with upland habitats from BB, but similarity values were even lower when the salt marsh was compared with marsh or upland habitats (Fig. 2).

We documented a gradient of bird species richness from the coastal marsh (lower richness) to the upland habitats (higher richness; Figs. 3 and 5). Along this gradient, we identified four bird species assemblages across all habitats and sites (Fig. 4). They were (1) a group of generalist species using lower-marshes dominated by *S. perennis* and *S. alterniflora* marshes; (2) a group of salt marsh specialist and generalist species using middle marshes represented by ungrazed and grazed *S. densiflora* marshes and *J. acutus* marshes; (3) a group of tall grass bird species using middle–upper marshes and grasslands represented by *Cortaderia selloana*, *Schoenoplectus californicus*, and *S. maritimus*; and (4) a group with a low number of representative species was characterized by middle–upper marshes and shrublands from Bahía Blanca (Fig. 5).

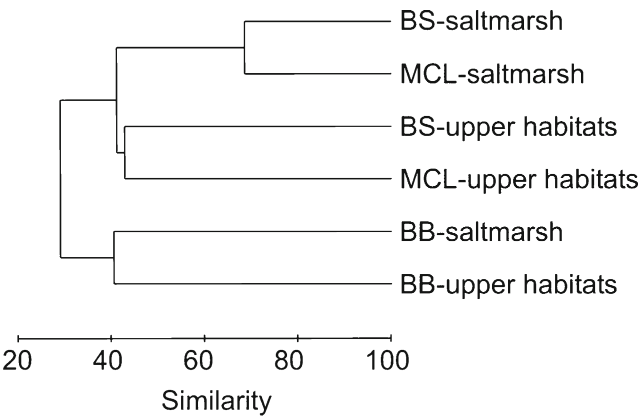


Fig. 2 The cluster diagram shows bird species similarities among typical salt marsh and upland habitats from three sites along the Southeastern South America

Lower marshes were habitats with the relatively most challenging conditions to terrestrial organisms due to seawater flooding and/or hypersaline soils. Only plant species characterized by a relatively low height and cover occupied these habitats, resulting in low VOR values (Figs. 3 and 6). Bird species observed in lower marshes were generalists such as yellow-winged blackbird and chimango caracara. They only bred in these habitats when increased nutrient levels led to increased VOR values, as in the eutrophized *S. alterniflora* marsh (Fig. 6).

Middle marshes have lower levels of salinity and flooding relative to lower marshes. The most common middle marsh plant species is *S. densiflora*, which is inhabited by the most habitat-constrained bird species we recorded, such as bay-capped wren-spinetail, dot-winged crake, Hudson's canastero, and sedge wren. Vegetation height was always lower than 1 m in the middle marsh, while VOR values were intermediate between those for the lower and upper marshes (Figs. 3 and 6).

Upper marshes had a more complex vegetation structure, with plant heights higher than 1.5 m and high VOR values (Figs. 3 and 6). Upper marsh soils were rarely flooded and/or only flooded by freshwater. The upper marsh bird assemblage was more diverse and was represented by typical grassland/fresh marsh species such as warbling doradito, sulphur-bearded spinetail, great Pampa-finch, and spectacled tyrant (Fig. 3; Table 3).

Middle and upper marshes and shrublands from Bahía Blanca showed a low number of species representatives of other groups such as chimango caracara, sedge wren, and spectacled

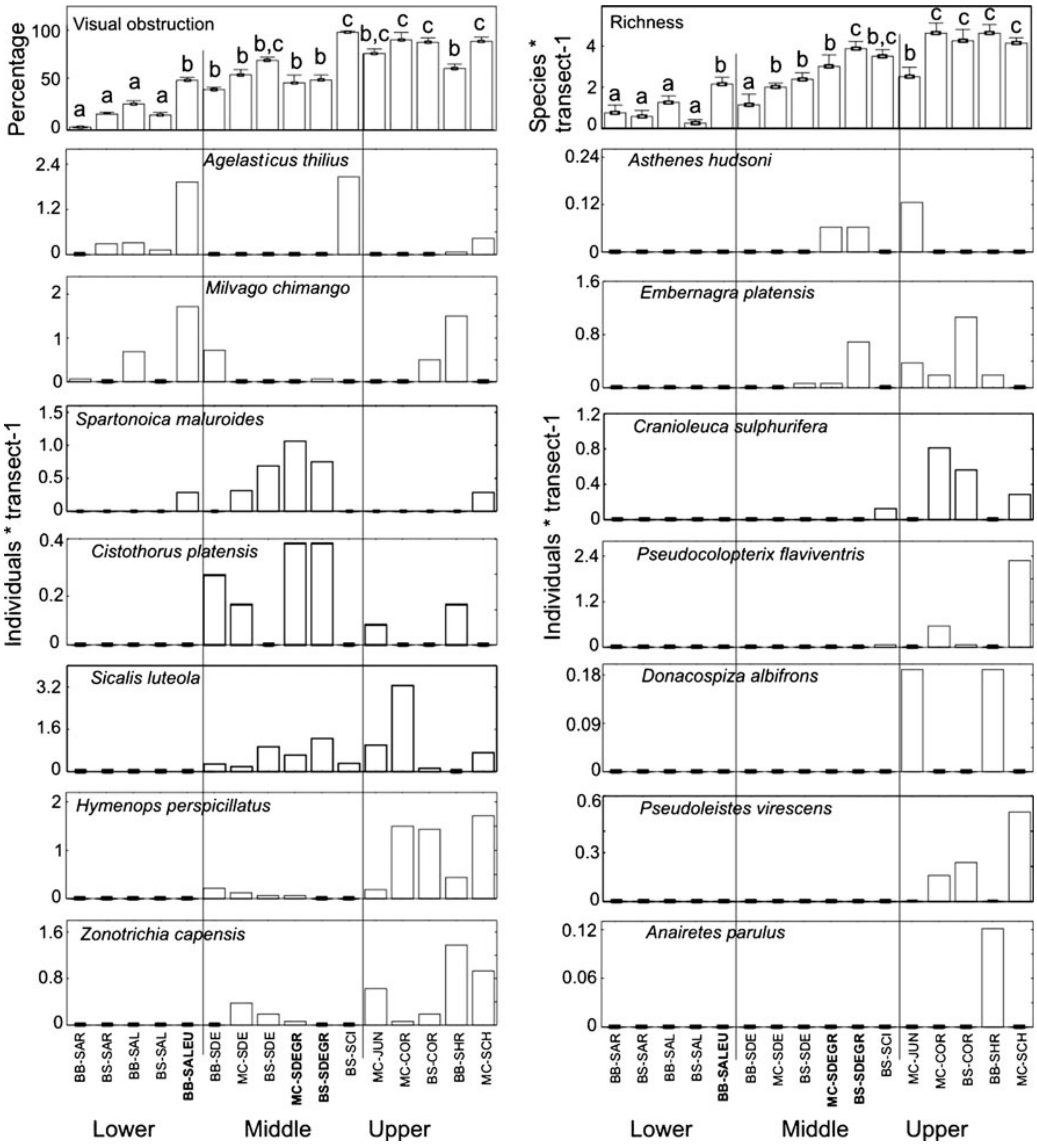


Fig. 3 Number of species and individuals and vegetation visual obstruction (VOR) recorded for salt marsh and outside salt marsh habitats from Bahía Samborombón, Laguna Mar Chiquita, and Bahía Blanca (see references of habitat in Table 1). The sequence of habitats along the *X*-axis is roughly ordered from the lowest part of the intertidal (*left*) to the highest part, with the disturbed habitats (i.e., by cattle grazing and sewage discharge) highlighted in *bold*. *Bars* for richness and VOR represent mean values and standard error; for bird species, only mean values are represented. *Different letters in the upper bar* represent significant differences as determined using an a posteriori LSD test ($P<0.05$) only for visual obstruction and richness

tyrant (Table 3). However, a specific group of birds was only found in the shrublands, a habitat recorded in the southern part of the study (Table 2).

Non-aerial insectivorous species showed more segregation among habitats than other trophic guilds. Non-aerial insectivorous species that were taxonomically and morphologically similar were well-segregated by habitat, especially furnariid species that use the vegetation structure to feed and nest. Within this group, bay-capped wren-spinetail was almost exclusively constrained to *S. densiflora* marshes, sulphur-bearded spinetail was best represented in *C. celloana* marshes, and wren-like rushbird was recorded only in *Scirpus* marshes. Another furnarid, the short-billed canastero, was only represented in the BB shrubland-dominated upland habitat, habitat not represented in MCL and BS. In contrast, generalist emberizid species had high overlap in habitat use, determined

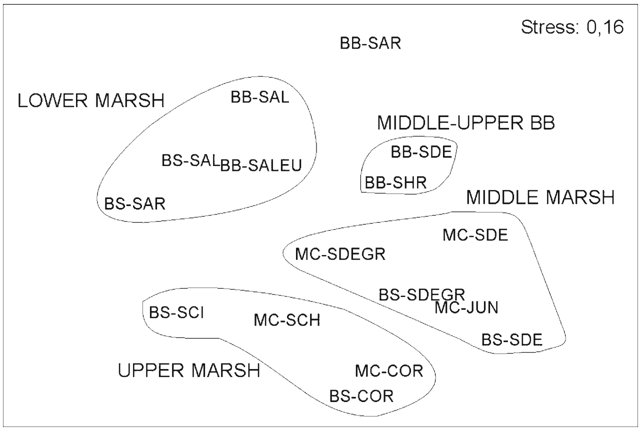


Fig. 4 Nonmetric multidimensional scaling of salt marshes and adjacent habitats from Bahía Samborombón, Laguna Mar Chiquita, and Bahía Blanca (see references of habitat in Table 1). *Lines* represent habitats that are grouped by bird species similarities

by the predominant use of upland, mainly *C. celloana* habitats, by great Pampa-finch, black-and-rufous warbling-finch, long-tailed reed-finch, and rufous-collared sparrow. Aerial insectivores (i.e., flycatchers: warbling doradito and spectacled tyrant) had the same pattern as emberizids, with high overlap in habitat use in the upper habitats.

Thirteen bird species were recorded nesting on coastal marsh and surrounding habitats (Table 4). From our sampling, the most common species nesting on coastal marsh habitats was yellow-winged blackbird, chimango caracara, and bay-capped wren-spinetail. However, only the bay-capped wren-spinetail was not recorded nesting in habitats other than salt marshes.

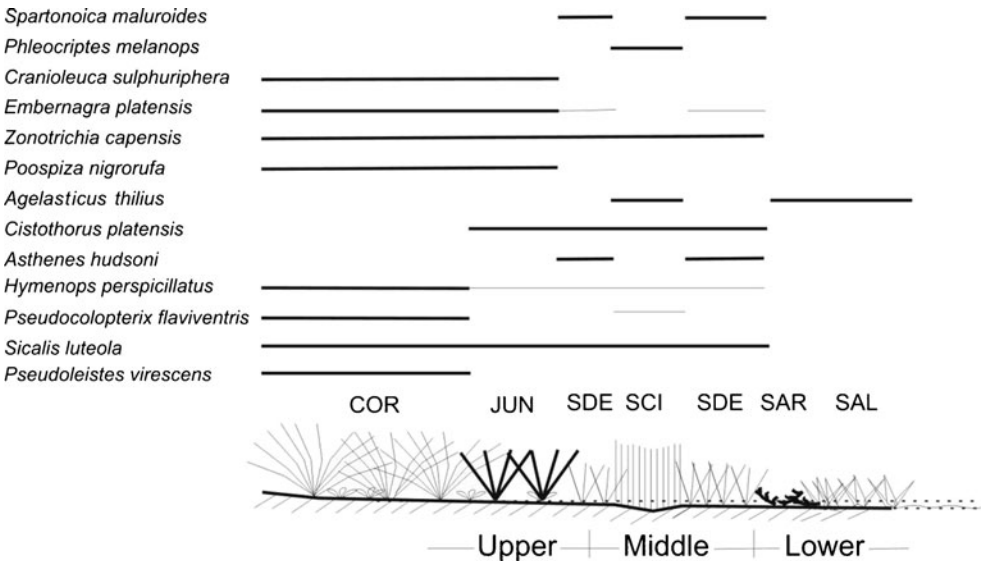
Discussion

Our results show that 20 species frequently used coastal marshes. The number of migratory species was relatively low, but a large part of many species' populations decrease in coastal marshes during the winter season, probably by moving further north. Bird species assemblages were more similar between brackish water-dominated marsh sites than between the marsh and upland habitats at the same site. Four bird assemblages were associated with the tidal level and/or site: lower marsh, middle marsh, upper marsh and grasslands, and middle and upper marshes and shrublands from Bahía Blanca. Bird richness increased steadily along the tidal gradient.

The number of species recorded in SESA coastal marshes is relatively high compared with the coastal marshes of North America (Greenberg and Maldonado 2006). This difference can be partially explained by the large bird diversity in the Neotropical Region (Sibley and Monroe 1990) and/or by the relative similarity between coastal marsh and upland grassland habitats (Soriano et al. 1991), which means that many grassland species can opportunistically use coastal marshes. For at least 7,000 years, coastal marshes have been mostly immersed in a grassland matrix (pampas region; Prieto 1996; Vilanova et al. 2010), facilitating movements between marsh and upland habitats and allowing the mixing of both bird faunas. Despite this mixing, coastal marsh and upland habitats showed typical bird assemblages. SESA coastal marshes can be seen as an impoverished version of upland grasslands, but not a randomly selected subset since similarity values indicate that the filter to the local grassland bird community is allowing similar species into the marsh at both northern sites (MCL and BS).

There were no salt marsh-exclusive species, in contrast with the number of endemic species recorded for NENA salt marshes (Greenberg and Maldonado 2006). This result may be due to the isolating effect of the forested upland habitats along NENA coasts (Bailey 1995), in contrast to the grassland and shrubland habitats along SESA coasts (Soriano et al. 1991). The most specialized bird within the observed

Fig. 5 Schematic representation of bird species using the different habitats along the tidal gradient. Vegetation profile represents an averaged profile of Bahía Samborombón and Laguna Mar Chiquita



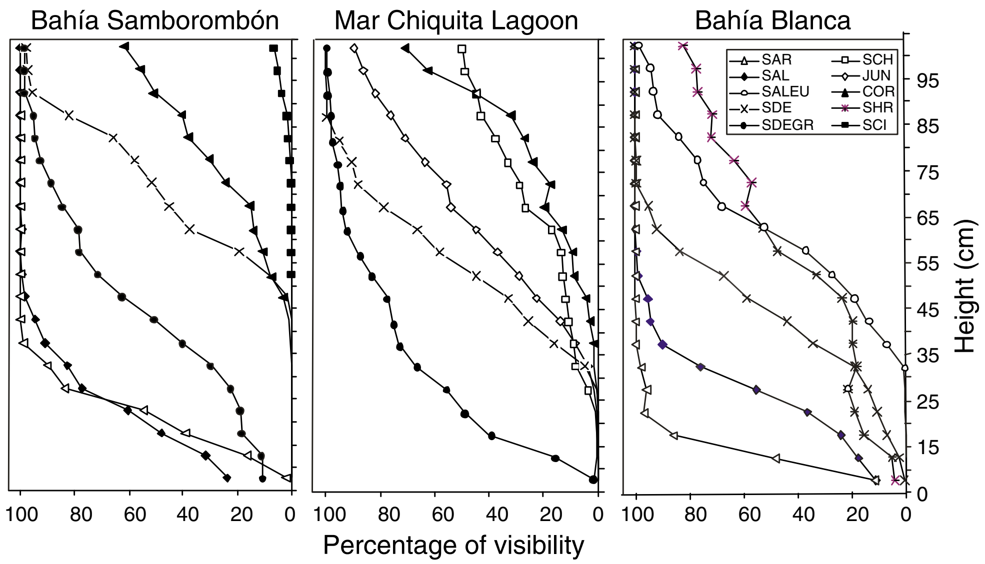


Fig. 6 Visual obstruction (VOR) expressed as the percentage of visibility for salt marshes and adjacent habitats from Bahía Samborombón, Laguna Mar Chiquita, and Bahía Blanca (see references of habitat in Table 1). *Symbols* represent the mean value for each height of VOR method

habitats was the bay-capped wren-spinetail, a furnarid species (Cardoni et al. 2012). Bay-capped wren-spinetail also use other habitats along their distribution (Cardoni et al. 2013), but show a strong association with South American saltmarshes (Isacch et al. 2004; Isacch and Cardoni 2011; Cardoni et al. 2011). In addition, comparisons of coastal and inland marsh populations show significant phenotypic differences in bill shape and plumage coloration (melanism), a convergent pattern with North American sparrows (Cardoni et al. 2013), suggesting that there are strong selective pressures associated with saltmarsh environments. Furnarids showed the largest habitat segregation of all groups considered, with bay-capped wren-spinetail almost exclusively constrained to *S. densiflora* marshes, sulphur-bearded spinetail best represented in *C. celloana* grasslands, and wren-like rushbird in *Scirpus* marshes. The high association of bay-capped wren-spinetail with *S. densiflora* marsh could be a consequence of a high tolerance for marsh habitat but poor competitive ability in upland habitat. The presence of this species in other habitats without the presence of morphologically similar furnarids (Isacch and Martínez 2001) could support this idea.

Table 3 Analysis of the contribution of each species to the average of the Bray–Curtis similarity between groups of samples (SIMPER analysis) indicating contribution of species to separate groups of habitats for coastal marshes and adjacent habitats from the Southeastern South America. Between brackets are values of average similarity for each group

	Contribution %	Cumulative %
Lower marsh (37.9)		
Yellow-winged blackbird	76.04	76.04
Chimango Caracara	17.34	93.38
Middle–upper BB (32.7)		
Chimango Caracara	75.79	75.79
Spectacled Tyrant	12.63	88.42
Grass Wren	7.37	95.79
Middle marsh (40.1)		
Bay-capped Wren-Spinetail	34.06	34.06
Grassland Yellow-finch	26.34	60.41
Correndera Pipit	12.69	73.1
Grass Wren	7.79	80.89
Great Pampa-finch	4.32	85.21
Rufous-collared sparrow	4.01	89.22
Spectacled Tyrant	2.78	92
Upper marsh (30.1)		
Spectacled Tyrant	23.3	23.3
Grassland Yellow-finch	16.4	39.71
Yellow-winged blackbird	15.05	54.75
Sulphur-bearded Spinetail	12.58	67.33
Rufous-collared sparrow	12.2	79.53
Great Pampa-finch	9.6	89.13
Warbling Doradito	2.81	91.93

Even when they are not migratory, populations of most marsh bird species leave partially or totally during the winter season, indicating that salt marshes do not fulfill ecological requirements for the birds year-round and/or that other habitats are relatively better than salt marshes during winter. A factor contributing to partial migration may be the marked decrease in arthropod abundance during winter, as arthropods are an important food resource for most birds (furnarids, tyranids, and icterids) in SESA coastal marshes (Canepuccia et al. 2009). Arthropods are also a major resource for emberizid species such as great Pampa-finch (Ferman and Montalti 2010; Montalti et al. 2005). Seeds are not important food resources for coastal marsh birds, but some natural (i.e., burrowing crab bioturbation; Cardoni et al. 2007) and/or anthropogenic disturbances (i.e., sewage discharge; Cardoni et al. 2011) can cause local increases in the production of seeds and hence of seed-

Table 4 Number of nests for bird species breeding in salt marsh and adjacent habitats from Bahía Blanca (BB, sea water marshes), and Bahía Samborombón (BS), and Mar Chiquita Lagoon (MCL, brackish water marshes)

	BB			BS+MCL				
	SALEU	SDE	SHR	SDE	SCI	JUN	SCH	COR
Bay-capped Spinetail	X	–	–	X	–	X	–	–
Yellow-winged Blackbird	X	–	–	–	X	X	X	–
Caracara Chimango	X	X	X	X	–	X	–	X
Cinereous Harries	–	–	–	X	–			
Long-winged Harrier	–	–	–	X	–			
Grass Wren	–	X	–	X	–	X	–	X
Great Pampa-finch	–	–	X	X	–	X	–	X
Grassland Yellow-finch	–	X	–	X	X	X	–	X
Sulphur-bearded Spinetail	–	–	–	–	–	–	X	X
Spectacled Tyrant	–	–	–	X	–	X	–	X
Wren-like Rushbird	–	–	–	–	X	–	X	–
Warbling Doradito	–	–	–	–	X	–	X	X
Short-billed Canastero	–	–	X	–	–	–	–	–

eating birds (Cardoni et al. 2007, 2011). Seed availability in coastal marshes of other regions is largely influenced by seed burial (Espinar et al. 2005) or dispersal by the tide (Wang et al. 2009).

Bird assemblages were associated with different habitats along the tidal gradient and sites (Fig. 2). There was an assemblage representative of the lower marshes, irrespective of the locality. The vegetation of lower marshes was dominated by *S. alterniflora* and *S. perennis*, and this habitat was mainly used by yellow-winged blackbird and chimango caracara (Fig. 5). Yellow-winged blackbird is a typical sedge marsh species (Canevari et al. 1991), and we presume that salt marsh vegetation structure is similar to that of a sedge marsh. Yellow-winged blackbird was only recorded breeding in eutrophized *S. alterniflora* marshes, where the vegetation structure significantly increased (Cardoni et al. 2011; this study). These characteristics indicate the high tolerance of this icterid species to seawater conditions (Cardoni et al. 2011), when a suitable vegetation structure is available. Yellow-winged blackbird only uses the lower salt marsh to breed, when the structure of vegetation increases (e.g., by sewage discharges), but it is noteworthy that this response is not adaptative because all nests are lost with the frequent extreme floods (Cardoni et al. 2011). A raptor species, chimango caracara, also uses eutrophized *S. alterniflora* marshes to breed, and again all nests are lost to floods (Cardoni et al. 2011). Thus, eutrophized *S. alterniflora* marshes may be "ecological traps" (sensu Gates and Gysel 1978), where the increased vegetation structure is an erroneous cues of suitable nesting habitat, hiding the adverse cues of flooding (Kokko and Sutherland 2001).

Middle marshes from northern sites (MCL and BS), where brackish conditions dominate, are best represented by a typical assemblage dominated by bay-capped wren-spinetail, sedge wren, great Pampa-finch, and grassland yellow-finch (Fig. 5). This is the typical coastal marsh assemblage of SESA. Although the presence of the dot-winged crake, a vulnerable species (IUCN 2012), was only recorded in *S. densiflora* marshes from BS, it should be noted that this enigmatic species was also recorded in other studies performed in MCL and BB coastal marshes (Martínez et al. 1997; Isacch et al. 2004; Cardoni et al. 2007; Cardoni 2011), thus it should be also considered within the typical coastal marsh bird assemblage. The most common disturbances on brackish water-dominated marshes are fire and cattle grazing, which decrease tall grass cover (Isacch et al. 2004; Isacch and Cardoni 2011; Cardoni et al. 2012). Under those disturbances, Hudson's canastero and correndera pipit became part of the bird assemblage of brackish water-dominated marshes, using open areas within the tall grass matrix. However, when the intensity of fire and grazing increase, Hudson's canastero tends to disappear, while correndera pipit remain and increases in abundance (Isacch et al. 2004; Cardoni 2011; Isacch and Cardoni 2011).

The upper marshes of the northern sites are the transition between coastal marsh and tall grasslands from the Pampas region (Isacch et al. 2006). The upper vegetation assemblages spread far from the upper limit of the tidal level because the topography is flat and soils are salty (Vervoost 1967). A peculiarity of this littoral system is the lack of clear limits between salt and freshwater marsh habitats. The bird assemblage of the upper habitats has higher richness than the other two lower habitats and was dominated by typical grassland–fresh marsh species, such as the sulphur-bearded spinetail, the warbling doradito, the spectacled tyrant, the grassland yellow-finch, and the great Pampa-finch (Fig. 5). In contrast, the middle–upper marsh and shrubland assemblage from Bahía Blanca (southern marsh) have low similarity with northern marshes (Fig. 2), which can be determined by the relatively low number of species recorded in Bahía Blanca and by the influence of a different biogeographic region (Cabrera and Willink 1973) which determines the developing of shrublands in the upper part of the coastal marsh (Verettoni 1961).

Most species recorded on coastal marshes were terrestrial birds, which respond to vegetation structure (Isacch and Martínez 2001; Isacch et al. 2004; Cardoni et al. 2007, 2011; Isacch and Cardoni 2011). A main component of bird habitat selection is vegetation structure (e.g., Mac Arthur and Mac Arthur 1961; Wiens 1973; Roth 1976). Vegetation species and structure changes along the coastal marsh are mainly due to physical conditions (e.g., topography, flooding, and saline concentration). Thus, evidence suggests that bird richness increase is associated with an increase in vegetation structure, although this pattern may be due to correlated differences in the physical conditions of the marsh as well.

Coastal marshes are patchily distributed along the worldwide coasts (Adam 1990). They are inhabited by a relative low but specialized group of species, many of them terrestrials adapted to live in this ecotonal coastal habitat (Greenberg and Maldonado 2006). Despite the fact that all SESA coastal marsh birds found in our study have distributions that are not constrained to coastal marshes, we identified a typical coastal marsh bird assemblage. These species also depend on interior lowland tall grasslands from the pampas, which have been heavily degradated (Azpiroz et al. 2012). However, some of these grasslands are being replaced by croplands (Herrera et al. 2009), due to the availability of new technologies and market conditions (Satorre 2005; Trigo 2005). As a consequence of the expansion of crop frontiers, the displacement of livestock to marginal areas due to agriculture (as lowland tall grasslands) constitutes an additional threat to the ecological integrity of these highly vulnerable grassland relicts (Bilenca and Miñarro 2004; Ghersa and Martinez-Ghersa 1991). Therefore, our results also highlight the importance of coastal marshes, specifically middle marshes dominated by *S. densiflora* and *J. acutus*, as refuges for the conservation of many pampas tall grassland birds.

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