

Changes in bird assemblages in a wetland ecosystem after 14 years of intensified cattle farming

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Abstract Human activities have modified wetlands all over the world. Water control structures that are frequently implemented in these ecosystems to keep lands free of flooding can decrease or degrade habitat for biodiversity. The Paraná River Delta, one of the largest wetlands in Argentina, has recently experienced rapid cattle grazing intensification facilitated by water control structures, resulting in extensive conversion of wetlands to pastures. It is unclear if this loss of wetlands has had a negative impact on the highly diverse bird community. Here, we evaluated the changes in bird assemblages in the Lower Delta of Paraná River after 14 years of cattle grazing intensification. We compared point count data from 1997 to 1999 with data collected in 2012 and 2013 using the same survey methods. We assessed the temporal changes in bird richness and composition using paired permutation tests and multivariate analysis. We related the bird composition to landscape changes to analyse if avian changes were associated with landscape dynamics. We found that after 14 years, the bird community differed greatly. In general, species richness decreased, especially in wet years. We found fewer wetland species in recent surveys; in particular we did not register saffron-cowled blackbird (*Xanthopsar flavus*), a species listed as globally vulnerable. Changes in bird composition were associated with an increase in bare soil due to land-use changes. Even though inter-annual differences in precipitation and river stage have great effects on the species present in the surveys, the absence of many wetland species in recent wet years, that is when habitat is suitable for them, is most likely due to changes in land cover. Globally, agricultural land use makes inroads into many wetlands, eroding their quality and extent. Maintenance of wetland species requires that conservation efforts focus on these vulnerable ecosystems before full-scale land conversion occurs.

Key words: biodiversity loss, grazing lands, Lower Delta of Parana River, wetland conversion, wetlands birds.

INTRODUCTION

Human activities have altered, degraded or eliminated more than 60% of the world's wetlands during the 20th century with dramatic consequences for biodiversity (O'Connell 2003; Gardner *et al.* 2015). Some wetlands have been over-exploited for their fish and water, whereas others have been drained and converted to agriculture (Van Asselen *et al.* 2013). This is unfortunate, because the conversion of wetlands erodes and degrades the biodiversity they support and the ecosystem services they provide (Zedler & Kercher 2005). An accurate assessment of the full ecological effects of wetland conversion depends on

knowing the time scale over which this ecosystem responds (Metzger *et al.* 2009). Hence, it is important to quantify the temporal patterns of wetland loss and the effects on biodiversity in order to identify sustainable wetland-use strategies.

Wetlands are among the most productive ecosystems in the world, they offer a great variety of goods and services and they provide critical habitat for flora and fauna representing highly diverse ecosystems (Zedler 2003; Mitsch & Gossilink 2007). Land-use changes that modify wetlands' original vegetation are one of the main threats to global biodiversity (Sala *et al.* 2009). It is estimated that 54% of vertebrate populations that depend on wetlands are decreasing due to wetland conversion or degradation (Dudgeon *et al.* 2006). Loss of wetland cover has been implicated in the decline of many wetland-dependent

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Accepted for publication April 2018.

species, including birds (Riffell *et al.* 2001; Quesnelle *et al.* 2013; Yuan *et al.* 2014).

Birds are important components of wetlands' biodiversity and very sensitive to habitat change (Weller 1999). The diversity of avian life history traits, coupled with the ease of detecting and recognizing birds (Wiens 1992) makes them useful indicators of landscape change effects on biodiversity (Gregory *et al.* 2003). Many studies show a reduction in bird species richness and abundance as a result of land-use changes (Newton 2004; Lepczyk *et al.* 2008; Schrag *et al.* 2009) while others show a decline of habitat specialists and a functional homogenization of bird communities in disturbed landscapes (Devictor *et al.* 2008; Clavel *et al.* 2011). In wetlands, many bird populations are declining because of the reduction in wetland cover (Findlay & Houlihan 1997; Naugle *et al.* 1999), others are affected by wetland patch isolation (Brown & Dinsmore 1986; Whited *et al.* 2000), while yet others are affected by urban development (Deluca *et al.* 2004) or drainage structures (Maclean *et al.* 2011). Understanding the relationship between birds and landscape changes can be useful to make predictions about future distributions of species and to anticipate conservation challenges as human activities affect wetlands.

Birds also respond to the natural cycling of wetlands. The dynamic nature of wetlands' hydrology maintains their status as wetlands over long time horizons, but on an annual basis, sites can vary greatly in their suitability for species with specific niche requirements related to degree of soil moisture and water level (Ward *et al.* 2010). This is the case of many wetland birds that occupy wetlands only when they are in certain water levels. For instance, inter-annual variability in precipitation affects wetland water levels and habitat structure, which in turn affects density and reproduction of wetland-nesting birds (Fletcher & Koford 2004). These conditions can vary naturally due to precipitations and river stages or because of human influence, either by regulating water levels (Baschuk *et al.* 2012) or by draining wetlands (Duncan *et al.* 1999). Both land use and climate variables thus affect wetland bird richness and abundance greatly (Forcey *et al.* 2011). Therefore, it is important to understand the effects of permanent alteration of wetlands independent of the natural cycling of wetlands to develop conservation strategies.

The Paraná River Delta is one of the most important wetlands in South America due to its broad extent and location at the end of Del Plata basin, but it is being modified quite rapidly (Baigún *et al.* 2009). Water control structures have accompanied the intensification of cattle activity, turning cyclically flooded ecosystems into grasslands that do not flood (isolated from river overflows and/or drained), so that

they resemble the dry grasslands of the Pampas, in a process locally called *pampeanización* (sensu Galafassi 2005). In the Lower Delta of Paraná River, 35% of freshwater marshes were converted to permanently dry grasslands in the last 14 years (Sica *et al.* 2016). These land-use and land-cover changes can alter habitat availability, and are likely to have affected the bird community in the Lower Delta, especially those species that are dependent on wetland habitat.

Our goal was to analyse the changes in the bird community of the Lower Delta after 14 years of intensified cattle grazing. In particular, we addressed the following questions: (i) Did species richness change within this time period, independent of changes expected due to water level alone? (ii) Is species' habitat affiliation (e.g. wetland affiliate, grassland affiliate, or generalist) associated with species response to land-use and land-cover changes? (iii) Did land-use conversion from wetlands to dry grasslands correspond with the loss of wetland affiliate bird species and the increased number of species with more terrestrial affiliations?

METHODS

Study area

The Paraná River Delta spreads along the final 300 km of the Paraná river from Diamante City ($-32^{\circ}4'S$; $60^{\circ}39'W$) to the vicinity of Ciudad Autónoma de Buenos Aires ($-34^{\circ}19'S$; $58^{\circ}28'W$; Fig. 1). The region has a humid temperate climate with precipitation evenly distributed throughout the year (Trewartha & Horn 1980). The regional hydrological regime is characterized by frequent flooding events caused by precipitation in the high Del Plata basin that modules Paraná River stage in the low basin (Lower Delta), and by local precipitation (Malvárez 1999). This dynamic hydrological pattern along with the geomorphology of the region has determined the extended presence of vegetation adapted to flooding conditions or to alternate periods of hydric excess and deficit defining the region as a vast wetland macro mosaic (Kandus *et al.* 2006). In addition, the Paraná River flows from tropical to temperate latitudes, its delta displays a peculiar biogeographical profile mixing both subtropical and temperate species resulting in a very high biodiversity (Malvárez 1999).

The Lower Delta is the most southern portion of the Paraná River Delta ($-33^{\circ}45'S$; $58^{\circ}51'W$; Fig. 1). We studied the non-insular part of the Lower Delta (south of Entre Rios Province). This complex flood plain covers approximately 4500 km² and has high environmental heterogeneity composed of freshwater marshes dominated by *Scirpus giganteus* or *Schoenoplectus californicus*, grasslands dominated by *Panicum miloides* and *Cynodon dactylon* and forest patches of *Prosopis nigra* and *Acacia caven* (Kandus *et al.* 2006; Bó *et al.* 2010). The area provides habitat to a large number of bird species including endangered ones for Argentina (López-Lanús *et al.* 2008) such as black and white monjita (*Heteroxolmis*

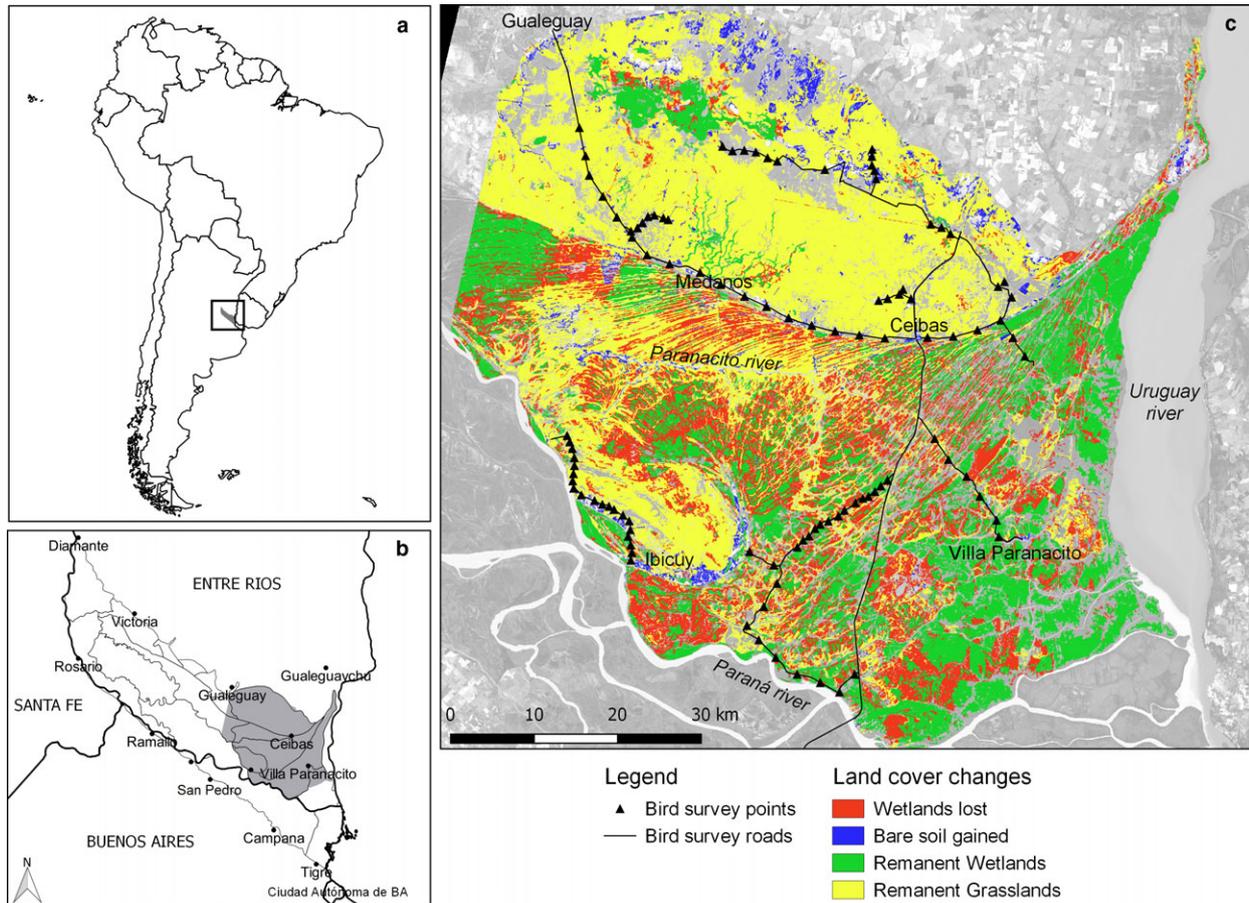


Fig. 1. (a) Location of the Paraná River Delta in South America (outlined in black). (b) Location of the non-insular part of the Lower Delta of Paraná River in Argentina (in grey). (c) Study area with main land-cover changes (source Sica *et al.* 2016) and point count survey location, shown as triangles, which were distributed along secondary and tertiary roads. [Colour figure can be viewed at wileyonlinelibrary.com]

dominicana), yellow cardinal (*Gubernatrix cristata*), straight-billed reedhaunter (*Limnocites rectirostris*), dot-winged crane (*Laterallus spilostris*) and saffron-cowled blackbird (*Xanthopsar flavus*; classified as vulnerable by the IUCN, BirdLife International 2016).

The Paraná River Delta was historically used as seasonal cattle grazing lands but land-use patterns have shifted towards more intensive and permanent grazing systems. Concomitantly, cattle numbers have increased by an order of magnitude in a single decade from 160 000 in 1997 to 1 500 000 animals in 2007 (Quintana *et al.* 2014). This intensification was possible due to the construction of water control structures such as ditches, polders and levees aimed to protect farmlands and urbanizations from seasonal flooding. This resulted in an area within polders of 241 000 ha (almost 14% of the region) and 5181 km of levees in 2012 (Minotti & Kandus 2013). Such land-use intensification caused major land-cover changes. For instance, in the Lower Delta, freshwater marshes, one of the dominant land covers in 1999 covering 41.3% of the total area, decreased to 24.2% while grasslands, which covered 43.0% of the area in 1999, expanded to 58.3% (Sica *et al.* 2016). Bare areas, including roads, urban areas and overgrazed grasslands also increased by 187% (Sica *et al.* 2016).

Bird surveys

We conducted 98 point counts over two multi-year time periods: October–November 1997 and 1999 and October–November 2012 and 2013. We registered all species seen or heard during a 15-min period (Ralph *et al.* 1993). The points were located on secondary and tertiary roads in 1997. All public, available roads detected in the study area by 1990s were sampled, the first survey point was randomly placed and the next points were spaced systematically at 1 or 3 km intervals (Ralph *et al.* 1995). By 2010s some had been converted to primary roads (Fig. 1, Appendix S2). We carried out all counts within a fixed radius circle of 100 m, between 06.00 and 10.30 hours and between 16.00 and 19.30 hours to reduce bias due to inactivity of birds around midday (Ralph *et al.* 1993). Even though avian sampling methods have advanced considerably since the 1990s including estimates of detectability (Gu & Swihart 2004), we replicated the original field protocol for purposes of comparison.

For the first time period, two observers sampled 46 point counts in 1997, and the same observers sampled 52 additional points in 1999. For the second time period, two different observers conducted all 98 point counts both in

2012 and 2013. Bird survey points were relocated using GPS and the field experience of some of the authors who were involved in the initial bird survey point selection in the years 1997 and 1999.

Habitat affiliation

We classified all species in guilds according to their habitat affiliation based on information in the literature (Fracassi 2001; Rocha 2008; Magnano 2011; De Stéfano *et al.* 2012; Narosky & Yzurieta 2013) (Appendix S1). Guilds were not mutually exclusive because many birds use different habitat types to fill different needs (e.g. reproduction, roosting and foraging) (Wiens 1992). We summarized species habitat affiliation in four guilds: (i) wetland species, including birds that require permanent or semi-permanent flooded vegetation or open water (Anseridae, Rallidae, Ardeidae, Ciconiidae, Icteridae, Limnortities [Furnariidae]); (ii) grassland species, which include birds requiring open habitats with herbaceous cover like pipits [Motacillidae] and sparrows [Emberizidae]; (iii) shrubland species, including those that require trees (such as Picidae and Cuculidae); (iv) generalist species including those that are common in many habitat types including urban and suburban systems (such as Columbidae and cowbirds [Icteridae]) (de la Peña 2005; Narosky & Yzurieta 2013).

Landscape variables

We used land-cover maps for each time period, developed from Landsat images between 1999 and 2013 (Sica *et al.* 2016), to calculate land-cover descriptive metrics. We delineated circular buffers of 200 m radius centred on each bird survey point, and within each buffer we calculated the area (ha) covered by five different habitat types (wetland, grassland, open water, bare soil and shrubland) for each time period.

Data analysis

As the study area has a complex hydrological regime with high inter-annual variability in water level due to fluctuations in river stage and local precipitation (Bó & Malvárez 1999), we compared maximum river stage in each bird survey year (maximum annual river stage height from Paraná River at San Pedro harbor, Prefectura Naval Argentina 2017) and mean accumulated precipitation during bird surveys (mm of precipitation accumulated in pluviometers placed in the town of Médanos and in Holt Ibicuy train Station, Entre Ríos province during October–November each survey year, Dirección de Hidráulica de Entre Ríos 2016; Appendix S3) as an indicator of wetland water level. Maximum river stage height was very high, close to the human evacuation threshold (3.6 m) in 1997. In the remaining survey years maximum river stage height approximated the long-term mean (2.62 m in 1999, 2.44 m in 2012 and 2.18 m in 2013). Mean accumulated precipitation during bird surveys (October–November) was high in

1997 (244 mm) and 2012 (300.5 mm); it was lower in 2013 (208 mm), whereas it reached the lowest value in 1999 (56 mm). Thus, regarding wetland water level, wet (1997 and 2012) and dry (1999 and 2013) years were observed. To avoid confounding effects of varying river stage and precipitation, we compared 1997 and 1999 surveys independently against each of the recent surveys (1997 *vs.* 2012 and 2013 independently, 1999 *vs.* 2012 and 2013 independently). By comparing bird counts in all possible combinations of river stage and precipitation in the 1990s and 2010s we can identify the effect of water level independently from other changes occurred in the area. For instance, if we find differences in the bird community comparing wet years (1997 *vs.* 2012), it is likely that these differences are not only related to the natural hydrologic dynamics.

Changes in species richness and frequency of occurrence

We compared observed and estimated bird species richness between time periods. We calculated the number of species in each survey retaining only those point counts that were sampled in both time periods. We estimated the total number of species in each survey using a bootstrap nonparametric estimator due to the large number of rare species detected (species that appeared in only one sampling point). This estimator takes into account the probability that a species will be surveyed as the number of point counts is increased (Magurran 2004). We also calculated mean avian species richness per survey point for the entire avian assemblage and within each habitat guild, and compared point-level species richness between time periods using paired permutation tests with the survey points as replicates.

To assess changes in frequency of occurrence of species, we constructed 2×2 presence/absence contingency tables for each species in each survey comparison. In these tables, we categorized each survey point according to the species' permanence. We then tested for changes in frequency of occurrence among time periods using McNemar's test with exact *P*-values (Agresti 2007). All analyses were conducted using R statistical software (R Core Team 2016) and appropriate contributed packages.

Changes in avian community patterns

To quantify changes in bird assemblages, we calculated dissimilarity indices between surveys. A high dissimilarity between species surveyed in the first and second time period indicates that the bird community changed. This change can be due either to species turnover (species surveyed in the first period are different than species surveyed in the second period) or by differences in nestedness, which is the loss or gain of species making the community in one period a subgroup of the community in the other period (Baselga *et al.* 2015). To identify if the community changed over time, we calculated dissimilarity among surveys using the Sorensen dissimilarity index (β_{sor}) and both components: species turnover (β_t) and nestedness (β_n). These

analyses were conducted using the package betapart in R (Baselga & Orme 2012).

To explore patterns of change in bird composition between surveys, we performed nonmetric multidimensional scaling ordination (NMDS). Using the Sorensen dissimilarity index, we ordered bird survey points according to the species present and graphed them in a two-dimensional plot. In addition, to test if the ordination of the points was associated with landscape changes, we calculated the correlation between the NMDS ordination axes and the landscape variables.

RESULTS

We recorded a total of 162 species belonging to 40 families (Appendix S1). Over one-third (64 species) were wetland birds, 59 were generalists, 49 were shrubland birds and 13 were grassland species. Most records were resident species, except for pectoral sandpiper (*Calidris melanotos*) and barn swallow (*Hirundo rustica*) that migrates to North America during austral winter; and streaked flycatcher (*Myiodynastes maculatus*), tropical kingbird (*Tyrannus melancholicus*), red-eyed vireo (*Vireo olivaceus*), grey-breasted martin (*Progne chalybea*) and brown-chested martin (*Phaeo-progne tapera*) that migrates to north of South America during austral winter. No austral winter migrants were included.

Only few bird survey points remained in a similar condition in the two time periods studied (Appendix S2). Wetlands were lost and converted into dry grasslands in more than 60% of the bird survey points that included this vegetation in 1999. Bare soil expanded in 54% of the points. This expansion was related to overgrazing and road construction (29 bird survey points were carried out on secondary roads in 1997/99 which became primary roads by 2013; Appendix S2).

Changes in species richness and frequency of occurrence

The difference in observed species richness was large between time periods especially between wet and dry years (Table 1). For example, all comparisons against 1997 (the wettest year from the first period) showed a decrease in number of species in the second period, even when comparing 1997 versus 2012 (the wettest year from the second period, Table 1). By contrast, comparisons against 1999 (the driest year of the first period) did not show the same trend (Table 1). Estimated richness was larger than observed richness in all surveys and we found similar differences among years (Table 1).

Comparing point-level species richness between 1997 and recent years, we found that the mean overall

richness ($S_{97} = 15.85 \pm 0.61$ vs. $S_{12} = 11.11 \pm 0.45$; $S_{13} = 11.02 \pm 0.47$), mean wetland species richness ($Swet_{97} = 5.20 \pm 0.51$ vs. $Swet_{12} = 2.69 \pm 0.28$; $Swet_{13} = 2.11 \pm 0.31$) and mean generalist species richness ($Sgeneral_{97} = 8.95 \pm 0.39$ vs. $Sgeneral_{12} = 7.06 \pm 0.49$; $Sgeneral_{13} = 7.09 \pm 0.42$) decreased significantly over time. Mean shrubland species richness ($Sshrub_{97} = 1.41 \pm 0.22$ vs. $Sshrub_{12} = 1.26 \pm 0.25$; $Sshrub_{13} = 1.87 \pm 0.33$) and grassland species richness ($Sgrass_{97} = 0.93 \pm 0.17$ vs. $Sgrass_{12} = 0.72 \pm 0.19$; $Sgrass_{13} = 0.63 \pm 0.18$) showed no significant difference (Fig. 2a,b). When comparing surveys from 1999 against recent years, mean generalist species richness ($Sgeneral_{99} = 7.90 \pm 0.38$ vs. $Sgeneral_{12} = 6.42 \pm 0.29$; $Sgeneral_{13} = 6.13 \pm 0.26$) declined and mean shrubland species richness ($Sshrub_{99} = 1.17 \pm 0.22$ vs. $Sshrub_{12} = 2.03 \pm 0.30$; $Sshrub_{13} = 2.11 \pm 0.28$) increased significantly over time (Fig. 2c,d). Mean wetland species richness ($Swet_{99} = 1.25 \pm 0.21$ vs. $Swet_{12} = 2.23 \pm 0.26$; $Swet_{13} = 1.44 \pm 0.24$) only increased significantly when comparing the driest year of the first period and the wettest year of the second period (Fig. 2c).

When comparing species frequency of occurrence between surveys, we found that many wetland species were only recorded in the first period (Table 2). This was the case for rufescent tiger heron (*Tigrisoma lineatum*), yellow-rumped marshbird (*Pseudoleistes guirahuro*), unicolored blackbird (*Agelaius cyanopus*), great grebe (*Podiceps major*), roseate spoonbill (*Platalea ajaja*), spotted rail (*Pardirallus maculatus*) and fulvous whistling duck (*Dendrocygna bicolor*) (Appendix S1). In particular, saffron-cowled blackbird which uses both flooded grasslands and freshwater marshes throughout its life cycle was not registered in any of the recent surveys. Moreover, typical wetland species such as the great white egret (*Ardea alba*), the piebald duck (*Netta peposaca*), the southern screamer (*Chauna torquata*) and the wood stork (*Ciconia maguari*) showed a significant decrease in frequency of occurrence (Appendix S1).

Many shrubland species were registered only in the second period (Table 2). Such was the case for the short-billed canastero (*Asthenes baeri*), tufted tit-spinetail (*Leptasthenura platensis*), black-capped warbling

Table 1. Observed species richness (S_{obs}), estimated species richness (S_{est}) and standard error (SE) for each survey

		S_{obs} ($S_{est} \pm ES$) in the first period	S_{obs} ($S_{est} \pm ES$) in the second period
Comparisons against the wettest year of the first period			
1997 vs.	2012	107	92 (104.89 \pm 3.53)
	2013	(118.71 \pm 3.85)	98 (111.83 \pm 3.7)
Comparisons against the driest year of the first period			
1999 vs.	2012	81	94 (104.89 \pm 3.74)
	2013	(90.78 \pm 3.31)	86 (97.58 \pm 3.84)

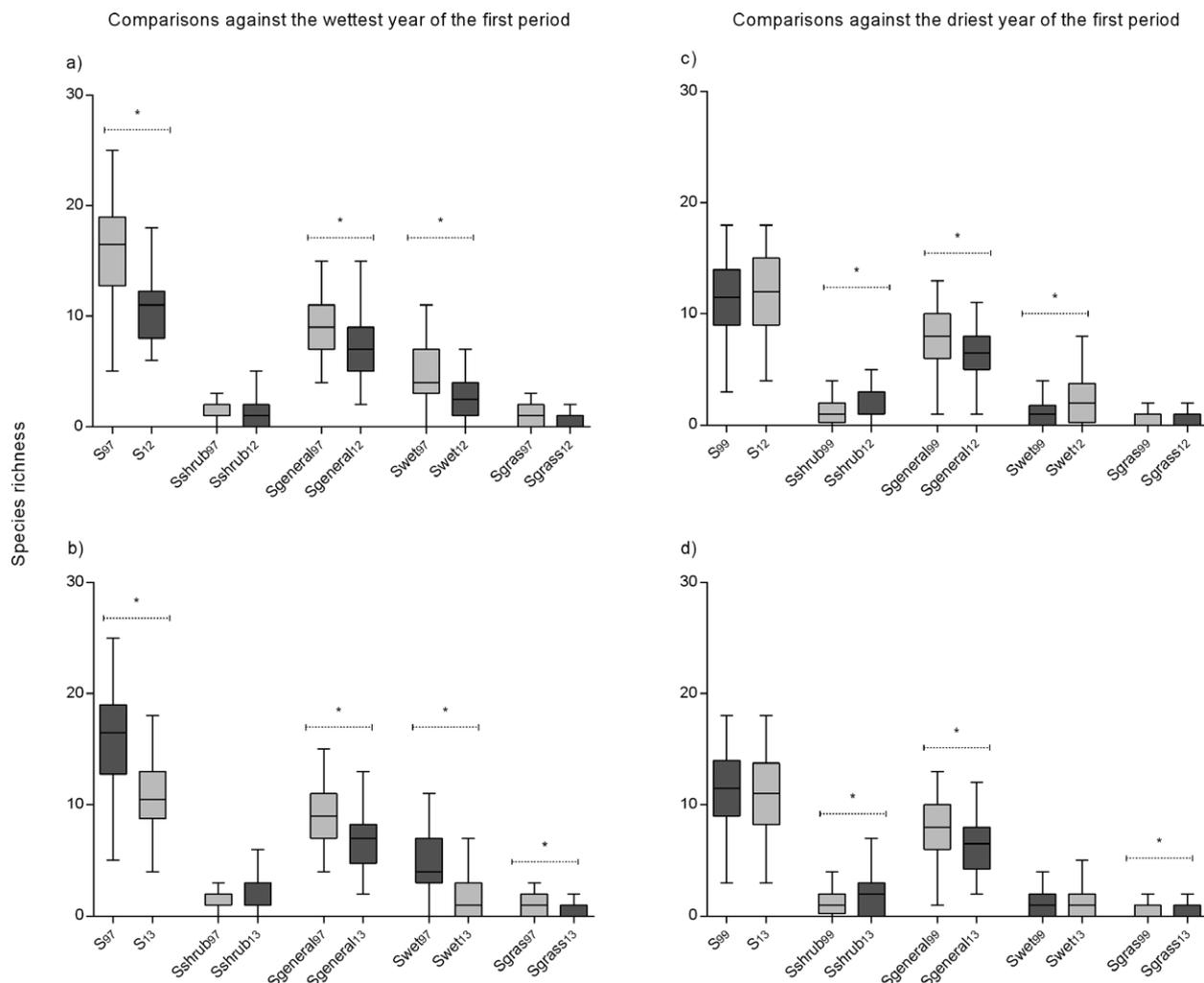


Fig. 2. Box plot of species richness for each habitat guild and the entire bird community in the non-insular area of the Lower Delta of the Paraná River. S: the entire community, Sshrub: shrubland species, Sgeneral: generalist species, Swet: wetland species, Sgrass: grassland species. *Indicates significant differences in mean richness using a paired permutation test between time periods. (a, b) Show comparisons for 1997 versus 2012, 2013 respectively. (c, d) Show comparisons for 1999 versus 2012, 2013 respectively.

finch (*Poospiza melanoleuca*), brown cacholote (*Pseudoseisura lophotes*), sooty-fronted spinetail (*Synallaxis frontalis*), striped cuckoo (*Tapera naevia*), among others (Appendix S1). Even though most generalist species did not differ in frequency of occurrence between the two time periods (Table 2), species like shiny cowbird (*Molothrus bonariensis*), black-and-rufous warbling finch (*Poospiza nigrorufa*), house wren (*Troglodytes aedon*) and rufous-collared sparrow (*Zonotrichia capensis*) increased significantly their frequency of occurrence (Appendix S1).

Changes in avian community patterns

Community dissimilarity between time periods was high for all comparisons ($\beta_{\text{sor}} > 0.65$). Turnover of

species was higher than nestedness ($\beta_t > \beta_n$) indicating that a large proportion of the species surveyed in the second period (2012 and 2013), were distinct from those surveyed in the first period (1997 and 1999) (Appendix S4). However, species nestedness was greater in comparisons against 1997 (the wettest year) than in comparison against 1999 (the driest year, Appendix S4).

The NMDS showed strong differences in bird composition over the two time periods (Fig. 3). All comparison showed that points surveyed in the first period clustered separately from those surveyed in the second period (Appendix S6). In most comparisons there was a clear change direction showing that the bird composition changed similarly in all surveyed points (Fig. 3). This change in species composition correlated with landscape variables, in

Table 2. Temporal changes in frequency of occurrence among bird habitat guilds in the non-insular area of the Lower Delta of the Paraná River

	Years of comparisons	Species absent in the second period (%)	Species that decreased [†] in frequency (%)	Species that increased [†] in frequency (%)	Species absent in the first period (%)
Wetland species	97-12	34.0	10.0	2.0	10.0
	97-13	40.4	11.5	0	13.5
	99-12	28.9	5.3	7.9	36.8
	99-13	28.9	2.6	2.6	26.3
Grassland species	97-12	25.0	0	0	0
	97-13	37.5	0	0	12.5
	99-12	22.2	0	11.1	11.1
	99-13	62.5	12.5	12.5	12.5
Generalist species	97-12	20.0	10.0	8.0	8.0
	97-13	17.0	11.3	1.9	11.3
	99-12	17.0	6.4	4.3	10.6
	99-13	19.6	17.4	13.0	8.7
Shrubland species	97-12	22.6	0.0	0.0	32.3
	97-13	14.7	2.9	0.0	38.2
	99-12	11.8	0.0	0.0	52.9
	99-13	25.8	3.2	3.2	45.2

[†]All species included have significantly increased/decreased ($P < 0.05$) their frequency of occurrence according to McNemar's test.

particular an increase in bare soil (Fig. 3, Appendix S5).

DISCUSSION

Bird assemblages sampled in the non-insular area of the Lower Delta of Paraná River differed strongly at two distinct points in time (1997–1999 *vs.* 2012–2013). Changes were primarily due to high species turnover, loss of some species, especially wetland affiliates, and gain of other species, especially terrestrial (grassland and shrubland) affiliates. The wetland affiliate group experienced the greatest loss of species, especially when comparing between years with high river stage and precipitation. While bird community differences between periods were due in part to natural hydrological dynamics (e.g. more wetland species richness in wet years in contrast to dry ones), we think that human-caused changes in the landscape very likely played a strong role in these differences as well (e.g. lower wetland species richness in recent wet year than in previous one). Particularly, the extended wetland conversion occurred in the area over the analysed time period may have had strong consequences for bird assemblages in the non-insular part of the Lower Delta.

Many wetland birds not only depend on wetland vegetation but also on specific water level conditions (Ward *et al.* 2010). For instance, in periods with low precipitation, the accumulation of water is scarce and large-bodied species move greater distances to different wetlands to find optimal conditions (Chase 2007;

Lemoine *et al.* 2007). A general drying of habitat leads to the reduction in the feeding or nesting habitat needed by a variety of wetland-dependent species (Duncan *et al.* 1999). This reduction can occur due to the alteration of hydrological regimes by natural factors (extended flood events or droughts) or through the implementation of water control structures. In this study, both sources of habitat drying were evident. The drier conditions that occurred in the studied area in 1999, or even in 2013 (lower precipitation and lower river stage height) could explain the absence of many wetland birds in these surveys. However, in 2012, despite being the year with the highest precipitation and high river stage which allowed higher water accumulation, wetland species richness was lower than in 1997, the wettest year of the first survey period. This decline in wetland species is likely associated with the fact that by 2012 many wetland areas that were previously covered by freshwater marshes had been drained and transformed into cattle pastures (Sica *et al.* 2016). Inter-annual variability in population size as a result of breeding success, or variability in the timing of migration, may also impact the distribution of species (Siriwardena *et al.* 1999). These random inter-annual variations could explain the absence of certain species in the second period. However, we found a clear pattern which was consistent across all survey comparisons as well as with other studies in the region, where the number of species that reduced the frequency of observation was very high and most belonging to wetland habitat affiliation. Hence, we consider that the observed changes in species result

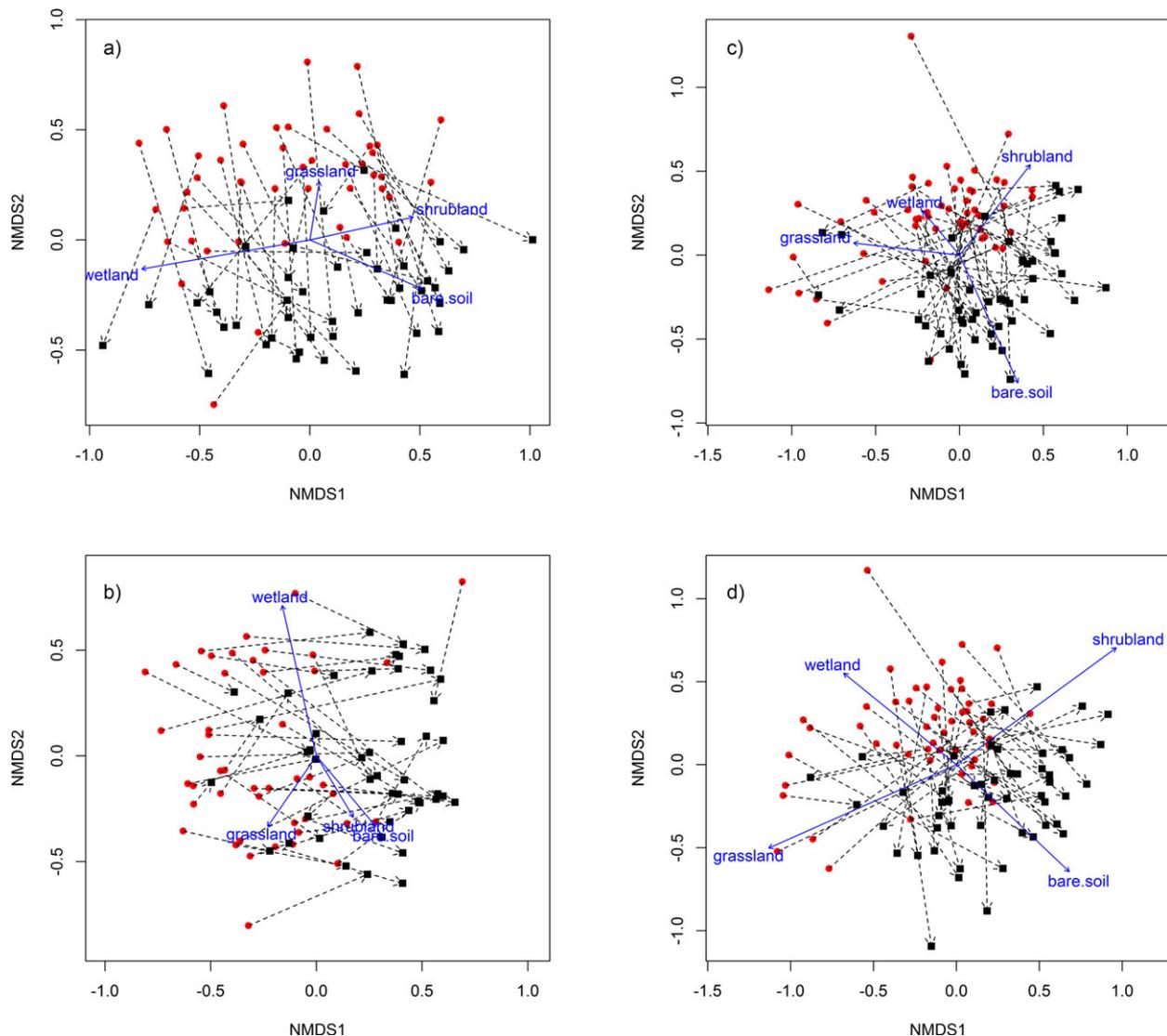


Fig. 3. Two-dimensional graphs showing the ordination of bird survey points in the first (red dots) and second (black dots) time periods and the direction of change in species composition (dotted arrows). Blue lines indicate the correlation between the ordination axes and landscape variables (larger lines, greater correlation). (a, b) 1997 *versus* 2012, 2013 respectively. (c, d) 1999 *versus* 2012, 2013 respectively. [Colour figure can be viewed at wileyonlinelibrary.com]

in a general pattern which is consistent with the loss of wetlands observed in the area.

Species composition was more different between time periods than within each period. The higher inter-period variability suggests that temporal changes in species composition had a greater effect in shaping the bird community than the naturally high landscape heterogeneity of the study area. The temporal change trajectories in bird composition in the non-insular area of the Lower Delta were associated with an increase in bare soil and, in some cases, with a decrease in wetland cover. Unlike most wetlands throughout the world where conversion is largely due to the expansion of croplands and settlements (Gerakis & Kalburtji 1998; Rebelo *et al.* 2009; Song *et al.*

2012), in the non-insular part of the Lower Delta intensification of cattle grazing is the main driver of landscape change (Quintana *et al.* 2014; Sica *et al.* 2016). This intensification is made possible by the development of water management infrastructure that makes lands suitable for cattle grazing thus reducing wetland extent and increasing grasslands and bare soil (Sica *et al.* 2016). The temporal changes in bird species composition indicate that the drying and draining of wetlands negatively affect biodiversity, a finding that is in line with patterns observed in other wetlands globally (Douglas & Johnson 1994; Gerakis & Kalburtji 1998; Smith & Chow-Fraser 2010).

As was expected, the different habitat guilds showed different trends. Wetland species were the

most negatively affected, particularly species like the southern screamer and the wood stork. These results are consistent with the findings of other studies, which documented changes in these species distribution due to habitat modification (Ryder 1967; Carrascal *et al.* 1993). For instance, in Buenos Aires province these species have declined over a period of 13 years of agriculture expansion, especially the wood stork, which was not detected in an area where it was very abundant prior to the agricultural expansion (Codesido *et al.* 2011).

The decrease in the occurrence of wetland species in disturbed ecosystems has been recorded in numerous studies examining the impact of agricultural expansion on wetlands (Duncan *et al.* 1999; Green *et al.* 2002). A particular case is saffron-cowled blackbird, one of the species recorded in the Lower Delta categorized as globally vulnerable (BirdLife International 2016) that was detected in the first period but not in the second one. This species inhabits open grasslands and wetlands in areas with high availability of insects. In Argentina, their populations are nowadays restricted to the south of Entre Rios, northern Corrientes and Misiones due to fragmentation and degradation of grasslands for agricultural use and conversion of wetlands mainly into rice production (Fraga *et al.* 1998). The non-insular area of the Lower Delta represents the southern limit of this species' range (BirdLife International 2016). This icterid forms mixed flocks (average 30 individuals) with the brown-and-yellow marshbird (*Pseudoleistes virescens*) and the black-and-white monjita (*Xolmis dominicanus*). The latter, listed as 'at risk' in Argentina (López-Lanús *et al.* 2008), was not detected in the second period but was observed in the first period outside of the survey limits (R. D. Quintana, pers. comm., 2017).

Contrary to the typical pattern in other altered wetlands (Duncan *et al.* 1999; Smith & Chow-Fraser 2010), in the Lower Delta generalist species did not colonize former wetlands as habitat became increasingly dry and the area of bare soil increased. Common species of disturbed or urban environments such as doves (*Zenaida auriculata*, *Columbina picui*) and parakeets (*Myiopsitta monacha*) did not increase. Grassland species like pipits (*Anthus* spp.), white-browed blackbird (*Sturnella superciliaris*) and rhea (*Rhea americana*) did not increase either, and in fact some even decreased in frequency of occurrence. This may indicate that the grazing lands that are replacing wetlands in the area are not high-quality grasslands habitats, and suggests that their usefulness for biodiversity can decline when they were converted to serve an economic purpose. Interestingly, many species associated with forests and shrublands such as woodcreepers (*Lepidocolaptes angustirostris* and *Drymornis bridgesii*) and spinetails (*L. platensis* and

S. frontalis) increased in frequency or even appeared only in recent surveys. These species are favoured in silvopastoral systems with low cattle density in other regions (Decarre 2015; Macchi *et al.* 2015), the same may happen in the Lower Delta where cattle grazing in native shrublands is a common practice.

Species loss, particularly wetland species, was lower than expected if we consider that wetland conversion towards dryer lands is widespread over the study area. This could have two potential explanations. First, landscape changes detected between 1999 and 2013 are not large enough to generate an immediate response of bird populations in Lower Delta potentially because of their plasticity associated with the high mobility of the species present in the area which allows them to face the changes (Lemoine *et al.* 2007). Second, bird populations may exhibit a delay in their response to changes in the landscape (Chamberlain *et al.* 2000; Metzger *et al.* 2009). If this is the case, then the reported period may be too short to detect a strong response and we are only detecting the beginning of the process. Hence, the true effect of wetland conversion could be even stronger than detected, especially for wetland species for which we already found clear effects of the landscape changes when we separated the effect of wetland water level.

The non-insular area of the Lower Delta of Paraná River is an example of wetland ecosystems being rapidly modified by human activities. Although the rate of wetland conversion around the world is ~50% in 150 years (O'Connell 2003; Finlayson, 2012), the conversion rate detected in the study area was very high (reduction of more than 40% of freshwater marshes in just 14 years; Sica *et al.* 2016). This fast pace of conversion and the expansion of water control structures in the area will continue unchecked if land-use regulations are not implemented, and it is possible that conversion may intensify further, with expanded anthropogenic changes to different land uses (e.g. agriculture, forestry or urban) or by a synergy with climate-change effects. To prevent major effects on biodiversity, additional conservation efforts are necessary. Some are in progress, such as a protocol for biodiversity management in afforestations (Fracassi *et al.* 2013) and guidelines for sustainable cattle management (Quintana *et al.* 2014) but their effectiveness depends on decision makers and land owners because there is no law that enforces protection of ecosystem integrity in the Lower Delta. However, such a law is not without precedent; in 2007 Argentina enacted a national law to protect its forests. If public and legislative support for a national law addressing wetland conservation and sustainable use were to be considered, our results could be useful inputs for planning human activities and biodiversity conservation in wetlands.

Understanding the effects of water level separately from the effects of land-cover change on bird community is a key point to take into account, as well as the recognition of possible time-lags in the response of birds. Wetlands around the world and the biodiversity they hold are at risk due to poor legislation (Keddy *et al.* 2009). Hence, incorporating this knowledge in legislation should be a priority in wetland regions worldwide.

ACKNOWLEDGEMENTS

We are gratefully to all the people that participated in the field surveys specially Natalia Garcia, Natalia Denkiewicz, Evelyn Figueroa Schibber and Ileana Martinez. We also thank Sebastian Dardanelli for his collaboration during survey design. This study was financially supported by several projects: PNNAT 1128053 and 1128052 (INTA), PICTOCIN I 0022, PIP 0092 (CONICET), PICT Bicentenario 2227 (ANPCyT) and a bilateral cooperation agreement between CSIC & CONICET (Programa de cooperación científica con Iberoamérica from the Spanish Ministry of Education). We are thankful to CONICET, the Fulbright commission and Bunge-Born Foundation for the scholarships that allowed the Yanina Sica's stay in SILVIS Lab.

REFERENCES

- Agresti A. (2007) *An Introduction to Categorical Data Analysis*. Wiley-Interscience, New York.
- Baigún C. R. M., Puig A., Minotti P. G. *et al.* (2009) Resource use in the Parana River Delta (Argentina): moving away from an ecophysiological approach? *Ecophysiol. Hydrobiol.* **8**, 245–62. <https://doi.org/10.2478/v10104-009-0019-7>
- Baschuk M. S., Koper N., Wrubleski D. A. & Goldsborough G. (2012) Effects of water depth, cover and food resources on habitat use of marsh birds and waterfowl in boreal wetlands of Manitoba, Canada. *Waterbirds* **35**, 44–55.
- Baselga A. & Orme C. D. L. (2012) Betapart: an R package for the study of beta diversity. *Methods Ecol. Evol.* **3**, 808–12.
- Baselga A., Bonthoux S. & Balent G. (2015) Temporal beta diversity of bird assemblages in agricultural landscapes: land cover change vs. stochastic processes. *PLoS ONE* **10**, e0127913. <https://doi.org/10.1371/journal.pone.0127913>
- BirdLife International (2016) Species factsheet: *Xanthopsar flavus*. [Cited 18 November 2016.] Available from URL: <http://www.birdlife.or>
- Bó R. F. & Malvárez A. I. (1999) Las inundaciones y la biodiversidad en humedales: un análisis del efecto de eventos extremos sobre la fauna Silvestre. In: *Temas Sobre Humedales Subtropicales y Templados de Sudamérica*, (ed A.I. Malvárez) pp. 147–68. Montevideo, MAB-ORCYT.
- Bó R. F., Quintana R. D., Courtalón P. *et al.* (2010) Efectos de los cambios en el régimen hidrológico por las actividades humanas sobre la vegetación y la fauna silvestre del Delta del Río Paraná. In: *Endicamientos y terraplenes en el Delta del Paraná* (eds D. E. Blanco & F. M. Méndez) pp. 33–64. Fundación para la Conservación y el Uso Sustentable de los Humedales, Buenos Aires.
- Brown M. & Dinsmore J. J. (1986) Implications of marsh size and isolation for marsh bird management. *J. Wildl. Manage.* **50**, 392–7. <https://doi.org/10.2307/3801093>
- Carrascal L. M., Bautista L. M. & Lázaro E. (1993) Geographical variation in the density of the white stork *Ciconia ciconia* in Spain: influence of habitat structure and climate. *Biol. Conserv.* **65**, 83–7.
- Chamberlain D. E., Fuller R. J., Bunce R. G., Duckworth J. C. & Shrubbs M. (2000) Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. *J. Appl. Ecol.* **37**, 771–88.
- Chase J. M. (2007) Drought mediates the importance of stochastic community assembly. *Proc. Natl Acad. Sci. USA* **104**, 17430–4.
- Clavel J., Julliard R. & Devictor V. (2011) Worldwide decline of specialist species: toward a global functional homogenization? *Front. Ecol. Environ.* **9**, 222–8.
- Codesido M., González-Fischer C. & Bilenca D. (2011) Distributional changes of landbird species in agroecosystems of central Argentina. *The Condor* **113**, 266–73.
- De Stéfano K., Merler J. A., Magnano A. L., Nanni A. S., Kandus P. & Quintana R. D. (2012) Relación entre la heterogeneidad ambiental y el patrón de distribución y la riqueza de aves en dos unidades de paisajes del Delta del Paraná. *Ornitol. Neotrop.* **23**, 169–84.
- Decarre J. (2015) *Diversity and Structure of Bird and Mammal Communities in the Semi-arid Chaco Region: Response to Agricultural Practices and Landscape Alterations*. Imperial College London, London.
- Deluca W. V., Studds C. E., Rockwood L. L. & Marra P. P. (2004) Influence of land use on the integrity of marsh bird communities of Chesapeake Bay, USA. *Wetlands* **24**, 837–47.
- Devictor V., Julliard R., Clavel J., Jiguet F., Lee A. & Couvet D. (2008) Functional biotic homogenization of bird communities in disturbed landscapes. *Global Ecol. Biogeogr.* **17**, 252–61.
- Dirección de Hidráulica de Entre Ríos (2016) *Hydrometeorology*. [Cited 18 November 2016.] Available from URL: <http://www.hidraulica.gov.ar/ema.php>
- Douglas A. J. & Johnson R. L. (1994) Drainage investment and wetlands loss: an analysis of the national resources inventory data. *J. Environ. Manage.* **40**, 341–55.
- Dudgeon D., Arthington A. H., Gessner M. O. *et al.* (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. *Biol. Rev. Camb. Philos. Soc.* **81**, 163–82.
- Duncan P., Hewison A. J. M., Houte S. *et al.* (1999) Long-term changes in agricultural practices and wildfowling in an internationally important wetland, and their effects on the guild of wintering ducks. *J. Appl. Ecol.* **36**, 11–23.
- Findlay C. S. & Houlahan J. (1997) Anthropogenic correlates of species richness in southeastern Ontario wetlands. *Conserv. Biol.* **11**, 1000–9. <https://doi.org/10.1046/j.1523-1739.1997.96144.x>
- Finlayson C. M. (2012) Forty years of wetland conservation and wise use. *Aquatic Conserv. Mar. Freshw. Ecosyst.* **22**, 139–43.
- Fletcher R. J. & Koford R. R. (2004) Consequences of rainfall variation for breeding wetland blackbirds. *Can. J. Zool.* **82**, 1316–25.

- Forcey G. M., Thogmartin W. E., Linz G. M., Bleier W. J. & Mckann P. C. (2011) Land use and climate influences on waterbirds in the Prairie Potholes. *J. Biogeogr.* **38**, 1694–707.
- Fracassi N. G. (2001) *Diversidad de mamíferos y aves en pajonales y forestaciones de salicáceas del Bajo Delta del río Paraná*. Master Thesis, Universidad de Buenos Aires, Buenos Aires.
- Fracassi N., Quintana R. D., Pereira J., Mujica G. & Landó R. (2013) *Protocolo de Estrategias de Conservación de la Biodiversidad en Bosques Plantados de Salicáceas del Bajo Delta del Paraná*. Ediciones INTA, Buenos Aires. [Cited 16 August 2016.] Available from URL: http://inta.gob.ar/sites/default/files/script-tmp-inta_-_conservacin_de_la_biodiversidad_en_plantacione.pdf
- Fraga R. M., Casañas H. & Pugnali G. (1998) Natural history and conservation of the endangered Saffron-cowled Blackbird *Xanthopsar flavus* in Argentina. *Bird Conserv. Int.* **8**, 255–67.
- Galafassi G. (2005) *La Pampeanización del Delta*. Extramuros ediciones, Buenos Aires.
- Gardner R. C., Barchiesi S., Beltrame C. et al. (2015) *State of the World's Wetlands and their Services to People: A Compilation of Recent Analyses*. Ramsar Convention Secretariat, Gland.
- Gerakis A. & Kalburtji K. (1998) Agricultural activities affecting the functions and values of Ramsar wetland sites of Greece. *Agric. Ecosyst. Environ.* **70**, 119–28.
- Green A. J., El Hamzaoui M., El Agbani M. A. & Franchimont J. (2002) The conservation status of Moroccan wetlands with particular reference to waterbirds and to changes since 1978. *Biol. Conserv.* **104**, 71–82.
- Gregory R. D., Noble D. G., Field R., Marchant J. H., Raven M. & Gibbons D. W. (2003) Using birds as indicators of biodiversity. *Ornis Hung.* **12–13**, 11–24. Available from URL: <http://www.ebcc.info/wpimages/other/bio-iindicators.pdf>
- Gu W. & Swihart R. K. (2004) Absent or undetected? Effects of non-detection of species occurrence on wildlife-habitat models. *Biol. Conserv.* **116**, 195–203.
- Kandus P., Quintana R. D. & Bó R. F. (2006) *Patrones de paisaje y Biodiversidad del Bajo Delta del Río Paraná. Mapa de ambientes (Patterns of landscape and biodiversity of the Lower Delta of the Paraná River. Map of environments)*, 1st edn. Pablo Casamajor, Buenos Aires.
- Keddy P. A., Fraser L. H., Solomeshch A. I. et al. (2009) Wet and wonderful: the world's largest wetlands are conservation priorities. *Bioscience* **59**, 39–51.
- Lemoine N., Schaefer H. C. & Bohning-Gaese K. (2007) Species richness of migratory birds is influenced by global climate change. *Global Ecol. Biogeogr.* **16**, 55–64. <https://doi.org/10.1111/j.1466-8238.2006.00252.x>
- Lepczyk C. A., Flather C. H., Radeloff V. C., Pidgeon A. M., Hammer R. B. & Liu J. (2008) Human impacts on regional avian diversity and abundance. *Conserv. Biol.* **22**, 405–16.
- López-Lanús B., Grilli P., Di Giacomo A. S., Coconier E. E. & Banchs R. (2008) *Categorización de las aves de la Argentina según su estado de conservación*. Aves Argentinas/AOP y Secretaría de Ambiente y Desarrollo Sustentable, Buenos Aires.
- Macchi L., Grau H. R. & Phalan B. (2015) Agricultural production and bird conservation in complex landscapes of the dry Chaco. *J. Land Use Sci.* **11**, 188–202.
- Maclean I. M. D., Wilson R. J. & Hassall M. (2011) Predicting changes in the abundance of African wetland birds by incorporating abundance–occupancy relationships into habitat association models. *Divers. Distrib.* **17**, 480–90.
- Magnano A. L. (2011) *Patrón espacial y temporal de la comunidad de aves en diferentes usos de la tierra del Bajo Delta del Río Paraná*. Universidad de Buenos Aires, Buenos Aires.
- Magurran A. E. (2004) *Measuring Biological Diversity*. Blackwell Science Ltd., Malden.
- Malvárez A. I. (1999) El Delta Del Río Paraná como mosaico de humedales. In: *Tópicos Sobre Humedales Subtropicales y Templados de Sudamérica* (ed A. I. Malvárez) pp. 35–53. UNESCO, Montevideo.
- Metzger J. P., Martensen A. C., Dixo M. et al. (2009) Time-lag in biological responses to landscape changes in a highly dynamic Atlantic forest region. *Biol. Conserv.* **142**, 1166–77. <https://doi.org/10.1016/j.biocon.2009.01.033>
- Minotti P. G. & Kandus P. (2013) *Actualización y profundización del mapa de endicamientos y terraplenes de la región del Delta del Paraná – 2013 Fundación para la Conservación y el Uso Sustentable de los Humedales*. Wetlands International LAC, Buenos Aires.
- Mitsch W. J. & Gossilink J. G. (2007) *Wetlands*. Wiley, Hoboken.
- Narosky T. & Yzurieta D. (2013) *Guía de Identificación de Aves de Argentina y Uruguay*. Vazques Mazzini Editores, Buenos Aires. Available from URL: http://www.vmeditores.com.ar/vm_publico/detalle.asp?id_titulo=28
- Naugle D. E., Higgins K. F., Nusser S. M. & Johnson W. C. (1999) Scale-dependent habitat use in three species of prairie wetland birds. *Landscape Ecol.* **14**, 267–76.
- Newton I. (2004) The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. *Ibis (Lond. 1859)*. **146**, 579–600.
- O'Connell M. J. (2003) Detecting, measuring and reversing changes to wetlands. *Wetl. Ecol. Manag.* **11**, 397–401.
- de la Peña M. R. (2005) *Reproducción de las aves argentinas (con descripción de pichones)*. L.O.L.A., Buenos Aires. Available from URL: <http://www.sidalc.net/cgi-bin/wxis.exe/?IsisScript=HAG.xis&method=post&formato=2&cantidad=1&expresion=mfn=017884>
- Prefectura Naval Argentina (2017) *River Stages*. [Cited 13 June 2017.] Available from URL: <http://www.prefecturanaval.gov.ar/alturas/index.php>
- Quesnelle P. E., Fahrig L. & Lindsay K. E. (2013) Effects of habitat loss, habitat configuration and matrix composition on declining wetland species. *Biol. Conserv.* **160**, 200–8.
- Quintana R. D., Bó R. F., Astrada E. & Reeves C. (2014) *Lineamientos para una ganadería ambientalmente sustentable en el Delta del Paraná* (eds C. Penedo & D. E. Blanco). Fundación Humedales/Wetlands International LAC, Buenos Aires.
- R Core Team (2016) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org/>
- Ralph C. J., Geupel G. R., Pyle P., Martin T. E. & DeSante D. F. (1993) *Handbook of Field Methods for Monitoring Landbirds*. Pacific Southwest Research Station, Albany, CA. Available from URL: <http://digitalcommons.unl.edu/cgi/viewcontent.cgi?article=1104&context=usdafsacpub>

- Ralph C. J., Droege S. & Sauer J. R. (1995) *Managing and monitoring birds using point counts: standards and applications*. USDA Forest Service Gen. Tech. Rep. PSW-GTR-149
- Rebelo L. M., Finlayson C. M. & Nagabhatla N. (2009) Remote sensing and GIS for wetland inventory, mapping and change analysis. *J. Environ. Manage.* **90**, 2144–53.
- Riffell S. K., Keas B. E. & Burton T. M. (2001) Area and habitat relationships of birds in Great Lakes coastal wet meadows. *Wetlands* **21**, 492–507.
- Rocha G. (2008) *Aves del Uruguay. El país de los pájaros pintados, Version 3*. Banda Oriental, Montevideo.
- Ryder R. A. (1967) Distribution, migration and mortality of the White-faced Ibis (*Plegadis chihi*) in North America. *Bird-Banding* **38**, 257–77.
- Sala O. E., Stuart Chapin F. III, Armesto J. J. *et al.* (2009) Global biodiversity scenarios for the year 2100. *Science* **287**, 1770–4.
- Schrag A. M., Zaccagnini M. E., Calamari N. C. & Canavelli S. B. (2009) Climate and land-use influences on avifauna in central Argentina: broad-scale patterns and implications of agricultural conversion for biodiversity. *Agric. Ecosyst. Environ.* **132**, 135–42.
- Sica Y. V., Quintana R. D., Radeloff V. C. & Gavier-Pizarro G. I. (2016) Wetland loss due to land use change in the Lower Paraná River Delta, Argentina. *Sci. Total Environ.* **568**, 967–78.
- Siriwardena G. M., Baillie S. R. & Wilson J. D. (1999) Temporal variation in the annual survival rates of six granivorous birds with contrasting population trends. *The Ibis* **141**(4), 621–36.
- Smith L. A. & Chow-Fraser P. (2010) Impacts of adjacent land use and isolation on marsh bird communities. *Environ. Manage.* **45**, 1040–51.
- Song K., Wang Z., Li L. *et al.* (2012) Wetlands shrinkage, fragmentation and their links to agriculture in the Muleng-Xingkai Plain, China. *J. Environ. Manage.* **111**, 120–32. <https://doi.org/10.1016/j.jenvman.2012.06.038>
- Trewartha G. & Horn L. (1980) *An Introduction to Climate*. McGraw-Hill, New York.
- Van Asselen S., Verburg P. H., Vermaat J. E. & Janse J. H. (2013) Drivers of wetland conversion: a global meta-analysis. *PLoS ONE* **8**, 1–13.
- Ward M. P., Semel B. & Herkert J. R. (2010) Identifying the ecological causes of long-term declines of wetland-dependent birds in an urbanizing landscape. *Biodivers. Conserv.* **19**, 3287–300.
- Weller M. W. (1999) *Wetland Birds: Habitat Resources and Conservation Implications*. Cambridge University Press, New York.
- Whited D. C., Galatowitsch S. M., Tester J. R., Schik K., Lehtinen R. & Husveth J. (2000) The importance of local and regional factors in predicting effective conservation. Planning strategies for wetland bird communities in agricultural and urban landscapes. *Landscape Urban Plan.* **49**, 49–65.
- Wiens J. A. (1992) *The Ecology of Bird Communities*. Cambridge University Press, New York.
- Yuan Y., Zeng G., Liang J. *et al.* (2014) Effects of landscape structure, habitat and human disturbance on birds: a case study in East Dongting Lake wetland. *Ecol. Eng.* **67**, 67–75. <https://doi.org/10.1016/j.ecoleng.2014.03.012>
- Zedler J. B. (2003) Wetlands at your service: reducing impacts of agriculture at the watershed scale. *Front. Ecol. Environ.* **1**, 65–72. [https://doi.org/10.1890/1540-9295\(2003\)001\[0065:waysri\]2.0.co;2](https://doi.org/10.1890/1540-9295(2003)001[0065:waysri]2.0.co;2)
- Zedler J. B. & Kercher S. (2005) Status, trends, ecosystem services, and restorability. *Rev. Lit. Arts Am.* **39–74**. <https://doi.org/10.1146/annurev.energy.30.050504.144248>

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. List of species registered in the Lower Delta of Paraná river (–33°45'S; 58°51'W) and their habitat affiliations.

Appendix S2. Land-cover changes occurred on each bird survey point between 1999 and 2013 in the Lower Delta. We calculated land-cover change as the subtraction of the area covered by each land-cover type (in hectares) in the second period and the first one (land cover₂₀₁₃ – land cover₁₉₉₉). Hence, negative values mean land-cover loss while positive values mean expansion.

Appendix S3. Accumulated precipitation (mm) during bird surveys (October and November 1997, 1999, 2012 and 2013). Data registered in two pluviometers in Entre Ríos province (Dirección de Hidráulica de Entre Ríos 2016). A pluviometer placed in the town of Médanos (representative of the study area as it extends less than 50 km away from this town) and another pluviometer placed in Holt Ibicuy (a train station 36 km south from Médanos).

Appendix S4. Community dissimilarity between time periods showing species turnover (β_t) and nestedness (β_n).

Appendix S5. NMDS summary for each temporal comparison and the correlation between the ordination axes (NMDS1 and NMDS2) and the landscape variables.

Appendix S6. Two-dimensional graphs showing the NMDS ordination of bird survey points considering species present in each survey.