Avian communities in *Spartina maritima* restored and non-restored salt marshes

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Capsule Salt marsh restoration with the native halophytes *Spartina maritima* and *Zostera noltii* can lead to significant improvement in habitat, increasing bird diversity over a 2-year period.
Aims To assess the evolution of the avian communities in *S. maritima* restored salt marshes 2 years after planting, in comparison with adjacent non-restored marshes in the Odiel Marshes (southwest Iberian Peninsula).
Methods Bird censuses were conducted from October 2008 to September 2009 in rectangular plots in three locations in both restored and non-restored marshes during high tides and low tides.
Results A total of 44 bird species, including 20 shorebird species, were recorded. Most species belonged to Charadriidae, Scolopacidae, Laridae and Sterninae. Eight threatened bird species were recorded in restored marshes. Ecological diversity of the avian communities varied between 1.13 and 1.77. Restored marshes showed higher ecological diversity and evenness and lower Simpson dominance index than non-restored marshes.
Conclusion Salt marsh restoration with the native halophytes *S. maritima* and *Z. noltii* can lead to significant short-term (over 2 years) improvements in bird diversity.

Salt marsh habitats are recognized for their importance for many bird species, both migratory and resident, as habitats for feeding, resting and breeding (Howe 1987, Ferns 1992, Hughes 2004, Laegdsaard 2006). For example, many shorebird species, with extremely high energy requirements and very high feeding rates (Nagy 2001), feed on invertebrates living in sediments that, in turn, feed on detritus produced by marsh vegetation (Chung 1993, Rowcliffe *et al.* 1995, Brown & Atkinson 1996). Other birds nest only on certain salt marsh plants (Post & Greenlaw 1994).

Destruction and alteration of habitat is the greatest threat for marsh birds (e.g. Howe *et al.* 1989, Yalden 1992, Goss-Custard *et al.* 1995, Weber *et al.* 1999, Figuerola & Amat 2003, Rosa *et al.* 2003). Alteration of habitats can arise through introduced plant species. For example, Gan *et al.* (2009) described how exotic *Spartina* can have negative impacts on local bird communities. Odiel Marshes, the study area considered here, has been invaded by dense-flowered cordgrass *Spartina densiflora* Brong. to a high degree (Nieva *et al.* 2001).

The creation and restoration of salt marsh habitats are critical for maintaining bird biodiversity in the face of salt marsh degradation and destruction (e.g. Zedler 1993). Ecological restoration that increases habitat heterogeneity has been linked to diversity and abundance of salt marsh birds (Greenlaw 1983, Craig & Beal 1992, Reinert & Mello 1995). Restored salt marshes provide new habitats for obligate species, which breed and forage only in salt and brackish marshes, and facultative species, which breed or forage in other habitats as well (Lewis & Casagrande 1997).

Monitoring is essential to assess the success of salt marsh restoration projects. To this end, changes in the avian community should be taken into account to assess the evolution of restored marshes. The complexity of the marsh bird community can be a measure of the success of the project (Lewis & Casagrande 1997) because shorebirds are a good indicator of environmental health (Beintema 1983). This is because salt marsh birds require numerous elements for their survival and operate at higher

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trophic levels (Burnett *et al.* 2005; Rodewald & Brittingham 2007, Nur *et al.* 2008). In addition, birds are also valuable as ecosystem change indicators because they often respond to cumulative effects of environmental influences on the system (Sekercioglu 2006).

Although there are many studies monitoring the bird communities in wetlands when the tidal influences have been restored (e.g. Brawley *et al.* 1998, Warren *et al.* 2002, Konisky *et al.* 2006, Gallego-Fernández & García-Novo 2007, Raposa 2009), only a handful of studies analyse bird responses to *Spartina* plantations (Zedler 1993, Melvin & Webb 1998, Havens *et al.* 2002). In this study we assess the development of the avian community in restored low salt marshes. Small Cordgrass *Spartina maritima* (Curtis) Fernald and Dwarf Eelgrass *Zostera noltii* Hornem. plantations two years after planting (Castillo & Figueroa 2009) were compared to adjacent degraded and non-restored marshes invaded by *S. densiflora* in an area of international importance for migratory shorebirds (the Odiel Marshes, southwest Iberian Peninsula). We hypothesized that salt marsh restoration with native halophytes would increase bird community complexity (species richness, ecological diversity and density) in comparison with degraded salt marshes invaded by the South American neophyte *S. densiflora*.

METHODS

Study site

The study was carried out at Odiel Marshes in the joint estuary of the Odiel and Tinto rivers (37°15′–37°37′N, 6°57′–6°58′W; southwest Spain). These salt marshes are located on the South Atlantic coast of the Iberian Peninsula near the city of Huelva (Spain). They occupy some 1758 ha. The tidal range (mean spring) is 2.97 m (0.40–3.37 above Spanish Hydrographic Zero, SHZ). The sediment salinity at low marshes ranges between 7 and 36 milliSiemens cm^{-1} (Curado *et al.* 2013).The climate is essentially Mediterranean, but modified with oceanic influences. Mean annual precipitation is 506 mm with a coefficient of variation of 31% (Rubio 1985).

Odiel Marshes are a site of international importance for migratory waders through the East Atlantic flyway (Garrido-Guil 1996, Sánchez *et al.* 2006). The high ecological values of Odiel Marshes has led them to be protected as a Ramsar site (Bernués 1998), as a UNESCO Biosphere Reserve, as a Natural Park (Paraje Natural) and as a Special Protection Area for Birds of the European Union (EU-SPA). Odiel Marshes is an obligatory stopping place for thousands of shorebirds migrating through the East Atlantic flyway for resting and refuelling (Sánchez *et al.* 2006). Fishing and shell-fishing occurs on these salt marshes. Odiel Marshes are polluted with metals coming from industrial activities in the estuary and long-term mining activities carried out landward at the Iberian Pyrite Belt (Curado *et al.* 2010). Furthermore, *S. densiflora*, which colonizes a wide range of habitats and competitively displaces native species, has been an invasive species in these marshes for over a century (Nieva *et al.* 2001).

Our study was carried out in low marsh areas and adjacent bare intertidal mudflats at two sites described in Curado *et al.* (2013). (1) Restored salt marshes planted from November 2006 to January 2007 with *S. maritima* (relative cover about 50%), the perennial glasswort *Sarcocornia perennis* (Miller) Scott subspecies *perennis* and *Z. noltii* (isolated individuals). Sea purslane *Atriplex portulacoides* L., *Suaeda maritima* (L.) Dumort. and isolated clumps of the invasive *S. densiflora* have also colonized these marshes. Restored marshes were located next to Huelva's Chemical Pole, one of the biggest industrial concentrations in Spain, extending over more than 1500 ha (Castillo & Figueroa 2009). (2) Adjacent non-restored salt marshes invaded by *S. densiflora* Brongn. (relative cover about 20%) with high erosion rates (Castillo *et al.* 2000), which were similar to the restored marshes prior to their restoration (Fig. 1). By necessity, restored marshes were compared with degraded marshes because no preserved marshes of *S. maritima* remained at channel bank in the Odiel Marshes.

Bird censuses

Bird censuses were conducted in 2.3 ha rectangular plots during high tides (between the lower distribution limit of the *Spartina* spp. band (+ 1.5 m above SHZ) and the upper distribution limit of salt marshes (about + 3.4 m SHZ)) and 5.80 ha plots during low tides (between the average tide level during low tide sampling (+ 0.8 m SHZ) and the upper distribution limit of salt marshes). These areas were defined to include every type of habitat (drainage channels, bare patches, intertidal ponds, mudflats, *Spartina* prairie and Chenopodiaceae community) that emerged at low and high tide. Three sampling points were established along 3 km of the

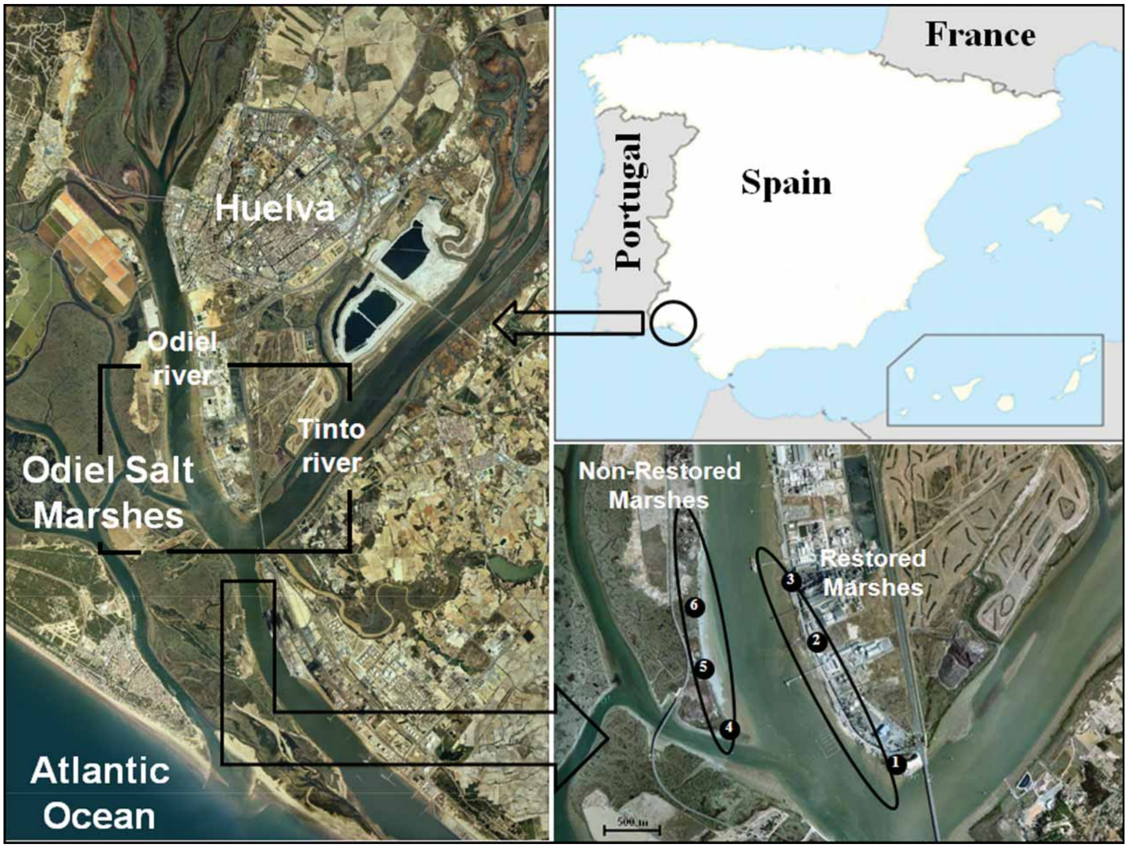

Figure 1. Location of Odiel Marshes on the Iberian Peninsula and position of sampling points for bird censuses in Odiel Marshes (1–3, restored marshes; 4–6, non-restored marshes).

shoreline in the restored marshes and non-restored marshes.

Censuses were carried out on clear mornings between 7:00 and 11:00 a.m. when low or high tide occurred between 9:00 and 10:00 a.m., during rising tides close to high tide level and ebbing tides close to low tide level (Dias *et al.* 2006). Observations were always made for 20 min at each sampling point using 8× binoculars and a 20–60× spotting scope, from a distance greater than 50 m to minimize disturbances. An initial scan covering all the sampling area was carried out slowly at the beginning of the 20-min period and then birds entering the area were counted. Censuses were performed weekly from October 2008 to September 2009 for each sampling point. Each sampling point was visited 3–5 times per season (autumn (October–November 2008), winter (December 2008–February 2009), spring (March–May 2009) and summer (June–August 2009)), at both low and high tides (e.g. see Havens *et al.* 1995, Neckles *et al.* 2002 for similar methodologies). Thus, every marsh area (restored and non-restored) was visited between 9 and 15 times every season both at low and high tide. Every marsh area was sampled during each sampling day, except during summer when just three points were visited on each day due to high temperatures that reduced bird activities. Every day the sampling was started in a different marsh to reduce effects related to daily changes in bird distribution. All observed bird species and the number of individuals of each species were recorded.

Data process and statistical analysis

Ecological diversity was calculated using the Shannon–Weaver index (H′), based on the inventoried data and abundance of each species (Shannon & Weaver 1949), which is sensitive to changes in rare taxa (Magurran 1988, Krebs 1994). Evenness (J), Maximum Ecological Diversity (H_{max}) and Simpson dominance index (D) of the bird communities were also calculated (Simpson 1949).

Rank/abundance diagrams were used as a method of representing the distribution of individuals amongst species within the community (see Whittaker 1975). Such graphs display community composition and allow a degree of biological interpretation not possible with single number diversity and equitability measures. They can illustrate differences in numerical dominance and in the presence of rare species between marshes and tidal levels through the year (Thrush 1986).

Similarity in species composition between marshes was investigated by calculating the Sørensen similarity index (Jongman *et al.* 1995). This index measures similarity of species between two communities but does not take abundances into account: $Sør = 2C\ /\ A + B$, where C is the number of species shared by the two considered marsh areas, and A and B are the species richness of the two considered marsh areas. Values of $Sør$ vary between 0 and 1; 0 indicates that the two marshes have no common species and 1 that the two marshes have the same species composition. Similarity percentages (SIMPER) analysis, based on the similarity matrix obtained from the Bray–Curtis index, was used

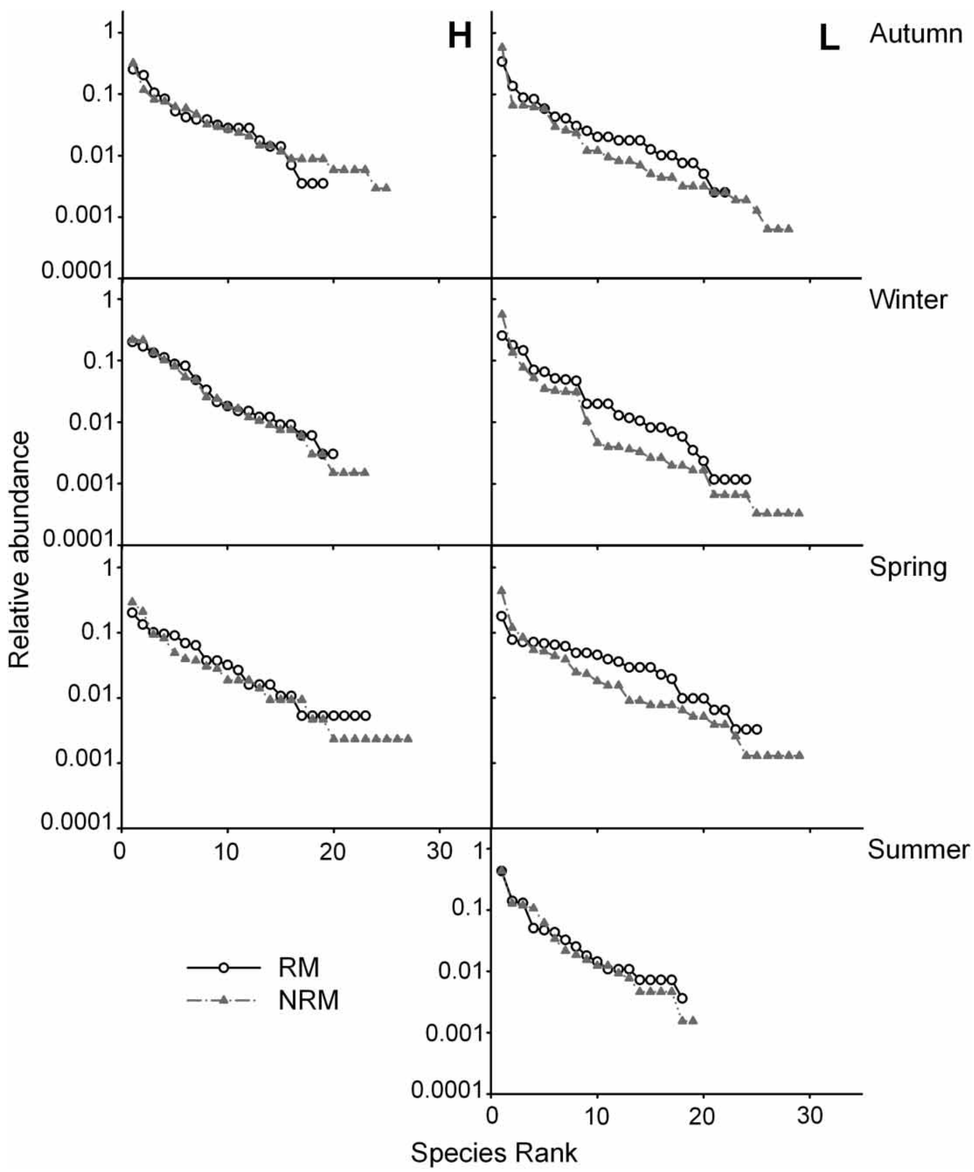

Figure 2. Rank-abundance diagrams (semi-logarithmic scale) for the bird communities at high tide (H) and low tide (L) in autumn, winter, spring and summer in restored and non-restored *Spartina maritima* marshes in the Odiel Marshes (southwest Iberian Peninsula). For each curve, a steep slope indicates low ecological diversity and high dominance, and a long tail indicates the presence of many rare species.

to calculate the contribution of each taxon to the dissimilarity between marshes areas (software package PRIMER 5.2.8; Clarke 1993).

Bird species density (number of birds ha^{-1}) for every sampling point was determined as the mean of densities recorded on every sampling day ($n = 3–5$) for the most abundant species and genus (*Arenaria interpres*, *Pluvialis squatarola*, *Calidris* spp., *Charadrius* spp., *Larus* spp., *Limosa* spp., *Numenius* spp. and *Tringa* spp.).

Statistical analyses were carried out with SPSS release 18.0 (SPSS Inc., Chicago, IL, USA). Data were tested for normality using a Kolmogorov–Smirnov test, and for homogeneity of variance with a Levene's test. Diversity indexes were compared using marsh area (restored and non-restored marshes), tidal level (low and high tide) and season (autumn, winter, spring and summer) as fixed factors. We used the Akaike Information Criterion (AIC) to define the best model for each measure of ecological diversity using R software 2.15.2 (R Foundation for Statistical Computing). We chose AIC for model selection because it provides an objective method for selecting the most parsimonious model that still provides an adequate fit to the data (Akaike 1973). The model with the lowest AIC value was considered the best-fitting model. We compared models by calculating the difference in support (Δ_i (AIC) = [AIC_i – min (AIC)]). We did not consider models that differed from the top models within 2 Δ_i (AIC) units of the best model to be supported (Burnham & Anderson 2002). Akaike weights (w_i AIC) were calculated for each model to examine the relative likelihood of the model given the data. These resulting weights sum to one across all models and are interpreted as probabilities where a model with an Akaike weight approaching one is strongly supported by the data (Johnson & Omland 2004). Annual densities were compared using *t*-test or *U*-test.

RESULTS

A total of 44 bird species, including 20 shorebird species, were recorded in the two marsh areas (36 spp. in restored and 40 spp. in non-restored marshes). In general, the total number of bird species recorded in non-restored marshes during the year was higher than in restored marshes due to the presence of rare species. The main differences were primarily recorded during low tides, when the slope of the rank-abundance curve was less marked for restored than for non-restored marshes, denoting a higher evenness for restored marshes (Fig. 2).

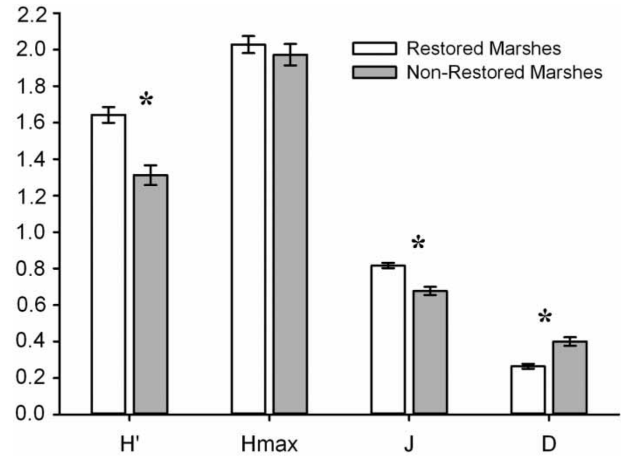

Figure 3. Mean annual ecological diversity (H′), maximum diversity (H_{max}), evenness (J) and dominance (D) for the bird communities in restored and non-restored *Spartina maritima* marshes in the Odiel Marshes (southwest Iberian Peninsula). *Significant differences between marshes for each diversity metric.

The number of shorebird species was relatively similar between marsh areas, varying between 1 and 2 species between restored and non-restored marshes for every season and tidal level. Most species belonged to Charadriidae, Scolopacidae, Laridae and Sterninae. Four species were recorded only in restored marshes (*Alcedo atthis*, *Anthus pratensis*, *Phylloscopus collybita* and *Tringa ochropus*), and eight species appeared very rarely and only in non-restored marshes (*Acrocephalus scirpaceus*, *Buteo buteo*, *Circus pygargus*, *Himantopus*

Table 1. Best models determined using Akaike Information Criterion (AIC). Index: H′, Ecological Diversity; H_{max}, Maximum Diversity; J, Evenness; D, Dominance. Model parameters: marsh (restored or non-restored marshes), tide state (high or low tide) and season (autumn, winter, spring or summer); K_i, number of parameters for model *i*; AIC_i, Akaike's Information Criterion; Δ_i (AIC), [AIC_i – min (AIC)]; w_i (AIC), the Akaike weight.

Index	Models	K_i	AIC_i	Δ_i (AIC)	w_i (AIC)
H′	marsh × season	2	194.5	0.0	0.9
H_{max}	marsh × tide state × season	3	197.7	0.0	1.0
J	marsh × tide state	2	–116.2	0.0	0.8
D	Marsh	1	–107.5	0.0	0.5
	marsh × tide state	2	–106.8	0.8	0.6
	marsh × season	2	–105.8	1.7	0.9

Table 2. Variation in the average abundance (A. Abun.), average dissimilarity (A. Diss.), the ratio of dissimilarity: standard deviation (Diss : SD; a measure of variation in the contribution to dissimilarity), contribution to dissimilarity (Cont. Diss.) (%) and contribution to accumulated dissimilarity (Ac. Diss) (%) of the most relevant bird taxa in restored marshes (RM) and non-restored marshes (NRM) in Odiel Marshes (southwest Iberian Peninsula). Taxa are listed in decreasing order according to their contribution to the average dissimilarity between marshes.

Species	A. Abun.		A. Diss.	Diss : SD	Cont. Diss. (%)	Ac. Diss (%)
	Dissimilarity between areas					
	RM	NRM	Average dissimilarity (29.9 %)			
Calidris alpina	2.4	5.7	2.7	4.7	8.8	8.8
Podiceps nigricollis	0.0	2.0	1.6	5.2	5.3	14.1
Pluvialis squatarola	1.9	3.5	1.3	2.5	4.4	18.5
Limosa lapponica	1.0	2.4	1.3	1.2	4.3	22.8
Calidris canutus	0.0	1.5	1.2	4.5	3.9	26.7
Pandion haliaetus	0.0	1.4	1.1	10.1	3.6	30.3
Limosa limosa	2.4	3.6	1.0	1.6	3.5	33.7
Sterna albifrons	0.9	2.2	1.0	1.8	3.4	37.2
Circus aeruginosus	0.3	1.5	1.0	2.2	3.1	40.3
Hydroprogne caspia	0.3	1.4	0.9	1.9	2.9	43.2
Tringa nebularia	2.1	1.2	0.9	1.5	2.9	46.1
Vanellus vanellus	0.0	1.1	0.9	1.3	2.9	49.0
Larus ridibundus	3.3	3.2	0.9	2.6	2.8	51.8
Arenaria interpres	3.0	2.0	0.8	1.2	2.8	54.7

himantopus, *Larus audouinii*, *Larus genei*, *Recurvirostra avosetta* and *Vanellus vanellus*). Fifteen threatened bird species were recorded at restored and non-restored marshes. Eight of them, Osprey *Pandion haliaetus*, Common Kingfisher *Alcedo atthis*, European Shag *Phalacrocorax aristotelis*, Kentish Plover *Charadrius alexandrinus*, Western Marsh-harrier *Circus aeruginosus*, Eurasian Curlew *Numenius arquata*, Black-tailed Godwit *Limosa limosa* and Eurasian Spoonbill *Platalea leucorodia*, fed in restored marshes (G. Curado, pers. obs.).

Ecological diversity and evenness were higher and dominance was lower at restored than at non-restored marshes. Maximum ecological diversity was similar for both marsh areas (Figs 2 & 3). Based on AIC, the models with greatest support were those that included the marsh type (Table 1). This parameter was the only one statistically significant in every model except for those predicting maximum ecological diversity. We did not find any significant interactions between parameters ($P > 0.05$).

Marsh areas showed a Sørensen similarity index of 0.84. *Calidris alpina*, *Podiceps nigricollis*, *Pluvialis squatarola* and *Limosa lapponica* were the species contributing mainly to the dissimilarity between restored and non-restored marshes (SIMPER analysis, average dissimilarity = 29.9%) (Tables 2 and 3). Restored marshes showed 81% similarity, with *Larus ridibundus*, *Charadrius hiaticula* and *Arenaria interpres* representing about 20% of this similarity. Non-restored marshes showed 79% similarity, with *Calidris alpina*, *Limosa limosa* and *Pluvialis squatarola* contributing about 21%.

Table 3. Mean annual shorebird and gull density (ind. ha^{-1}) of more abundant species and genera in *Spartina maritima* restored and non-restored marshes ($n = 21$).

	Annual average densities (ind. ha^{-1})	
Species	Restored	Non-restored
*Arenaria interpres****	1.0 ± 0.2	0.2 ± 0.1
Calidris spp.**	1.0 ± 0.4	7.6 ± 2.2
Charadius spp.	1.6 ± 0.4	1.0 ± 0.2
Larus spp.	2.2 ± 0.6	2.8 ± 1.1
Limosa spp.*	0.3 ± 0.1	2.8 ± 1.0
Numenius spp.	0.6 ± 0.1	0.6 ± 0.1
*Pluvialis squatarola****	0.2 ± 0.0	1.6 ± 0.4
Tringa spp.	0.9 ± 0.2	2.1 ± 0.6

t-test or *U*-test: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Arenaria interpres occurred in higher densities in restored than in non-restored marshes (Mann–Whitney *U*-test, $U = 83.0$, $P < 0.001$), while *P. squatarola*, *Calidris* spp. and *Limosa* spp. showed the opposite pattern (Mann–Whitney *U*-test: *P. squatarola*, $U = 74.5$, $P < 0.001$; *Calidris* spp., $U = 113.0$, $P < 0.01$; *Limosa* spp., $U = 136.0$, $P < 0.05$). The density of the other analysed groups was similar between restored and non-restored marshes (Table 3).

DISCUSSION

In agreement with our hypothesis, marshes restored with *S. maritima* and *Z. noltii* showed higher ecological diversity than non-restored marshes only 2 years after planting. This rapid response by birds may be related to the rapid growth of *S. maritima* and *Z. noltii* transplants. The lineal expansion of *S. maritima* rhizomes on bare sediments has been calculated to be 1.1 ± 0.0 cm month^{-1} in the restored area (Castillo & Figueroa 2009), and the spread of *Z. noltii* by seeds and rhizomes was very active (G. Curado, pers. obs.).

The availability of food seems to be the main environmental factor in determining the suitability of a particular habitat for marsh bird species (Weller 1994, Desholm 2000, Ma *et al.* 2007). *S. maritima* and *Z. noltii* act as marsh-structuring halophytes (Castellanos *et al.* 1994, Figueroa *et al.* 2003, Bouma *et al.* 2009), increasing habitat diversity, providing organic matter and stabilizing sediments (Salgueiro & Caçador 2007, Widdows *et al.* 2008). Thus, plantations would increase environmental heterogeneity in restored marshes, increasing the diversity of birds' foraging habitats (Weller & Spatcher 1965) because microhabitats are home for different invertebrates and fish species in low marshes (Nienhuis & Groenendijk 1986, Cardoso *et al.* 2007, MacKenzie & Dionne 2008, Parker *et al.* 2008). In addition, some birds such as geese feed directly on leaves and rhizomes of *Spartina* (Chung 1993) and of *Zostera* (Inger *et al.* 2006, Moore & Black 2006). However, because most shorebirds feed in intertidal mudflats without vegetation where invertebrates are more abundant (Davis & Moss 1984, Rosa *et al.* 2003), we must also consider that the secondary production of non-vegetated areas depends on adjacent vegetated marshes as a source of detritus for saprovore invertebrates (Valiela *et al.* 2000). In support of this, we recorded that restored marshes maintain higher diversity, densities and biomass of benthic macroinvertebrates compared to non-restored marshes (unpublished data). In addition, some macroinvertebrate groups are mainly associated with vegetated areas (Arocena 2007). On the other hand, Ruddy Turnstone showed high densities in restored marshes, which may be related to large numbers of shell fragments that increase the environmental heterogeneity (Whitfield 1990).

Our results met expectations that marsh birds colonise restored ecosystems quickly (Hemesath & Dinsmore 1993, Brawley *et al.* 1998, Passell 2000, Gallego-Fernández & García-Novo 2007, Raposa 2009). Avian community diversity metrics described in this study 2 years after restoration (about 1.63) were higher than those found in other restored salt marshes planted with *S. alterniflora* and other halophytes in the USA between 3 and 15 years after restoration (ecological diversity between 0.26 and 0.92; Melvin & Webb 1998, Armitage *et al.* 2007), and lower than those recorded in North American *S. alterniflora* mature restored marshes (12 years after restoration; ecological diversity between 1.83 and 2.12; Havens *et al.* 2002). Although both study locations showed high similarity in their communities (0.84 according with Sørensen similarity index), differences in ecological diversity were recorded. These differences between restored and non-restored marshes seemed to be related to changes in the relative abundance of certain species.

Non-restored marshes, partially colonized by invasive *S. densiflora* and containing extensive tidal mudflats with low vegetation cover, offered a more homogeneous environment, specifically favouring a few dominant bird species which exploited available resources very efficiently, increasing dominance and decreasing ecological diversity and evenness in comparison with restored marshes. For example, Dunlin *Calidris alpina*, the most abundant migrant shorebird in the Atlantic East (Smith & Piersma 1989), prefers intertidal mudflats without vegetation for feeding (Goss-Custard & Moser 1988), and in our study was much more abundant in non-restored than in restored marshes. This shorebird species was the highest contributor to the dissimilarity between bird communities in restored and non-restored marshes. Previous work has linked low bird diversity and species richness with plant invasions in marshes (Benoit & Askins 1999, Gan *et al.* 2009) and it has been shown that the bird communities recovered after removal of invasive species (Patten & O'Casey 2007).

The absence of some occasional species recorded in non-restored marshes compared to restored marshes may be related to high exposure to human impacts such as noise and the presence of pedestrians and vehicles in restored marshes. Many of the rarest bird species are very sensitive to human disturbance, and the presence of urban areas and other infrastructure can adversely affect some marsh birds (De Boer 2002, Rosa *et al.* 2003, Armitage *et al.* 2007). In addition, the proximity of the non-restored marshes to different ecosystems such as terrestrial pasturelands or salt pans, none of which occurred close to restored marshes because that space was occupied by infrastructure, may influence the presence of rare species such as Eurasian Buzzard *Buteo buteo* and Montagu's Harrier *Circus pygargus* that hunt for prey on neighbouring pasturelands, Black-Winged Stilt *Himantopus himantopus* which is typical of salt pans, or Eurasian Reed Warbler *Acrocephalus scirpaceus* which is associated with patches of Common Reed *Phragmites australis* (Cav.) Trin. ex Steud.

Our study helps to clarify how salt marsh restoration using *S. maritima* and *Z. noltii* in European estuaries enhance the bird communities in the short-term. However, studies analysing the relationship between salt marsh restoration and parallel changes in the macroinvertebrates and shorebird communities are required in order to improve our understanding about the development and maturation of restored marshes.

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