Comparing the diversity and composition of waterbird functional traits between natural, restored and artificial wetlands

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Summary

1. The restoration of degraded areas and the creation of artificial ecosystems have partially compensated for the continuing loss of natural wetlands. However, the success of these wetlands in terms of the capacity of supporting biodiversity and ecosystem functions is unclear. Research is needed to improve our understanding of the value of restored and constructed wetlands to functional diversity of freshwater fauna.

2. We compared natural, restored and artificially created wetlands present within the Doñana Natural Space, Spain and valued as important for waterbirds. We evaluated if these wetlands are equivalent in terms of waterbird functional trait diversity and composition, during both the wintering and breeding seasons. We modeled functional diversity measures and functional group species richness describing species diet, body mass and foraging techniques with GLMMs in 20 wetlands monitored between 2006 and 2011. We used three different statistical approaches to evaluate the robustness of our results.

4. Artificial wetlands constructed for conservation failed to reach the functional diversity of natural and restored wetlands. Unexpectedly, artificial ponds constructed for fish production performed better, and even exceeded natural wetlands for functional richness during winter. Fish ponds stood out as having a unique functional composition, connected with increase in richness of opportunistic gulls and decrease of species sensitive to high salinity. Overall, the functional structure of breeding communities was more affected by wetland type than wintering communities.

5. Our findings suggest that compensating the loss of natural wetlands with restored and artificial wetlands results in systems with altered waterbird-supported functions, such as seed dispersal or nutrient cycling. Protection of natural Mediterranean wetlands is vital to maintain the original diversity and composition of waterbird functional traits. Furthermore, restoration must be prioritized over the creation of artificial wetlands, which, even when intended for conservation, may not provide an adequate replacement.

Introduction

The loss of natural ecosystems by anthropogenic impacts has reached extreme proportions, causing severe declines in biodiversity and their associated ecosystem services (Albert et al., 2020). For example, wetlands have lost 43% of their area between 1997 and 2011, currently covering only 0.9% of the earth's surface (Costanza et al., 2014). Wetlands provide many ecosystem functions such as carbon storage, water purification, biodiversity conservation, food production, nutrient fixation, and flood prevention (Zedler & Kercher, 2005). The maintenance of these functions depends on physical, chemical and biological processes sustained by various groups of organisms that are part of the freshwater ecosystems (Millennium Ecosystem Assessment, 2005). However, these processes are being lost through extensive drainage, degradation, and fragmentation of natural wetlands (Dixon et al., 2016, Davidson et al., 2018).

The restoration of degraded areas and the creation of artificial ecosystems have been used to compensate for the loss of natural systems in both terrestrial and aquatic ecosystems, including wetlands (Race & Fonseca, 1996; Sudding, 2011). However, the success of the construction of wetlands in terms of the capacity of these areas in supporting ecosystem services is not well understood, especially because it depends on how wetland construction was executed (Moreno-Mateos et al., 2017; Wiegand et al., 2017). Also, restoration practices are often ineffective in recovering original levels of ecosystem functions in wetlands (Moreno-Mateos et al., 2012). Nevertheless, restored and artificial wetlands have become increasingly common, with constructed wetlands such as ricefields, reservoirs and fish ponds occupying extensive areas (Perennou et al., 2012; Pekel et al., 2016; Davidson et al., 2018). Given continuous loss of natural wetlands and increases in areas occupied by restored and artificial wetlands, it is vital to investigate to what extent these modified habitats sustain the original biological communities and their ecological functions.

As ecosystem processes depend on their biological components, changes in the diversity of functional traits present in animal (e.g. waterbird) or plant communities may be related to altered ecosystem functioning. Functional traits are characteristics of the organisms that express the way through which they interact with the ecosystem (Violle et al., 2007). In fact, trait-based approaches are the best option for increasing our understanding of ecosystem functions if the measurement of functions themselves is not possible (Gagic et al., 2015), e.g.

81 due to logistic or economic restraints. For this approach, it is possible to calculate
82 multifunctional diversity measures for a community, based on functional trait values for its
83 component species. The use of a functional diversity approach enables both the
84 understanding of which functional traits of a community are maintained, and how the
85 functional structure of this community may vary in space and time (Almeida et al., 2018,
86 2019). Understanding variation in functional diversity is important if we are to maintain
87 functions performed by the communities, and consequently the functions of the ecosystem
88 itself (Tilman et al., 1997; Diaz & Cabido, 2001). Here, we used different facets of functional
89 diversity to provide a complementary perspective, together describing the distribution of
90 species and their respective abundances within a functional space built from their functional
91 trait values.

92 Waterbirds are among the best known and most important animal communities in
93 wetlands, as they sustain various ecological functions including nutrient cycling, dispersal of
94 propagules, ecosystem engineering, and biological control (Green & Elmberg, 2014).
95 Maintaining their roles in wetlands is essential to sustain the functioning of these aquatic
96 ecosystems, as birds also regulate populations of other organisms such as fish (Gawlik, 2002;
97 Steinmetz et al., 2003), invertebrates (Hamilton et al., 2006; Rodriguez-Perez & Green,
98 2012), and aquatic plants (van Altena et al., 2016). Thus, birds can be important indicators
99 of the functions provided by wetlands (Amat & Green, 2010; Green & Elmberg, 2014).
100 Moreover, waterbird communities also represent a useful tool to investigate wetland
101 functional diversity, as they are easy to monitor and bird counts represent the best established
102 form of long-term environmental monitoring for many wetlands, as happens in the
103 Mediterranean region, and in many wetlands around the world protected as Ramsar sites
104 (Kleijn et al., 2014). We measured functional traits of waterbirds and assigned them to
105 different functional groups with respect to resource use, as birds perform most of their
106 ecological roles through resource acquisition and consumption (Sekercioglu, 2006; Green &
107 Elmberg, 2014).

108 Here, we evaluate functional structure (i.e., distribution of species and their
109 abundances in the functional trait space) and functional group richness (i.e., number of
110 species belonging to a group of species that obtain resources in a similar way) of waterbird
111 communities of natural, restored, and artificial wetlands in Doñana Natural Space, south-

west Spain. We considered restored wetlands as previously drained areas that were restored to a wetland state by removing drainage systems and that have a natural hydrology, while artificial wetlands were created on dry land or previously drained wetlands and are maintained with artificial hydrology. We divided artificial wetlands into two categories, separating those that were created for fish production from those that were primarily created for conservation purposes. Doñana is one of the most important areas for waterbirds in Europe and in the Mediterranean region, and many of its created and restored sites aim to benefit birds (Rendón et al., 2008; Sebastián-González & Green, 2014; 2016). Doñana holds a range of natural, restored and artificial wetlands within the same complex, allowing a meaningful comparison between these different habitat types. We expected that restored and artificial wetlands would not function as natural wetlands, but that restored wetlands would be more similar to natural wetlands than the artificial systems. Among the artificial wetlands, we expected that those designed with conservation purposes would function more similarly to natural wetlands than fish ponds.

We tested the hypotheses that: (i) natural wetlands support higher levels of waterbird functional diversity than restored and artificial wetlands; (ii) restored wetlands support higher waterbird functional trait diversity than artificial wetlands; and (iii) artificial wetlands created with conservation purposes support higher functional diversity than fish ponds. We tested these hypotheses separately for wintering and breeding waterbird communities. For a better comprehension of the functional structure of the communities, we used four measures of functional trait diversity as complementary indices (Mason et al., 2005; Laliberté & Legendre, 2010) and investigated differences in functional group richness between wetland types. We expected that (iv) artificial wetlands used for fish production would only favor the occurrence of piscivorous species.

Methods

Study Area

The Doñana Natural Space (108 429 ha) is composed of a mosaic of aquatic and terrestrial environments located in the estuary of the Guadalquivir River, south-western Spain (Fig. 1). Situated in a floodplain fed by rain and river waters, its dynamics depend largely on a yearly variable rainfall that is concentrated mainly between October and March. Its climate

is Mediterranean with Atlantic influence, presenting mild and short winters and dry, hot summers. The area is catalogued as a Ramsar site, a European Union Special Protected Area, and partly as a UNESCO World Heritage Site (Green et al., 2017, 2018). Doñana is one of the last major natural coastal ecosystems in Europe and has international importance for breeding, staging and wintering birds. Doñana's aquatic ecosystems are highly heterogeneous and today form a complex mosaic of natural, restored, and artificial wetlands (Green et al., 2017, 2018). To evaluate differences in bird functional traits among these wetland types, we evaluated 5 natural and 5 restored wetlands, together with 5 fish ponds and 5 other artificial wetlands distributed across the protected area (Fig. 1, Table S1). We have used all the sites for which similar monitoring data was available, except for the fish ponds, for which we randomly chose five sites from the 36 monitored fish ponds. This was because we wanted a balanced design, and such large numbers of sites were not available for the other wetland categories. Furthermore, we wanted our results to be comparable to earlier work on taxonomic and phylogenetic measures of waterbird diversity using the same study sites (Sebastián-González & Green, 2016).

The original Doñana marsh was extensively drained during the 20th century, during which large parts of it were transformed into agricultural areas, rice fields, salt pans and fish farms (Rendon et al., 2008). Restoration projects took place in the late 20th and beginning of the 21st centuries, aiming to recover part of the former hydrology of the wetlands (García & Marín, 2006). The natural and restored wetlands we studied are mainly temporary natural marshes fed by surface flow and direct rainfall, with some dune ponds fed by aquifers. These habitats, which have a natural or seminatural hydrology, flood during the rainy season and usually dry out between July and October (Díaz-Delgado et al., 2016; Green et al., 2017). Wetland restoration and construction took place during a joint ecotourism-aquaculture project in Veta la Palma in the early 1990s (two restored sites and seven constructed sites), and a project to recover some of the original hydrology of the marsh system in the early 2000s (three restored sites and two constructed sites, García & Marín, 2006). One of the artificial sites was created separately to provide an attraction at a visitor center for Doñana National Park (Santoro et al., 2010). The artificial wetlands were created by the construction of dykes to allow the water level to be raised above surrounding land. Thus, although located in former temporary marsh areas, they had an artificial hydrology and relatively stable water levels.

Five of them were extensive fish ponds used to raise estuarine fish of commercial value, in which the food supply available to waterbirds has been relatively well studied (Rodríguez-Pérez & Green 2012, Walton et al., 2015a, 2015b; Sebastian-Gonzalez & Green, 2017).

Waterbird surveys

Wetlands were surveyed monthly between 2006–2011 by experienced observers as part of a monitoring program carried out by the Doñana Biological Station (EBD-CSIC, <http://icts.ebd.csic.es/documents/20181/231243/Protocolo_20_Censos+terrestres+aves+acuaticas.pdf/30df6a74-929a-4bec-8241-57ffb811f993 >). All aquatic birds in the wetlands were identified to species and counted, while those in flight were excluded. Every wetland was visited on a vehicle, in a single morning, and surveyed from one or more positions along the shoreline with binoculars (8 x 50) and a telescope (20 x 60). Counts were performed monthly during breeding (from April to June) and wintering (from December to February) seasons, between the 10th and the 20th of each month. The order of the counted sites varied among months. We considered data on each season in each year, by summing waterbirds found in the three surveys performed within the same season and the same year into one datum.

Functional traits

To calculate functional diversity, we used information on 15 functional traits that represent different aspects of the waterbirds ability to exploit resources (Table 1, Table S2). Information for all traits were sourced from Wilman et al. (2014). Body mass strongly relates to metabolic rate, indicating the amount and size of food required for a given individual (Luck et al., 2012). Percentages of diet composition and stratum use indicate the main items consumed by species, and where they are acquired, and thus are related to functions performed by species such as population control, propagule dispersal, scavenging, nutrient cycling, and ecosystem engineering (Green & Elmberg, 2014). Plasticity of diet and strata represent the level of specialization associated with a given species and were calculated as the number of different diet items (from 1 to 7: invertebrates, fish, vertebrates, carcasses, fruits, seeds or plant material) and number of strata used (from 1 to 5: below surface, around surface, ground, understory or mid-high). Higher values for both plasticities indicate less

dependence on a particular food item or stratum (Luck et al., 2013), although it is important to note that these data were not collected from the study area (where no such data were available), but from the literature. To calculate functional diversity indexes, percentages of diet items and of feeding strata were assigned weights so that all percentages were put together to represent the trait sets ‘diet items’ and ‘feeding strata’. For this, we calculated for each percentage the weight: $W_i = 1/N_i$, where N_i is the number of traits (seven diet items and five feeding strata) by which the trait set i was divided (Laliberté & Legendre, 2010). For example, the trait set “diet items” was comprised of seven traits (each of the items with percentage data), each of them with weight $1/7$, so that when combined, they complete the “weight of one” representing diet items.

Functional diversity and functional groups

In order to evaluate changes in functional structure, we calculated functional diversity measures for each wetland ($n=20$), in each year, for wintering and breeding counts. For each season in each year, we calculated four multidimensional indices: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) (Mason et al., 2005; Villéger et al., 2008), and functional dispersion (FDis, Laliberté & Legendre, 2010) to describe the functional structure of the communities. Functional richness (FRic) represents the size of the functional space occupied by a community and is calculated as the convex hull volume of the community (Fig. 2a). It considers the most extreme points of the functional space, and is correlated with species richness. Functional evenness (FEve) describes how evenly the abundances of species are distributed in the functional space (Fig. 2b). Low values of FEve indicate that functional differences between species are very variable (Villéger et al., 2008). Functional divergence (FDiv) defines how far the abundances of the species are from the center of the functional space (Fig. 2c). Low levels of FDiv are associated with a low niche differentiation among species, meaning that the most abundant species are very similar and may compete (Mouchet et al., 2010). Functional dispersion (FDis) is the dispersion of species in the trait space, and represents the mean distance of species to the centroid of the community, weighted by their abundances (Fig. 2d; Villéger et al., 2008; Laliberté & Legendre, 2010). Decreases in FDis mean that abundances of species with trait values further

away from the centroid decreased, indicating lower use of the margins of the functional space.

We calculated the functional space from a PCoA constructed from traits of all species from all years, from both wintering and breeding counts. We computed the functional distances between pairs of species using the Gower distance (Gower, 1966). Then, we performed a Principal Coordinates Analysis (PCoA; Gower, 1966) on the functional distance matrix and used the PCoA axes to represent new trait values. For the FRic calculation, only two PCoA axes were used, as the number of axes cannot be superior to the number of species, and some sites presented low species richness. We estimated the functional diversity indices from PCoA axes and species abundance data. Computing the functional space was not possible for 12 of the 248 samples containing fewer than three species, so they were removed from further analyses. We calculated functional diversity indexes with the dbFD function from the FD package (Laliberté & Legendre, 2010) within the R environment, version 3.0.1 (Laliberté et al., 2014; R Core Team, 2017).

To evaluate whether the functional composition of the waterbird community varied among wetland types, we classified all occurring species into functional groups, according to the manner in which these species acquire their resources in the water. We considered eight functional groups: small wading birds, large wading birds, vegetation gleaners, dabbling ducks, diving ducks, opportunistic gulls, surface fishers and diving fishers (see Table 2 for the species belonging to each functional group). These groups were similar to those defined by Ramírez et al. (2018) for a larger geographical area, although we excluded the raptor group as they rarely occurred in our study wetlands. The species *Anser anser* was also removed from the analyses as it was not considered to belong to any of the identified groups. We calculated the absolute species richness for each functional group as the total number of species registered in each wetland (n=20), in each year, for wintering and breeding counts. To compensate for the possible effect of wetland size in our analysis we have also considered the relative species richness for each functional group, calculated as the richness for group i divided by total species richness in the sampled site. This was calculated for each functional group and also for each wetland in each year, for wintering and breeding counts. Relative species richness indicates how much of the total richness of a community is

represented by a given functional group, so that changes in it represent changes in the representativeness of each group in the total community.

Data analyses

We used Generalized linear mixed models (GLMMs) to compare waterbird functional diversity and functional group richness between wetlands of four types: natural, restored, artificial created for conservation purposes, and artificial created as fish ponds, separately for wintering and breeding seasons (*Approach 1*). We constructed models for all the functional diversity indexes and for absolute and relative richness of each functional group. Mixed effects models allow a random term to be included in the model, which can be used to account for non-independence between some of the samples (Zuur et al., 2009). As our data involved repeated samples in many years for each site, we used the sampled year as a random variable to control for possible temporal pseudoreplication. As restored wetlands occupied larger surface areas when fully inundated than other wetlands (see Fig. 1), we included total waterbird count per site as a covariate in the models to account for these differences in wetland size. Thus, the analyses test for differences in functional diversity for a given bird abundance. We used the Gaussian distribution in functional diversity models and the poisson distribution for the functional group models. All models were constructed with the glmer function of the lme4 package (Bates et al., 2015) and overdispersion was checked for the poisson models with the function dispersion_glmer of the blmezo package (<https://stat.ethz.ch/pipermail/r-sig-mixed-models/2011q1/015392.html>).

For each functional diversity index and functional group, we constructed two models, one null model including only the random term and the covariate, and a second model also including the variable “wetland type” (natural, restored, artificial created for conservation and artificial fish ponds). We compared each pair of models using the Akaike information criterion (AIC). We constructed confidence intervals and performed pairwise comparisons among least-squares means of the wetland types for each model using the lsmeans function of the lsmeans package (Lenth, 2016).

To verify the robustness of our results, we used two other analytical approaches. First, using a randomization approach (*Approach 2*), we recalculated the GLMMs for each season using year as a random factor, abundance as a covariate, and the wetland type as explanatory

variable, but randomizing the position of observed values of functional diversity indices and functional group richness. We repeated this analysis 1000 times to identify the range of values that the coefficient of the explanatory variable can take for a random relationship between the dependent and explanatory variables. We used standardized effect sizes (SES) to evaluate the probability that the models with the randomized variables would produce coefficients for wetland type with a value of the magnitude observed in our GLMM model.

Finally, we also compared functional diversity between the different wetland types in each season while removing the effect of repeatedly measuring the same wetland through time (*Approach 3*). To do this, we repeated the GLMMs with year as a random variable, abundance as a covariate, and wetland identity as an explanatory factor. We calculated the predicted diversity of each wetland ($n = 20$) according to the model estimates and performed ANOVAs to compare these predicted values between the four wetland types (natural, restored, artificial created for conservation and artificial fish ponds). We performed post-hoc Tukey HSD tests when ANOVAs had significant results.

Results

A total of 2 353 605 individuals from 88 species were recorded in 12 (two per year during six years) surveys for all the 20 wetlands in Doñana (see Table S3). The inclusion of the wetland type variable (to distinguish between natural, restored and the two types of artificial sites) in the GLMMs (*Approach 1*) significantly improved the model fit for most of the functional diversity indexes and functional groups (Table 3). Results from our three analytical approaches mostly agreed, supporting the existence of functional differences among the waterbird communities of the four wetland types. In addition, differences between wetland types were generally larger during the breeding season (Figs 3-5, Tables S4-S6).

Functional diversity indices

For functional diversity indexes of wintering communities, wetland types improved model fit only for Functional Richness (FRic), while for breeding communities wetland type inclusion improved model fit of all functional diversity indexes. Surprisingly, highest FRic values were found in restored wetlands and artificial fish ponds. According to all analytical approaches, breeding communities were mostly different in artificial wetlands created for

conservation, with lower values of FRic, Functional Divergence (FDiv) and Functional Dispersion (FDis) and a trend towards higher Functional Evenness (FEve, Fig. 3).

Functional groups

For two (small wading birds and opportunistic gulls) of the eight functional groups during winter, we found that model fits were improved by “wetland type” inclusion for both absolute (i.e. number of species) and relative (i.e. proportion of all species) richness (Figs. 4a, k, 5a, k). These models suggested lower small wading bird species richness for natural wetlands, and higher opportunistic gull richness for artificial fish ponds. Large wading birds were found to present higher richness in restored wetlands according to models fitted to absolute richness, but this pattern was not supported in the relative richness models (Figs. 4c, 5c). Finally, differences in diving ducks richness were only true when relative richness was evaluated, with artificial wetlands built for conservation presenting lower values of relative richness in relation to natural wetlands (Figs. 4i, 5i).

During the breeding season, both absolute and relative richness model fits were improved by “wetland type” inclusion for small wading birds, large wading birds, dabbling ducks, diving ducks, opportunistic gulls, surface fishers and diving fishers. In other words, “wetland type” was important for all functional groups except vegetation gleaners, for which models did not support differences among wetland types in any case; (Figs. 4, 5). Although the exact differences among wetland types varied a little according to the way in which richness was considered (usually with predicted values for restored wetlands being lower and those of artificial wetlands built for conservation being higher for models fitted with relative richness), general results were very similar. We found lower small wading bird richness in natural wetlands, but lower large wading bird richness in artificial fish ponds (Figs. 4b, d, 5b, d). Both dabbling and diving ducks had higher than expected relative richness (Approach 3) in natural wetlands (Figs. 4h, j, 5h, j). Opportunistic gulls showed consistently higher richness in fish ponds (Figs. 4l, 5l). Finally, surface fishers showed lower richness in artificial wetlands built for conservation (Figs. 4n, 5n), while diving fishers showed lower richness in fish ponds (Figs. 4p, 5p).

Discussion

Our results show that artificial wetlands constructed for conservation purposes support waterbird communities with a lower functional diversity (FDiv, FDis and FRic) than those in natural and restored wetlands in Doñana Natural Space. Furthermore, the level of functional diversity supported by artificial wetlands varies greatly between those constructed for conservation and fish ponds. Fish ponds performed surprisingly well, and were not outperformed by natural wetlands for any of the diversity indices. Indeed, together with restored wetlands, they had higher functional richness than natural wetlands in winter.

Because created wetlands designed for conservation purposes (Art) performed worse than fish ponds (Afp), some of our initial hypotheses were not supported. The former perhaps performed badly owing partly to a combination of relatively small size (in some cases) and artificial hydrology (constructed using dykes to hold surface or ground water that was pumped in, topping up water occasionally after levels drop through evaporation). Although also based on dyke construction, fish ponds have a more sophisticated water circulation system with input from the Guadalquivir estuary, circulating water through the ponds, and then an outflow into a lower part of the estuary, providing a continuous supply of nutrients and dissolved oxygen to benefit fish stocks (Walton et al., 2015a). However, the reasons for these unexpected differences in performance require further investigation.

Important seasonal effects were observed for the differences among wetland types, which were more pronounced during the breeding season. This may be because the breeding season is when birds are more faithful (i.e. less mobile, with a smaller home range) to the wetlands where they are counted. While wintering birds typically move daily among different water bodies of a wetland complex, breeding individuals are less mobile, and tend to feed in their breeding areas (Bowler et al., 2005; McDuie et al., 2019). Many wintering waterbirds are also nocturnal foragers that move to different resting sites during the day (Herring & Collazo, 2005; Kleyheeg et al., 2017; Guillemain et al., 2010). For example, from October to December wintering ducks and godwits roosting in Doñana fish ponds often fly to feed in ricefields during the night (Kloskowski et al., 2009; Márquez-Ferrando et al., 2014). In contrast, lesser black-backed gulls *Larus fuscus* make similar movements to feed in ricefields during the day (Martín-Vélez et al., 2020). Thus, many wintering birds in our study area may be present at a given wetland, but not functionally active in it in terms of consumption, and thus not dependent on wetland characteristics other than quality of roosting sites. On the other

hand, these waterbirds remain functionally active in any wetland they visit in terms of nutrient transport, and may contribute to eutrophication of wetlands (Martín-Vélez et al., 2019). It is also possible that differences among wetland types were more pronounced during the breeding season owing to greater spatial heterogeneity in food supply, salinity and other environmental variables. However, while high summer temperatures and lack of rainfall may be expected to generate such heterogeneity, the hydrological conditions in natural and restored wetlands are also highly variable during winter due to fluctuating rainfall (Díaz-Delgado et al. 2016).

The only groups that presented consistent habitat use in both seasons were those of small wading birds and opportunistic gulls. Opportunistic gulls showed higher richness in fish ponds, which is likely related to their preference for establishing breeding colonies in this area (as for other Laridae, Ramírez et al., 2012) as well as their use of ponds as roost sites when making daily flights to feed in ricefields or landfills outside our study area (Martín-Vélez et al., 2020). Small wading birds were less represented in natural wetlands than in all other wetland types. This may be related to the lower salinity of natural wetlands, as these birds are adapted to feed in saline environments, which in Doñana also support higher densities of benthic invertebrates, their main prey (Frisch et al. 2006; Kloskowski et al., 2009; Ramírez et al., 2018).

Functional diversity indices

Even though we controlled for differences in waterbird abundance among the wetland types in our models, it is possible that the greater abundance in restored wetlands (due to their larger surface area, see also Sebastián-González & Green, 2014) still influenced functional richness. FRic is mathematically dependent on species richness and is highly influenced by outliers (Villéger et al., 2008). Therefore, the high FRic found for restored wetlands (Fig. 3) must be treated with caution. Our FRic models also indicated that fish ponds support species with different combinations of functional traits compared to other wetland types, especially during winter. Nevertheless, these functionally different species were probably present at low abundances, as neither FDiv nor FDis were higher in fish ponds. During the breeding period, the model for FRic indicated that communities in Art wetlands were formed by functionally similar species (Fig. 3b), although this may be linked to their

smaller areas and consequently a lower species richness (Sebastián-González & Green, 2014). Moreover, the most abundant species in Art wetlands shared similar functional traits (Fig. 3f, h). Overall, Art consistently showed lower functional diversity indices during the breeding season, indicating that their waterbird communities may support less ecosystem functions than do natural and restored wetlands as well as fish ponds in Doñana.

Although the functional space occupied by waterbird communities in any wetland type was generally similar for breeding and wintering periods, there was a higher proportion of individuals with extreme trait combinations during the breeding period, as indicated by generally higher FDiv and FDis values. This suggests that (except for Art) the most abundant breeding species tend to be more functionally different from one another than the most abundant wintering species in all wetland types. This may indicate lower inter-specific competition during winter, although Sebastián-González & Green (2017) found no evidence in Afp ponds for a seasonal change in interspecific competition based on co-occurrence of closely related species. Similarly, Bidwell et al. (2014) found no evidence of interspecific competition on spatial distribution of breeding ducks in a prairie wetland complex. Alternatively, the seasonal changes in FDiv and FDis may be related to the particularly high abundances of several duck species in winter (Rendon et al., 2008). Nevertheless, such seasonal changes may be subject to long term trends, as happened in wetlands of eastern Spain over a 28-year period, where FDis increased for wintering waterbird communities, whereas FDiv decreased for breeding communities (Almeida et al., 2019).

Functional groups

In natural wetlands, and especially in the breeding season, the groups that tended to have higher than expected representativeness in the waterbird communities were dabbling ducks, diving ducks and diving fishers, while the groups with lower than expected representativeness were the small wading birds and opportunistic gulls. Interestingly, these were the groups that showed contrary trends in the other wetland types. In particular, fish ponds showed almost the exact opposite, with relative richness being lower than expected for dabbling ducks and diving fishers yet higher than expected for small wading birds and opportunistic gulls. Fish ponds provide good habitat for small wading birds owing to shallow areas ideal for larger birds such as godwits, stilts and avocets, together with occasional

drawdowns for pond maintenance (Márquez-Ferrando et al., 2014, Sebastian-Gonzalez & Green, 2017). Higher richness of ducks in natural wetlands is consistent both with previous analyses of aerial counts from Doñana that showed that many duck species favor natural marshes over fish ponds (Rendón et al., 2008), and with their negative relation with salinity across south-west Spain (Ramírez et al., 2018). This is likely related to both their avoidance of higher salinity wetlands for breeding (Gutierrez, 2014), and their dependence on seeds from the greater abundance and richness of wetland plants found in natural wetlands (Grillas et al., 1993; Soons et al., 2016). Diving fishers, such as grebes and terns may be favored by a higher diversity of macroinvertebrates in the natural wetlands, as well as the diversity of plants for nesting, both of which are related to the low salinity and are favored by high spatial and temporal variation in depth within this natural marsh system (Grillas et al., 1993; Green et al., 2018). It may seem paradoxical than diving fishers had lower richness in fish ponds, but this may be related to lower and more stable depth in these wetlands.

In Art wetlands, surface fishers seem to be replaced by large wading birds. The low richness of surface fishers in these sites may be connected with the relatively small size of the wetlands, as terns and slender-billed gulls *Chroicocephalus genei* form colonies in relatively large wetlands in Doñana (e.g. Ramírez et al., 2012). Large wading birds may be absent in Afp because of their preference for less saline wetlands (Ramírez et al., 2018). The patterns found across south-west Spain by Ramírez et al. (2018) help to explain many of our results as fish ponds are of higher salinity than other wetlands (Frisch et al., 2006), due to their inputs from the Guadalquivir estuary and management to favour estuarine fish (Walton et al. 2015a, 2015b). Large wading birds such as purple heron *Ardea purpurea*, squacco heron *Ardeola ralloides* and glossy ibis *Plegadis falcinellus* are strongly associated with low salinity habitats, and prey on large insects, amphibians, crayfish and other species absent in the high salinity fish ponds (Macias et al., 2004; Montesinos et al., 2008). One exception is the greater flamingo *Phoenicopterus roseus*, which occurs in all wetland types but is particularly abundant in saline habitats such as Afp (Rendón et al., 2008).

Results for absolute and relative richness of different functional groups mostly coincided, and the differences between them were mainly for restored wetlands and Art. Comparative values for wading birds and ducks were higher in restored and lower in Art wetlands for absolute richness, but not for relative richness (i.e. the proportion of species

present that belonged to a given group). These differences may be caused by an influence of size differences in richness for these groups, as restored wetlands were the largest in our study system and some Art wetlands are the smallest. Nevertheless, by using relative richness we were able to remove any effect of wetland size.

Final considerations and conclusions

Artificial wetlands such as fish ponds, salt ponds or ricefields may be preferred as feeding habitat and support high numbers of individual species at specific times of the year (Masero, 2003; Márquez-Ferrando et al., 2014; Martín-Velez et al. 2020), showing that they have an important role for waterbirds in specific situations. Furthermore, differences in rainfall patterns among years may change the importance of each wetland type for birds, according to habitat availability, e.g. fish ponds act as a refuge for waterbirds during droughts (Kloskowski et al., 2009). Since all the studied ponds are part of one same wetland complex, birds may move among them taking advantage of the large variety of habitat options in close proximity. This intense movement among ponds enables birds to make different uses of each wetland type. Probably, differences in waterbird functional diversity would be even stronger among the wetland types if they were not part of a same wetland complex.

Although functional diversity indices showed no difference between fish ponds and natural wetlands, fish ponds showed differences in terms of functional group richness, favoring opportunistic species and limiting the richness of piscivorous birds such as large wading birds and diving fishers. Functional structure and composition have been shown to vary independently (Almeida et al., 2018). Hence, our results indicate that waterbird functional traits lost in fish ponds are substituted by other trait combinations, in a turnover that keeps functional structure levels similar to those of natural wetlands, but which reflects a different use of the wetlands by the birds. Likewise, habitat alterations have been found to selectively change functional composition for a wide range of other aquatic organisms such as plants, zooplankton or benthic invertebrates (Januschke et al., 2014; Baattrup-Pedersen et al., 2016; Braghin et al., 2018).

We recorded significant differences in functional diversity between wetland types, indicating differences in functions performed by waterbirds that may lead to differences in ecosystem functioning. Therefore, compensating the loss of natural wetlands with restored

and artificial wetlands can lead to systems with altered waterbird supported functions. Although restored wetlands and fish ponds are surprisingly resilient in their functional diversity, efforts to protect natural wetlands are more likely to be effective at maintaining the original functional diversity of waterbirds. Artificial wetlands constructed specifically for conservation aims performed especially badly, possibly due to hydrology, low productivity and/or small size. Artificial wetland use also affects community composition in terms of functional groups, and further investigation is required to improve understanding of to what extent waterbird functional diversity is supported by artificial wetlands in general. This requires research carried out at different spatial scales (both in the breeding and wintering range of migratory species, exploiting international censuses e.g. Pavon-Jordan et al. 2019), and covering major classes of wetlands not included in our study, such as reservoirs, ricefields or solar salt ponds. Wetlands constructed for conservation aims such as bird watching should also be compared with natural wetlands in other study areas, to establish whether our results reflect a widespread phenomenon and a need to rethink wetland design for conservation.

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Data Availability Statement

Data used in this study are available under request in the ICTS-RBD repository
<http://icts.ebd.csic.es/infraestructura-de-datos>

Conflict of Interest Statement

The authors have no conflict of interest to declare.

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Table 1. List of the functional traits compiled for waterbird species. Traits were sourced from Wilman et al. (2014), and are not based on data collected in the study area.

Functional trait code	Functional trait definition
Invertebrates	Percentage of diet composed of invertebrates
Fish	Percentage of diet composed of fish
Vertebrates	Percentage of diet composed of vertebrates
Carcasses	Percentage of diet composed of carrion
Fruits	Percentage of diet composed of fruits
Seeds	Percentage of diet composed of seeds
Plant material	Percentage of diet composed of other plant material
Diet plasticity	Number of items present in diet
Below surface	Percentage use of water below surface stratum for feeding
Around surface	Percentage use of water around surface stratum for feeding
Ground	Percentage use of ground stratum for feeding
Understory	Percentage use of understory stratum for feeding
Midhigh	Percentage use of midhigh stratum for feeding
Strata plasticity	Number of strata used in food acquisition
Body mass	Body mass in grams

769 Table 2. Functional groups considered in this study, respective codes, and waterbird species
 770 belonging to them. Species that breed regularly in the study area are indicated with an
 771 asterisk.

Functional group	Code	Species
Small wading birds	SWB	<i>Actitis hypoleucos</i> , <i>Arenaria interpres</i> , <i>Calidris alba</i> , <i>Calidris alpina</i> , <i>Calidris canutus</i> , <i>Calidris ferruginea</i> , <i>Calidris minuta</i> , <i>Calidris pugnax</i> , <i>Calidris temminckii</i> , <i>Charadrius alexandrinus</i> *, <i>Charadrius dubius</i> *, <i>Charadrius hiaticula</i> , <i>Gallinago gallinago</i> , <i>Glareola pratincta</i> *, <i>Himantopus himantopus</i> *, <i>Limosa lapponica</i> , <i>Limosa limosa</i> , <i>Numenius arquata</i> , <i>Numenius phaeopus</i> , <i>Pluvialis apricaria</i> , <i>Pluvialis squatarola</i> , <i>Recurvirostra avosetta</i> *, <i>Tringa erythropus</i> , <i>Tringa glareola</i> , <i>Tringa nebularia</i> , <i>Tringa ochropus</i> , <i>Tringa stagnatilis</i> , <i>Tringa totanus</i> *, <i>Vanellus gregarius</i> , <i>Vanellus vanellus</i> *
Large wading birds	LWB	<i>Ardea alba</i> *, <i>Ardea cinerea</i> *, <i>Ardea purpurea</i> *, <i>Ardeola ralloides</i> *, <i>Botaurus stellaris</i> *, <i>Bubulcus ibis</i> *, <i>Egretta garzetta</i> *, <i>Ixobrychus minutus</i> *, <i>Nycticorax nycticorax</i> *, <i>Phoeniconaias minor</i> , <i>Phoenicopterus roseus</i> *, <i>Platalea leucorodia</i> *, <i>Plegadis falcinellus</i> *
Vegetation gleaners	VGI	<i>Fulica atra</i> *, <i>Fulica cristata</i> *, <i>Gallinula chloropus</i> *, <i>Porphyrio alleni</i> , <i>Porphyrio porphyrio</i> *, <i>Rallus aquaticus</i> *
Dabbling ducks	DbD	<i>Anas acuta</i> *, <i>Anas crecca</i> , <i>Anas platyrhynchos</i> *, <i>Mareca penelope</i> , <i>Mareca strepera</i> *, <i>Marmaronetta angustirostris</i> *, <i>Spatula clypeata</i> , <i>Spatula discors</i> , <i>Spatula querquedula</i> , <i>Tadorna tadorna</i> *
Diving ducks	DvD	<i>Aythya ferina</i> *, <i>Aythya fuligula</i> , <i>Aythya nyroca</i> *, <i>Netta Rufina</i> *, <i>Oxyura leucocephala</i> *
Opportunistic gulls	OpG	<i>Chroicocephalus ridibundus</i> *, <i>Larus fuscus</i> , <i>Larus michahellis</i> *
Surface fishers	SfF	<i>Chlidonias hybrid</i> *, <i>Chlidonias leucopterus</i> , <i>Chlidonias niger</i> *, <i>Chroicocephalus genei</i> *, <i>Gelochelidon nilotica</i> *, <i>Hydrocoleus minutus</i>
Diving fishers	DvF	<i>Hydroprogne caspia</i> , <i>Phalacrocorax carbo</i> , <i>Podiceps cristatus</i> *, <i>Podiceps nigricollis</i> *, <i>Sternula albifrons</i> *, <i>Tachybaptus ruficollis</i> *

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Table 3. Generalized linear mixed models of waterbird functional diversity indexes and of absolute and relative species richness (SR) of functional groups in relation to wetland type for breeding and wintering seasons. All models include abundance as a covariate and year as a random variable. We present the coefficients of the models for the covariate, the explanatory variable, and the value of the ΔAIC between the null models and the models including wetland type. Natural wetlands are aliased. Negative ΔAIC values indicate lower AIC for the null model. See Table 2 for details of abbreviations of functional groups and Fig. 2 for diversity indices.

Index	Intercept	Abundance	Restored	Artificial for conservation	Artificial Fish pond	ΔAIC
Wintering						
<i>Diversity indices</i>						
FRic	0.5080	0.0568	0.1656	-0.0329	0.1898	17.66
FEve	0.4155	-0.0491	-0.0021	0.0392	-0.0074	-3.63
FDiv	0.6557	-0.1005	-0.0122	-0.0427	0.0448	-1.76
FDis	0.1082	-0.0076	0.0127	-0.0053	0.0127	-0.53
<i>Functional groups</i>						
SWB SR	1.0392	0.1811	0.6128	0.2472	0.3972	18.42
LWB SR	1.222	0.093	0.4199	-0.1629	0.0261	16.67
VGl SR	0.6061	0.0000	0.0357	-0.0561	0.2001	-4.38
DbD SR	1.4392	0.2399	-0.1183	-0.3357	-0.2015	0.62
DvD SR	0.2432	0.2113	-0.0156	-0.3421	-0.0325	-3.42
OpG SR	-0.1084	0.1305	0.2449	-0.9996	0.7251	30.49
SfF SR	-3.9205	0.612	2.6067	0.1355	2.2153	10.65
DvF SR	0.4667	0.1328	0.2572	-0.071	0.2514	-1.37
SWB relative SR	0.1516	0.01	0.0281	0.028	0.028	8.43
LWB relative SR	0.2003	-0.0206	0.0441	0.0408	-0.009	0.24
VGl relative SR	0.1106	-0.0136	-0.0377	-0.0171	-0.0295	-1.52
DbD relative SR	0.2609	0.0137	-0.0841	0.0321	-0.0743	7.62
DvD relative SR	0.0875	0.0051	-0.0374	-0.051	-0.0212	6.48
OpG relative SR	0.0447	-0.0007	0.0075	-0.0339	0.0592	46.72
SfF relative SR	0.0016	0.0064	0.0095	-0.0004	0.0111	4.13
DvF relative SR	0.0949	-0.0027	-0.0007	-0.0224	0.014	-1.38
Breeding						
<i>Diversity indices</i>						
FRic	0.5358	0.0250	0.1334	-0.1246	0.0689	24.06
FEve	0.4789	-0.0411	-0.0051	0.0787	-0.0011	2.03

FDiv	0.8610	0.0021	-0.0240	-0.1658	0.0021	31.87
FDis	0.1447	-0.0101	0.0112	-0.0397	-0.0075	23.69
<i>Functional groups</i>						
SWB SR	1.2145	0.1982	0.6903	0.0628	0.4039	8.45
LWB SR	1.7387	-0.0305	0.3105	-0.1079	-0.465	40.2
VGl SR	0.5506	0.0104	0.3339	-0.1435	-0.1651	2.71
DbD SR	1.1557	0.0738	0.0262	-0.4519	-0.3203	6.53
DvD SR	0.5888	0.0207	-0.1287	-0.691	-0.0149	5.54
OpG SR	-0.5072	0.0985	0.9167	-0.3153	1.1718	36.7
SfF SR	0.4094	0.1293	0.291	-0.5748	0.1507	9.51
DvF SR	0.3099	-0.0419	0.3306	-0.1626	-0.5022	6.99
SWB relative SR	0.1569	0.0137	0.0375	0.0369	0.037	3.54
LWB relative SR	0.3011	-0.0352	-0.0092	0.1124	-0.1137	42.57
VGl relative SR	0.089	-0.0032	-0.0019	-0.0026	-0.0098	-5.47
DbD relative SR	0.1601	-0.0023	-0.0408	-0.0066	-0.0366	5.13
DvD relative SR	0.0988	-0.0031	-0.0415	-0.0533	0.0003	23.16
OpG relative SR	0.0281	0.0044	0.0262	-0.0122	0.0836	74.95
SfF relative SR	0.0741	0.0091	-0.0022	-0.0454	0.0101	18.74
DvF relative SR	0.0769	-0.0049	-0.0106	-0.0225	-0.0371	1.89

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Figure 1. Location of the studied wetlands at the Doñana Nature Reserve, Southern Spain. Polygons represent maximum flooded areas for each wetland and do not correspond to actual wetland sizes during most of the study period, especially for the restored wetlands. Sampled sites are represented by numbers. Towns and roads are represented in grey. See wetland identification in Table S1.

Figure 2. Representation of functional diversity indices in the community trait space. For simplification, here functional space is constructed based on only two traits. Points represent species, which are plotted according to their trait values and with diameters proportional to their abundances. (a) Functional richness (FRic) is the amount of functional space filled by the community, calculated as the convex hull volume of the community (grey polygon). (b) Functional evenness (FEve) represents the regularity of the distribution of species' abundances in functional space, calculated as the minimum spanning tree (represented by the dashed line) linking species. (c) Functional divergence (FDiv) is the degree to which the abundance of a community is distributed towards the extremities of the occupied trait space, measured as the mean distance of all species to the center of gravity of the community (represented by the large, open circle). (d) Functional dispersion (FDis) is the mean distance of species (weighted by their abundances) to the centroid of the community.

Figure 3. Boxplots of predicted functional diversity indices for natural (Nat), restored (Res), artificial created for conservation (Art) and artificial fish pond (Afp) wetlands according to models in Table 2. The graphs show the predicted value and 0.95 confidence interval for each wetland type. Black and green letters above the bars represent results from post-hoc tests from approaches 1 and 2, respectively (see methods section). When letters are not shared, there is a statistically significant difference between wetland types, according to post-hoc tests from Table S4 (black letters) and Table S6 (green letters). Predicted value circles are colored according to Standardized Effect Size (SES) results from approach 3 (see Methods and Table S5) in orange (observed values are higher than expected at random), black (observed values according to expected at random) and blue (observed values lower than expected at random).

Figure 4. Boxplots of predicted absolute richness (SR) of each waterbird functional group for natural (Nat), restored (Res), artificial created for conservation (Art) and artificial fish pond (Afp) wetlands according to models in Table 2. The graphs show the predicted value and 0.95 confidence interval for each wetland type. Black and green letters above the bars represent results from post-hoc tests from approaches 1 and 2, respectively (see Methods). When letters are not shared, there is a statistically significant difference between wetland types, according to post-hoc tests from Table S4 (black letters) and Table S6 (green letters). Predicted value circles are colored according to SES results from approach 3 (see Methods and Table S5) in orange (observed values are higher than expected at random), black (observed values match those expected at random) and blue (observed values lower than expected).

830 Figure 5. Boxplots of predicted relative species richness (relative SR) of each waterbird
831 functional group for natural (Nat), restored (Res), artificial created for conservation (Art) and
832 artificial fish pond (Aff) wetlands according to models in Table 2. The graphs show the
833 predicted value and 0.95 confidence interval for each wetland type. Black and green letters
834 above the bars represent results from post-hoc tests from approaches 1 and 2, respectively
835 (see Methods). When letters are not shared, there is a statistically significant difference
836 between wetland types, according to post-hoc tests from Table S4 (black letters) and Table
837 S6 (green letters). Predicted value circles are colored according to SES results from approach
838 3 (see Methods and Table S5) in orange (observed values are higher than expected at
839 random), black (observed values match those expected at random) and blue (observed values
840 lower than expected).