A functional perspective for breeding and wintering waterbird communities: temporal trends in species and trait diversity

Waterbird functional diversity through time

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Abstract

Waterbird communities are prone to strong temporal changes both seasonally and annually, but little is known about how this affects their functional diversity and community assembly. Detecting temporal trends in taxonomic and functional diversity within (alpha diversity) and between (beta diversity) communities in breeding and wintering seasons could give insight into the ecological processes driving those trends. In this study, we investigated trends in wintering and breeding waterbirds within and between eleven wetlands in Mediterranean Spain, using a 28-year time-series up to 2017. We assessed the temporal trends in taxonomic and functional diversity measures, and compared observed functional diversity values with null expectations, in order to explore the mechanisms driving community assembly. We found increases over time in species richness and in the occupied functional space for both

wintering and breeding communities, indicating that species with distinct functional roles were added in both seasons. However, the distribution of the abundances in the functional space was different for breeding and wintering communities. Dissimilarity of species and functional traits decreased among wetlands, suggesting that some of the same functional traits were added to the different wetlands, increasing regional homogenization through time. This is reflected in increases over time in mean body mass, diet plasticity and in the importance of fish in waterbird diets, plus declines in the dietary importance of invertebrates and in plasticity of feeding strata. Furthermore, species composition between wintering and breeding communities, but not trait composition, has become more similar through time. Our results highlight that annual changes, and especially seasonal changes, in the composition of waterbird communities have different effects on their functional diversity, and are influenced by opposing community assembly mechanisms.

Keywords: beta diversity, functional structure, functional traits, Mediterranean, wetlands

Introduction

Quantifying and explaining changes in biological communities is a major challenge in ecology (Magurran and Dornelas 2010), and is the basis for forecasting future changes in biodiversity (Dornelas et al. 2012). Biological communities can be described using a wide variety of measures that take into account different aspects of biodiversity. To date, taxonomic measures, mainly species richness, have been the usual diversity aspects studied. The distribution of species and their abundances in functional space, i.e. the so-called functional structure of a community, is another important aspect of biodiversity that has gained attention during recent years (McGill et al. 2006, Naeem et al. 2012). Analyses of functional trait diversity may highlight patterns across ecosystems that are not apparent in taxonomic analyses (Boersma et al. 2016), as they better account for ecological differences among species. For example, changes in the distribution of species in the functional trait space may reveal the loss or gain of extreme trait values, the concentration of species abundances towards the extremes or the center of the occupied trait space, and the packing of individuals in the occupied space. These changes may alter the roles played by the community in the ecosystem. A set of complementary functional diversity indices may be used to identify different aspects of such changes (Mouillot et al. 2013).

As with taxonomic diversity, functional diversity can be measured both within (alpha diversity) and between (beta diversity) communities. The first component reflects the representativeness of a community in the trait space (Villéger et al. 2008, Laliberté and Legendre 2010). The second component represents the dissimilarity of functional composition between communities, and can be measured as the difference in functional space occupied by two or more communities (Villéger et al. 2011). Changes in beta diversity may indicate increases in homogeneity or heterogeneity of species and traits among communities.

Evaluating changes at both these levels of functional diversity gives insight into the environmental scale driving species and functional trait distributions (Mendez et al. 2012, Socolar et al. 2016). Moreover, investigating if trait distributions are dependent on species richness may reveal whether stochastic or deterministic ecological processes are acting on communities (Mouillot et al. 2007). Stochastic effects may indicate that observed diversity patterns are generated according to neutral processes (Hubbell 2001), while deterministic processes are niche-based. Deterministic processes are two-sided: on the one hand, interspecific competition limits similarity, favoring trait over-dispersion (MacArthur and Levins 1967); on the other hand, environmental filtering (Zobel 1997) selects which traits can persist, favoring trait grouping, as species present are likely to share filtered traits.

In the face of global environmental issues such as habitat loss and degradation or climate change, investigating temporal trends in diversity is one way to explore how such changes affect biological communities. Hence, long-term datasets are an essential resource in biodiversity research and monitoring (Mendez et al. 2012, Bonecker et al. 2013, Monnet et al. 2014). One of the aims of ecological monitoring is to detect changes in the structure and function of ecosystems, helping to detect and understand complex dynamic patterns (Magurran et al. 2010). Changes in diversity have a two-way relationship with the ecosystem, as biological communities are both products of environmental characteristics and interactions, and drivers of processes that maintain ecosystem functioning (Tilman et al. 1997, Diaz and Cabido 2007, Suding et al. 2008).

Waterbirds are among the best known ecological communities. They can be monitored with a unique degree of accuracy, in which all individuals can often be counted in wetland ecosystems with a clear boundary. Furthermore, they provide various ecological functions in wetlands including control of populations at lower trophic levels, propagate

dispersal and the resulting connectivity between different wetlands, ecosystem engineering, and scavenging (Green and Elmberg 2014, Green et al. 2016). At the same time, waterbirds are affected by high rates of wetland loss and degradation (Davidson 2014) that have caused population declines of many species (Wetlands International 2019). Furthermore, many waterbirds migrate during their annual cycle, resulting in seasonal changes in the assemblages in a given place, notably between the wintering and breeding periods. This poses a challenge to the study of waterbirds, as their assemblages may depend not only on local wetland conditions, but also on conditions of many other wetlands used during other stages of their annual cycle (Webster and Marra 2005). Although migration is well studied from individual and population perspectives, the communities that are composed by migrant and sedentary species have received little attention from the functional perspective. Thus, examining changes in the functional structure of waterbird seasonal communities over time (both within and between years, and between seasons) can help us better understand the dynamics of these communities (Barnagaud et al. 2017).

Strong temporal trends in the abundance of individual waterbird species and in total abundance have been documented in the Mediterranean region (Rendón et al. 2008, Mediterranean Wetlands Observatory 2012, Pagel et al. 2014, Martínez-Abraín et al. 2016), and other studies have addressed the relationship between taxonomic diversity and wetland management (Sebastián-González and Green 2016). However, despite the importance of Mediterranean wetlands and waterbird species, there is still no information on the functional diversity of waterbird communities in this region. In fact, the information on the functional diversity of waterbird communities in general remains scarce. To our knowledge, there are no studies on waterbird functional diversity that consider the entire avian community, only specific groups within it (e.g. wading birds, Almeida et al. 2017; and shorebirds, Mendez et

al. 2012). However, the waterbird community is composed of very distinct bird groups, and evaluating a single group of waterbirds gives an incomplete understanding of community changes and its consequences (Green and Elmberg 2014, Sebastián-González and Green 2014). In the face of wetland loss and degradation, and given the dependence of waterbirds on different wetlands along their migration routes, investigating waterbird trends at alpha and beta scales gives insights as to the factors driving changes in this community. Thus, ours is a unique study of changes in functional structure of a well-monitored group of organisms facing major habitat changes. Furthermore, most studies of taxonomic diversity of waterbirds focus on either the breeding season (e.g. Galewski and Devictor 2016) or the wintering period (e.g. Godet et al. 2011), whereas we compare breeding and wintering communities in the same wetlands.

We evaluated temporal trends in alpha and beta waterbird taxonomic and functional diversity along a 28-year data series of wintering and breeding communities at a regional scale in 11 protected wetlands in Comunidad Valenciana, Spain. Our approach allowed us to (i) investigate temporal changes in wintering and breeding waterbird communities within and among wetlands, considering species richness and multiple components of community functional structure; (ii) analyze whether the dissimilarity between wintering and breeding communities changes over time; and (iii) consider what processes drive the assembly of communities at alpha and/or beta scales. Although our time series does not allow direct inferences about cause-effect relationships, observed patterns point to potential ecological and anthropogenic drivers underlying the temporal trends.

Methods

Study area

The studied wetlands (n=11) are located in Comunidad Valenciana, South-eastern Spain, and were originally coastal lagoons in different stages of natural succession towards terrestrial ecosystems (Supplementary material Appendix Fig. A1). Coastal wetlands in this region have suffered extensive loss of suitable habitat for many animal groups, including waterbirds, prior to effective protection measures (which were adopted for the study sites between 1986 and 2005). More information on these sites can be found at <http://www.parquesnaturales.gva.es>.

Bird sampling

We used an official data set on annual breeding and wintering waterbird counts for a 28-year period (1990-2017, Supplementary material Appendix 1 Table A1), compiled by the environmental authority of Comunidad Valenciana region, which provided data on all 11 wetlands (data available at <http://www.bdb.gva.es/es/censos-d-aus-aquaticues>). Surveys were performed by experienced observers from the regional government, following a standardized protocol that has remained roughly constant during the study period. The accuracy of the counts is likely to vary among taxonomic groups (e.g. ducks are easier to count than rails). However, as we used breeding pairs searched for during several months in the breeding season and a coordinated survey in the wintering (see below for details), the error is not expected to be large. Also, this error is expected to be constant between years, so that it does not influence temporal trends.

Winter counts were performed simultaneously at all wetlands each year during two weeks, starting around the second weekend of January, in coordination with the International Waterbird Census (IWC, for further details see <http://www.wetlands.org/AfricanEurasianWaterbirdCensus/tabid/2788/Default.aspx>).

Wintering ducks, coots, or grebes (Podicipedidae) were counted from a distance and from fixed sites every year using spotting scopes. Other wintering bird groups such as herons, gulls or shorebirds were counted along fixed itineraries, with variable detection bandwidths depending on the study site. The exact monitoring protocol in each wetland was adapted to its characteristics, such as vegetation structure or wetland shape. Wintering marsh harriers were counted around sunset at communal roosts.

Breeding counts were mostly performed by the staff of protected areas over the whole breeding season (March-August), due to differences in breeding phenology of each species (e.g. Green et al. 1999). Counts were performed using specific and fixed methodologies for each species. Colonial species (herons, gulls, terns, shorebirds, and flamingo) were counted by visiting breeding colonies and counting individual nests at the peak of their breeding period. Non-colonial species (ducks, coots, and grebes) were conducted by surveys from motorized boats, counting nests or birds displaying breeding behavior or adults with chicks. Species with low detectability (rallid species, little bittern) were counted by prospecting the wetland thoroughly from manually-propelled boats in shallow areas. The standardized survey locates pairs with newly-hatched young (i.e. young that could not have been counted in the previous survey because they would not have hatched yet). For all species, we used the total number of different breeding pairs (i.e. pairs that were successful in their reproduction and produced young) counted per year in counts for 27 years, from 1990 to 2016.

Functional traits

We measured functional traits of waterbirds related to variation in the birds' ability to exploit resources, since resource acquisition and consumption are ways through which birds perform most of their ecological roles (Sekercioglu 2006, Green and Elmberg 2014).

We used 15 functional traits that represent different aspects of this variation (Table 1). The same functional traits were used to characterize wintering and breeding species. 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 such as population control, propagule dispersal, scavenging, nutrient cycling, and ecosystem engineering (Sekericioglu 2006). Body mass and percentages of diet composition and stratum use were sourced from Wilman et al. (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, scavenge, fruits, seeds or plant material) and number of strata used (from 1 to 5: below surface, around surface, ground, understory, mid-high). Higher values for both plasticities indicate less dependence on a particular food item or stratum (Luck et al. 2013). Percentages of diet items and of feeding strata were assigned weights, so that all percentages were put together to represent the trait groups ‘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 by which the trait group i was divided (Laliberté and Legendre 2010). For example, the trait group ‘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.

Alpha Diversity

In order to evaluate changes in diversity through time, we calculated diversity measures for each year and wetland (n=11), for wintering (n=28) and breeding (n=27) counts.

For each wetland in each year, we calculated species richness to represent taxonomic diversity; and functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) (Mason et al. 2005, Villéger et al. 2008), and functional dispersion (FDis, Laliberté and Legendre 2010) to represent functional diversity. Using different facets of functional diversity provides a complementary perspective, together describing the distribution of species and their respective abundances within functional space (Fig. 1). Functional richness (FRic) represents the size of the functional space occupied by a community (Fig. 1a), and is measured by the convex hull volume, where vertices of the hull are species with extreme trait values. Thus, FRic does not vary with presence or absence of species with average trait values, and increases in communities composed of species with more extreme traits. Functional evenness (FEve) corresponds to how evenly the abundances of species are distributed in the functional space (Fig. 1b), measured through the minimum spanning tree among species in the functional space. FEve shows higher values either when abundance is more evenly distributed among species, or when functional distances among them are more regular. Functional divergence (FDiv) is the degree to which the abundance of a community is distributed towards the extremities of the occupied trait space (Fig. 1c), measured as the mean distance of all species to the center of gravity of the community. High levels of FDiv then are associated with high niche differentiation among species, i.e. when the most abundant species are very dissimilar and hardly 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 (Fig. 1d), weighted by their abundances (Villéger et al. 2008, Laliberté and Legendre 2010). FDis increases when the abundances of species with trait values further away from the centroid increase, indicating higher use of the margins of the functional space. Each of these three components describes an independent

aspect of functional diversity, so that the simultaneous analysis of these components gives a more complete quantification of functional diversity.

To assess the functional space for all species, we performed a Principal Coordinates Analysis (PCoA, Gower 1966) computed 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 PCoA on the functional distance matrix and used the first six PCoA axes to construct the functional space from which FEve and FDis were calculated. For the FRic and FDiv 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 (22 sampling events had a species number between 3 and 5). This space constructed with two axes represented 25% of the total PCoA variance. From the scores of the species in the PCoA axes and the abundance of species, we estimated the functional diversity indices. Computing the functional space was not possible for 15 samples containing two or fewer species, so they were removed from further analyses. These samples were: Clot de Galvany wintering 1990, 1994, 1995, 1996, 1998 and breeding 1993, 1994, 1995, 1999; Prat de Cabanes-Torreblanca breeding 1992, 1996, 1999; Marjal de Xeresa-Xeraco wintering 1998; and PN Salinas de Santa Pola wintering 2002 and breeding 1999. We calculated functional diversity indices with the dbFD function from the 'FD' package (Laliberté and Legendre 2010) within the R environment, version 3.0.1 (Laliberté et al. 2014, <www.r-project.org>).

In order to understand how changes in specific functional traits may be linked to changes in functional structure, we estimated a one-dimensional index for each functional trait in each community, wetland and year: the community-weighted means of the trait values (CWM, Garnier et al. 2004). CWM represents the overall community-level trait values by

accounting for abundance of each species in each site. For example, CWMs are means of the percentage of each item in the diet (or percentage of each stratum, or plasticity of diet/strata) for the entire community.

Beta diversity

We calculated spatial (between wetlands) and temporal (between seasons) beta diversities for each year for the waterbird communities. Spatial beta diversity was calculated separately for wintering and breeding counts through multiple-site dissimilarity measures for taxonomic beta diversity as proposed by Baselga (2010), and analogously for functional beta diversity as proposed by Villéger et al. (2011). For both taxonomic and functional compositions (species abundances are taken into account for in these measures), we calculated multiple-site beta diversity as the Sorensen dissimilarity index, representing total variation between assemblages. As the multiple-site dissimilarity measure can only be calculated for a maximum of 10 sites, we removed one of the wetlands (Clot de Galvany-Balsares, which was the site for most surveys with species richness < 3 , preventing functional volume estimation) from these calculations. On the other hand, we measured temporal beta diversity as pairwise dissimilarity measures between the wintering and breeding periods for each site and year. Once again, we considered taxonomic and functional beta diversities as proposed by Baselga (2010) and Villéger et al. (2011). Functional space calculation was the same as for alpha functional diversity. The volumes of multivariate trait space shared by two wetlands, and the volume unique to each wetland, were used in the functional beta diversity calculations (Villéger et al. 2011). We performed beta diversity calculations using the ‘betapart’ package (Baselga et al. 2017), in the R environment (www.r-project.org).

Statistical analyses

We fitted Generalized Additive Mixed Models (GAMMs) to all alpha (including CWM) and temporal beta measures and Generalized Additive Models (GAMs) to spatial beta measures to analyze trends in waterbird communities for Valencian protected wetlands in the last 28 years. GAMMs and GAMs are flexible statistical tools that can be used to explore and obtain non-linear fits to any data structure (Wood 2006). As we had no *a priori* reasons for describing the shape of the relationship between our response variables and time, GAM (and GAMM) was an appropriate tool for our analyses. GAMMs were constructed including wetland identity as a random effect to account for variation introduced by each site in trends for alpha (including CWM) and temporal beta diversity measures. A first-order autocorrelation structure was added to all models to account for temporal dependence among samples. All response variables (alpha diversity indices, CWMs and beta diversity values) were transformed as $\log(x + 1)$ before model construction to improve normality, with the exception of species richness. We modeled species richness with the negative binomial distribution and the log link function to deal with overdispersion and other diversity indices (and CWMs) with the Gaussian distribution and identity link function, to which the log-transformed indices showed a good fit. Standardized residuals were plotted against fitted values and the resulting plots were inspected for homoscedasticity. Adjusted r-squares were calculated as the proportion of variance explained by the models. GAMM and GAM Models were constructed using the ‘mgcv’ package (Wood 2017) in the R environment.

In order to investigate the processes driving the functional diversity patterns, we compared observed values of functional alpha indices and functional beta diversity and expected values generated by null models, to test whether our observed functional diversity values were expected according to a stochastic model of trait assembly. Two different null

distributions of both alpha and beta diversity values were generated for each year. For the first null communities (null model 1), we kept the community data constant and randomized the traits associated with each species by shuffling the names of the species in the trait matrix. This kept the original species richness and abundance (in the case of abundance-weighted indices) of each wetland in each year, simply reassigning functional identities to species. For the second null communities (null model 2), we randomly assigned species to each sampling unit with frequencies proportional to those observed. Abundances for each species were chosen at random (without replacement) from the distribution of abundances that occurred in each place and time. Thus, species richness in the assemblages and species occupancy rates remained fixed, and only co-occurrences were varied. We generated wintering and breeding null models separately, as each season had a different species pool. For functional alpha diversity, we produced 999 null distributions for each wetland in each year, recalculating functional indices each time. As for functional beta diversity, which has a longer computation time, we calculated 99 null distributions for each year, recalculating functional beta diversity for the group of wetlands each time.

Separately for each null model, we compared observed values with randomly generated values in each wetland and year for alpha diversity, and in each year for beta diversity (separately for breeding and wintering communities). These comparisons were made via standardized effect sizes (SES, Gotelli and Rohde 2002), which were calculated according to the following equation:

$$SES = \frac{\text{observed} - \text{mean (expected)}}{SD \text{ (expected)}}$$

SES values larger than zero are greater than expected and those smaller than zero are less than expected. However, only values greater than 1.96 or smaller than -1.96 are

significantly greater or less than expected, with $\alpha = 0.05$ (Gotelli and Rohde 2002). Departures from null expectations indicate that functional diversity is non-random, suggesting deterministic community assembly processes. For alpha diversity, higher than expected SES values indicate trait over-dispersion (i.e. coexisting species are functionally complementary), while lower than expected SES values indicate trait convergence (i.e. coexisting species are functionally redundant). For beta diversity, departures from the null expectations suggest that there is higher/lower difference in trait composition between communities than would be expected from the difference in species composition. We compared SES results of both null models to verify if they showed the same pattern.

Results

Changes in species richness (SR) and functional richness (FRic) along the 28 years monitored were significant for both wintering and breeding communities (Fig. 2a-d). General additive mixed modeling (GAMM) smoothing terms indicate that SR and FRic increased linearly for breeding communities (Fig. 2b, d), and stabilized in the last decade for wintering communities (Fig. 2a, c). Functional dispersion (FDis) showed the same positive significant trend as SR and FRic for wintering communities (Fig. 2e), stabilizing in the last decade. On the other hand, for breeding communities, functional divergence (FDiv) showed a linear decreasing significant trend over time (Fig. 2f). Other indices showed no significant trends (see Supplementary material Appendix 1 Table A2 for results of all models).

General additive mixed modeling (GAMM) smoothing terms of CWM values (Supplementary material Appendix 1 Table A3) for each functional trait in each year revealed significant increases in the proportion of fish in the diet (Fig. 3a) and mean weighted body

mass (Fig. 3b) for both wintering and breeding communities through time, and in diet and strata plasticity for the breeding community (Fig. 3c). On the other hand, there were significant decreases in the proportion of invertebrates in the diet of the breeding community (Fig. 3a) and in strata plasticity of the wintering community (Fig. 3c). CWMs of other functional traits did not share the same clear trends for both communities (Supplementary material Appendix 1 Fig. A2).

Temporal changes in taxonomic and functional beta diversity between wetlands were also significant, and negative overall, for wintering and breeding communities of Valencian waterbirds (Fig. 2, Supplementary material Appendix 1 Table A4). GAM smoothing terms indicate that wintering birds' taxonomic and functional beta diversities showed similar trends, decreasing in the early years and then stabilizing or increasing slightly in recent years (Fig. 2g, i). Breeding bird taxonomic beta diversity and breeding bird functional beta diversity decreased linearly (Fig. 2h, j). Models fitted to beta diversity calculated between wintering and breeding communities revealed a negative temporal trend for taxonomic beta diversity, while functional beta diversity between seasons showed no significant changes over time (Fig. 4, Supplementary material Appendix 1 Table A5).

For alpha functional diversity, standardized effect sizes from both null models showed the same pattern (Supplementary material Appendix 1 Figs. A3 and A4), and were rarely statistically significant. In different years and in very few wetlands, communities showed significant differences from those expected, which occurred for all functional diversity indices, and with observed values both below and above those expected, without a clear pattern.

For beta functional diversity, results for the two null models differed. According to null model 1, observed beta functional diversity values were mostly and significantly above

expected values for wintering bird communities through all the monitored years, but showed no significant difference from expected values for breeding bird communities (Fig. 5a). According to null model 2, observed beta functional diversity values were also mostly and significantly above expected values for wintering bird communities through all the monitored years. On the other hand, observed values for breeding bird communities were significantly below the expected values for most years (Fig. 5b).

Discussion

Trends in alpha diversity

This is the first study to evaluate the temporal changes in alpha and beta functional diversity in Mediterranean waterbird communities. We show that the increase in mean species richness (SR) has occurred concomitantly with an increase in functional richness (FRic), represented by an expansion in the functional space occupied by both wintering and breeding local communities. This correlation between species and functional richness is expected given that the space occupied by a community tends to increase together with the number of species in it (Mason et al. 2013). This result also indicates that specific ecological trait values and/or combinations of trait values characterizing the species gained by the community were not present before. This was also demonstrated by changes in CWMs of body size, diet composition, and diet and strata plasticity. Our results suggest that the new species may be exploiting alternative trophic resources, and most likely increase the ecological functions provided by the community.

Despite similar increases in taxonomic and functional richness, other components of community functional structure showed different trends in time for the wintering and

breeding waterbirds. Wintering birds showed an increase in functional dispersion (FDis) through time, similar to the increase in SR and FRic. Both FDis and FRic estimate the spreading of species in the trait space defined by trophic resources and foraging strategies. However, FRic is very sensitive to outliers and does not integrate information on relative abundances (Laliberté and Legendre 2010). Thus, the similar trends found for FRic and FDis indicate that the feeding modes and diet of the new species responsible for the increase in FRic are not outliers in the functional space. An increase in FDis reflects an increase in the mean distance of species to the center of the functional space occupied by the community (Mouillot et al. 2013). This indicates that not only do the wintering communities occupy an increasingly larger functional space, as indicated by FRic, but also that the species added to the community (e.g. *Nycticorax nycticorax*, *Oxyura leucocephala*, *Tadorna tadorna*) have high abundances in relation to the rest of species in the communities, and so consistently occupy the margins of this space. The occupation of the margins of the space by new species adds new (i.e. not present before) traits to the community, and thus probably new ecological functions.

In contrast, breeding birds showed a decreasing trend in functional divergence (FDiv), reflecting a decrease in the proportion of total abundance represented by species that have more extreme traits. This may be associated to a low degree of niche differentiation among individuals within communities, meaning that most abundant species are similar and more subject to competition (Mouchet et al. 2010). FRic and FDiv trends indicate that breeding species that were added to the communities (e.g. *Gelochelidon nilotica*, *Larus melanocephalus*, and *Sterna sandvicensis*) have contributed with different combinations of foraging modes, diets, and body size (extreme trait values), but have relatively low abundances in terms of breeding pairs. Decreases in FDiv may also be related to decreases

in the size of breeding populations for some previously common species in the communities (*Fulica atra*, *Aythya ferina* and *Netta rufina*, Martínez-Abrain et al. 2016). Thus, we have found increases in the occupied functional space (FRic) for both wintering and breeding communities, but opposing trends for the abundances of the species responsible for this increased functional richness. However, the increase in occupied functional space indicates that species with distinct functional roles were added in both seasons.

Trends in beta diversity

Wintering and breeding waterbird communities became more functionally similar over time. Overall, we observed increases in local species and trait richness and decreases in the dissimilarity of species and functional traits among wetlands, suggesting that some of the same functional traits have been added to the different wetlands, increasing homogenization through time. These traits may be those of species with high diet and strata plasticity and broad habitat use (e.g. *Ardea alba*, *Plegadis falcinellus*, *Porphyrio porphyrio*), which have extended their ranges across much of the Iberian Peninsula (Rendón et al. 2008, Martínez-Abrain et al. 2016, Ramo et al. 2013). The decreasing trend in beta diversity for the wintering communities ceased in the last decade, as did the increase in alpha diversity (Figs. 2a, c, and 4a, c). It is unclear what may have caused this change. Multiple factors influence species abundance and distribution, and it can be difficult to make the distinction between natural and anthropogenic changes (Magurran et al. 2010). At the same time, linking increases in alpha diversity only to local events can be an oversimplification, especially in the case of waterbirds, which are very mobile and often depend on surrounding areas during part of the day. Furthermore, migratory species are also influenced by changes much farther away along the flyway (Almaraz et al. 2012). Overall, the decrease in beta diversity through time may

represent a decrease in the influence of local processes and an increase in the influence of regional processes in the composition of the communities (Bonecker et al. 2013), as supported by other studies in Mediterranean wetlands (Galewski et al. 2011, Godet et al. 2011, Santoro et al. 2013).

Taxonomic beta diversity between wintering and breeding seasons decreased through time, indicating that differences in species composition between seasonal communities have been reduced. Nevertheless, there is no trend in the functional differences between seasons. Increased similarity between seasons may be an indicator that some species started to reproduce in the wetlands, or stopped migrating during winter. However, these species may add only redundant functional traits to wetlands. Thus, they do not cause alterations in the functional space filled by local communities, and consequently have no influence on differences in functional composition between seasons.

Patterns of community assembly

Observed functional alpha diversity values were mostly similar to expected values, suggesting a predominantly random assembly process in waterbird communities. These results are not necessarily an indicator of neutral processes structuring the communities, as a similar pattern may arise when both functional attraction and repulsion act at the same time due to opposing factors (Helmus et al. 2007, Mouchet et al. 2010, Bidwell et al. 2014). Random alpha functional diversity values have also been found in bird assemblages elsewhere (Luck et al. 2013, Almeida et al. 2017), and may be a product of other stochastic processes such as random birth, death, and dispersal events masking trait-dependent community assembly processes (Caswell 1976, Sale 1977, Hubbell 2001). The detection of

470 trait-based assembly processes is also dependent on the pool of traits and functional diversity
471 indices used. We have used indices representing the most important complementary facets
472 of functional diversity, conducting a particularly thorough investigation into trait-dependent
473 community assembly, but future inclusion of other traits or the comparison with new null
474 models may reveal additional, unexplored patterns.

475 Wintering functional beta SES values were higher than random expectations in most
476 of the studied years (Fig. 5), indicating that trait dissimilarity between wetlands is higher than
477 would be expected according to dissimilarity in species composition. Differences in
478 community composition related to a more unpredictable variation in flooding levels among
479 wetlands may occur during winter (e.g. Meléndez-Pastor et al. 2010). As water levels
480 increase, some of the wetlands lose their shallow areas, impeding the occurrence of species
481 that are dependent on these areas, but which do occur in other wetlands. Thus, a high
482 heterogeneity met by wintering species makes species with different environmental
483 requirements use different wetlands, promoting the dissimilarity of species traits (Loreau
484 2000), and favoring a higher functional beta diversity among wetlands. Human use and
485 conservation efforts are generally similar in all study wetlands, so that differences in human
486 disturbance are not likely to cause this pattern. On the other hand, breeding functional beta
487 SES values showed distinct patterns according to the chosen null model. In this case,
488 observed beta diversity values were below random expectations only in model 2. This model
489 revealed that there is a lower than expected dissimilarity of traits in the breeding communities
490 for a given taxonomic dissimilarity. Breeding bird communities are thus more functionally
491 similar than would be expected. This indicates that environmental conditions during this
492 season allow the reproduction of very similar species in all wetlands. There is thus a higher
493 equivalence in the roles of breeding waterbirds among wetlands than of wintering birds.

These results suggest that niche-based processes strongly influence differences in functional composition among Valencian wetlands. As null model 2 represents real frequencies of occurrence of species, it is more sensitive to processes influencing communities. Using more than one null model helps to identify complementary patterns of community assembly, and is thus recommendable.

It is important to consider that such distinct patterns between wintering and breeding functional beta SES values do not necessarily reflect changes in the community structure between wetlands that occur from winter to summer. For instance, breeding bird counts include only reproducing species, meaning that other species that are present in the wetland but are not breeding are not taken into account. In contrast, all the species present in the wetland are included in the wintering communities. This characteristic of our breeding data, far from making it unsuitable for our analyses, means breeding communities include only waterbirds that are tightly dependent on their habitats. For this reason, breeding bird results may not have the same meaning as those for wintering communities.

Conclusions

Overall, we found that Valencian waterbird communities have gained species that represent different trait value combinations, and thus exploit resources in different ways. Although not demonstrated directly, this suggests a temporal increase in ecological functions provided by waterbirds in the studied wetlands. The change detected in dietary composition of waterbird communities, the increase in mean body size, and the changes in niche plasticity may partly reflect the role of invasive carp (*Cyprinus carpio*) and crayfish (*Procambarus clarkii*) as ecosystem engineers which have invaded the study area, driving major changes in functional and taxonomic community structure (Tablado et al. 2010, Maceda-Veiga et al.

2017). At the same time, differences in the trait space among wetlands have decreased, showing that the species acquired occupy similar niches in each wetland. The increase of waterbird trait diversity for local communities may have resulted from a) the recovery of species from historical declines caused by hunting and lethal pesticides, b) the addition of new species that are expanding their distribution in the area, c) regional temperature increase, and d) habitat protection (Ramo et al. 2013, Pagel et al. 2014, Galewski and Devictor 2016, Martínez-Abrain et al. 2016). Still, the environmental quality of these wetlands has not been fully restored (e.g. eutrophication is a widespread problem in Spanish protected wetlands, Green et al. 2017), and temporal information on environmental variables could help to explain our results. Unfortunately, data on environmental covariates that might affect the observed trends is not available. Nevertheless, our results provide a warning signal about changes in the prevailing functional traits that may, in the long term, change the composition of the waterbird community and its ecological functions.

Our results show that even though compositional aspects of the wintering and breeding waterbird communities change similarly through time, other facets of community functional structure have different trends. Furthermore, comparing both seasons revealed an increase in the similarity of wintering and breeding communities through time. Most previous studies of waterbirds focus on only one community, usually that present in winter (e. g. Godet et al. 2011, Mendez et al. 2012). Future research on the difference between seasonal communities in other places and ecological groups will help to evaluate the generality of our results. Moreover, we found that seasonal communities are driven by opposing assembly mechanisms, which may bring them to respond differently to environmental variation. Our study shows that evaluating community changes in only one season may reveal incomplete and potentially misleading patterns for waterbirds. Thus, we highlight that comparing

seasonally distinct communities provides a better understanding of the dynamics and changes of assemblages that comprise both sedentary and migrating species.

Acknowledgements

We are thankful to the anonymous work of a large number of dedicated people who carried out the bird counts over the years, especially to JA Gómez. This dataset was provided by the Servicio de Vida Silvestre, Generalitat Valenciana, in collaboration with SEO/BirdLife. We thank two anonymous reviewers for their helpful suggestions on the manuscript.

Funding

BAA received grant PDSE/88881.133362/2016-01 from the Brazilian Coordination for the Improvement of Higher Education Personnel (CAPES). ESG was supported by a Juan de la Cierva contract (Ministerio de Economía y Competitividad, IJCI-2015-24947) and Generalitat Valenciana (SEJI/2018/024).

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697 Tables

698 Table 1. Functional traits compiled for waterbird species. Traits were sourced from Wilman et al. (2014).

Functional trait code	Functional trait definition
Body mass	Body mass in grams
Invertebrates	Percentage of diet composed of invertebrates
Fish	Percentage of diet composed of fish
Vertebrates	Percentage of diet composed of vertebrates
Scavenge	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 of use of water below surface feeding stratum
Around surface	Percentage of use of water around surface feeding stratum
Ground	Percentage of use of ground feeding stratum
Understory	Percentage of use of understory feeding stratum
Mid-high	Percentage of use of mid-high feeding stratum
Strata plasticity	Number of strata used in food acquisition

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701 Figures

702

703 Fig. 1. Representation of functional alpha diversity indices and functional beta diversity in
 704 the functional space. For simplification, functional space is constructed based on only two
 705 traits. Points represent species, and are plotted according to their trait values. Point sizes are
 706 proportional to species abundances. (a) Functional richness (FRic) is the amount of functional
 707 space filled by the community, calculated as the convex hull volume of the community. (b)
 708 Functional evenness (FEve) represents the regularity of the distribution of species'
 709 abundances in functional space, calculated as the minimum spanning tree (represented by the
 710 dashed line) linking species. (c) Functional divergence (FDiv) is the degree to which the
 711 abundance of a community is distributed towards the extremities of the occupied trait space,
 712 measured as the mean distance of all species to the center of gravity of the community
 713 (represented by the black circle). (d) Functional dispersion (FDis) is the mean distance of
 714 species (weighted by their abundances) to the centroid of the community. (e) Functional

715 dissimilarity (beta diversity) is the amount of functional space not shared between two or
 716 more communities, represented by the non-overlapping volume of communities.

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719 Fig. 2. Significant temporal trends of alpha and beta diversity indexes. (a) wintering bird
 720 species richness, (b) breeding bird species richness, (c) wintering bird functional richness,

(d) breeding bird functional richness, (e) wintering bird functional dispersion, (f) breeding bird functional divergence, (g) wintering bird taxonomic beta diversity, (h) breeding bird taxonomic beta diversity, (i) wintering bird functional beta diversity, (j) breeding bird functional beta diversity in Valencian wetlands. Taxo.SOR and func.SOR stand for taxonomic Sorensen dissimilarity index and functional Sorensen dissimilarity index, respectively. Observed values for each wetland in each year are shown in grey. Colored lines represent General Additive Mixed Model smoothing terms for alpha indexes and General Additive Modeling smoothing terms for beta indexes. Shaded areas represent confidence intervals.

Fig. 3. Temporal trends of CWM values of (a) invertebrate and fish proportions in diet, (b) body mass, and (c) diet and strata plasticity for wintering and breeding waterbird communities in the Valencian wetlands. Dashed lines represent mean observed values. Solid lines represent General Additive Mixed Model smoothing terms in each case. Only statistically significant smoothing terms are shown. Blue and orange lines represent wintering and breeding communities, respectively. Different traits represented in the same graph vary in color intensity.

Fig. 4. Temporal trends of seasonal (a) taxonomic beta diversity, and (b) functional beta diversity in Valencian wetlands. Observed values for each wetland in each year are shown as grey connected dots. Lines represent General Additive Modeling smoothing terms in each case. Shaded areas represent confidence intervals. *** $p < 0.001$

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747 Fig. 5. Standardized effect sizes for differences between observed and expected values for
 748 beta functional diversity in wintering and breeding bird communities generated by (a) null
 749 model 1, not accounting for species frequencies of occurrence, and (b) null model 2,
 750 accounting for species frequencies of occurrence. Points below the inferior dashed line or
 751 above the superior dashed line indicate departures from the expected beta functional
 752 diversity.