

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

3 Waterbird functional diversity through time

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15

16 Abstract

17 Waterbird communities are prone to strong temporal changes both seasonally and annually,  
18 but little is known about how this affects their functional diversity and community assembly.

19 Detecting temporal trends in taxonomic and functional diversity within (alpha diversity) and  
20 between (beta diversity) communities in breeding and wintering seasons could give insight

21 into the ecological processes driving those trends. In this study, we investigated trends in  
22 wintering and breeding waterbirds within and between eleven wetlands in Mediterranean

23 Spain, using a 28-year time-series up to 2017. We assessed the temporal trends in taxonomic  
24 and functional diversity measures, and compared observed functional diversity values with

25 null expectations, in order to explore the mechanisms driving community assembly. We

26 found increases over time in species richness and in the occupied functional space for both

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

39

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

## 41 Introduction

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

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

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

75         In the face of global environmental issues such as habitat loss and degradation or  
76 climate change, investigating temporal trends in diversity is one way to explore how such  
77 changes affect biological communities. Hence, long-term datasets are an essential resource  
78 in biodiversity research and monitoring (Mendez et al. 2012, Bonecker et al. 2013, Monnet  
79 et al. 2014). One of the aims of ecological monitoring is to detect changes in the structure  
80 and function of ecosystems, helping to detect and understand complex dynamic patterns  
81 (Magurran et al. 2010). Changes in diversity have a two-way relationship with the ecosystem,  
82 as biological communities are both products of environmental characteristics and  
83 interactions, and drivers of processes that maintain ecosystem functioning (Tilman et al.  
84 1997, Diaz and Cabido 2007, Suding et al. 2008).

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

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

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

113 al. 2012). However, the waterbird community is composed of very distinct bird groups, and  
114 evaluating a single group of waterbirds gives an incomplete understanding of community  
115 changes and its consequences (Green and Elmberg 2014, Sebastián-González and Green  
116 2014). In the face of wetland loss and degradation, and given the dependence of waterbirds  
117 on different wetlands along their migration routes, investigating waterbird trends at alpha and  
118 beta scales gives insights as to the factors driving changes in this community. Thus, ours is a  
119 unique study of changes in functional structure of a well-monitored group of organisms  
120 facing major habitat changes. Furthermore, most studies of taxonomic diversity of waterbirds  
121 focus on either the breeding season (e.g. Galewski and Devictor 2016) or the wintering period  
122 (e.g. Godet et al. 2011), whereas we compare breeding and wintering communities in the  
123 same wetlands.

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

134

135 **Methods**

136 *Study area*

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

144

#### 145 *Bird sampling*

146 We used an official data set on annual breeding and wintering waterbird counts for a  
147 28-year period (1990-2017, Supplementary material Appendix 1 Table A1), compiled by the  
148 environmental authority of Comunidad Valenciana region, which provided data on all 11  
149 wetlands (data available at <http://www.bdb.gva.es/es/censos-d-aus-aquatiques>). Surveys  
150 were performed by experienced observers from the regional government, following a  
151 standardized protocol that has remained roughly constant during the study period. The  
152 accuracy of the counts is likely to vary among taxonomic groups (e.g. ducks are easier to  
153 count than rails). However, as we used breeding pairs searched for during several months in  
154 the breeding season and a coordinated survey in the wintering (see below for details), the  
155 error is not expected to be large. Also, this error is expected to be constant between years, so  
156 that it does not influence temporal trends.

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

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

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

180

### 181 *Functional traits*

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



185 We used 15 functional traits that represent different aspects of this variation (Table 1). The  
186 same functional traits were used to characterize wintering and breeding species. Body mass  
187 strongly relates to metabolic rate, indicating the amount and size of food required for a given  
188 individual (Luck et al. 2012). Percentages of diet composition and stratum use indicate the  
189 main items consumed by species, and where they are acquired, and thus are related to  
190 functions such as population control, propagule dispersal, scavenging, nutrient cycling, and  
191 ecosystem engineering (Sekercioglu 2006). Body mass and percentages of diet composition  
192 and stratum use were sourced from Wilman et al. (2014). Plasticity of diet and strata represent  
193 the level of specialization associated with a given species and were calculated as the number  
194 of different diet items (from 1 to 7: invertebrates, fish, vertebrates, scavenge, fruits, seeds or  
195 plant material) and number of strata used (from 1 to 5: below surface, around surface, ground,  
196 understory, mid-high). Higher values for both plasticities indicate less dependence on a  
197 particular food item or stratum (Luck et al. 2013). Percentages of diet items and of feeding  
198 strata were assigned weights, so that all percentages were put together to represent the trait  
199 groups ‘diet items’ and ‘feeding strata’. For this, we calculated for each percentage the  
200 weight:  $W_i = 1/N_i$ , where  $N_i$  is the number of traits by which the trait group  $i$  was divided  
201 (Laliberté and Legendre 2010). For example, the trait group ‘diet items’ was comprised of  
202 seven traits (each of the items with percentage data), each of them with weight  $1/7$ , so that  
203 when combined, they complete the “weight of one” representing diet items.

204

### 205 *Alpha Diversity*

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

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

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

234 To assess the functional space for all species, we performed a Principal Coordinates  
235 Analysis (PCoA, Gower 1966) computed from traits of all species from all years, from both  
236 wintering and breeding counts. We computed the functional distances between pairs of  
237 species using the Gower distance (Gower 1966). Then, we performed a PCoA on the  
238 functional distance matrix and used the first six PCoA axes to construct the functional space  
239 from which FEve and FDis were calculated. For the FRic and FDiv calculation, only two  
240 PCoA axes were used, as the number of axes cannot be superior to the number of species,  
241 and some sites presented low species richness (22 sampling events had a species number  
242 between 3 and 5). This space constructed with two axes represented 25% of the total PCoA  
243 variance. From the scores of the species in the PCoA axes and the abundance of species, we  
244 estimated the functional diversity indices. Computing the functional space was not possible  
245 for 15 samples containing two or fewer species, so they were removed from further analyses.  
246 These samples were: Clot de Galvany wintering 1990, 1994, 1995, 1996, 1998 and breeding  
247 1993, 1994, 1995, 1999; Prat de Cabanes-Torreblanca breeding 1992, 1996, 1999; Marjal de  
248 Xeresa-Xeraco wintering 1998; and PN Salinas de Santa Pola wintering 2002 and breeding  
249 1999. We calculated functional diversity indices with the dbFD function from the 'FD'  
250 package (Laliberté and Legendre 2010) within the R environment, version 3.0.1 (Laliberté et  
251 al. 2014, <[www.r-project.org](http://www.r-project.org)>).

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

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

259

#### 260 *Beta diversity*

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

279

280 *Statistical analyses*

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

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

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

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

$$324 \quad \text{SES} = \frac{\text{observed} - \text{mean (expected)}}{325 \quad \text{SD (expected)}}$$

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

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

337

## 338 Results

339

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

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

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

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

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

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



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

382

## 383 Discussion

### 384 *Trends in alpha diversity*

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

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

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

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

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

429

#### 430 *Trends in beta diversity*

431 Wintering and breeding waterbird communities became more functionally similar  
432 over time. Overall, we observed increases in local species and trait richness and decreases in  
433 the dissimilarity of species and functional traits among wetlands, suggesting that some of the  
434 same functional traits have been added to the different wetlands, increasing homogenization  
435 through time. These traits may be those of species with high diet and strata plasticity and  
436 broad habitat use (e.g. *Ardea alba*, *Plegadis falcinellus*, *Porphyrio porphyrio*), which have  
437 extended their ranges across much of the Iberian Peninsula (Rendón et al. 2008, Martínez-  
438 Abraín et al. 2016, Ramo et al. 2013). The decreasing trend in beta diversity for the wintering  
439 communities ceased in the last decade, as did the increase in alpha diversity (Figs. 2a, c, and  
440 4a, c). It is unclear what may have caused this change. Multiple factors influence species  
441 abundance and distribution, and it can be difficult to make the distinction between natural  
442 and anthropogenic changes (Magurran et al. 2010). At the same time, linking increases in  
443 alpha diversity only to local events can be an oversimplification, especially in the case of  
444 waterbirds, which are very mobile and often depend on surrounding areas during part of the  
445 day. Furthermore, migratory species are also influenced by changes much farther away along  
446 the flyway (Almaraz et al. 2012). Overall, the decrease in beta diversity through time may

447 represent a decrease in the influence of local processes and an increase in the influence of  
448 regional processes in the composition of the communities (Bonecker et al. 2013), as  
449 supported by other studies in Mediterranean wetlands (Galewski et al. 2011, Godet et al.  
450 2011, Santoro et al. 2013).

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

459

#### 460 *Patterns of community assembly*

461 Observed functional alpha diversity values were mostly similar to expected values,  
462 suggesting a predominantly random assembly process in waterbird communities. These  
463 results are not necessarily an indicator of neutral processes structuring the communities, as a  
464 similar pattern may arise when both functional attraction and repulsion act at the same time  
465 due to opposing factors (Helmus et al. 2007, Mouchet et al. 2010, Bidwell et al. 2014).  
466 Random alpha functional diversity values have also been found in bird assemblages  
467 elsewhere (Luck et al. 2013, Almeida et al. 2017), and may be a product of other stochastic  
468 processes such as random birth, death, and dispersal events masking trait-dependent  
469 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.

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

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

508

### 509 *Conclusions*

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

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

544

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555

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## 697 Tables

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

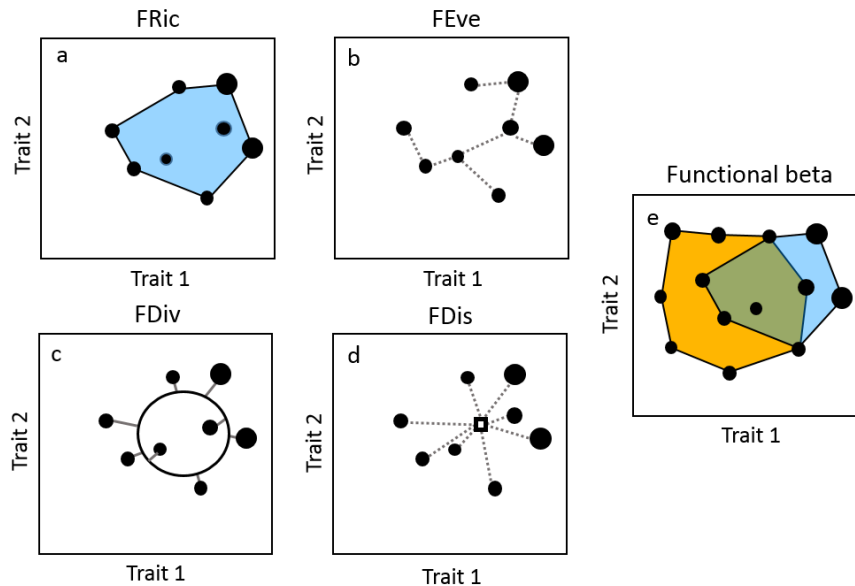
Functional trait code	Functional trait definition
Body mass	Body mass in grams
Invertebrates	Percentage of diet composed of invertebrates
Fish	Percentage of diet composed of fish
Vertebrates	Percentage of diet composed of vertebrates
Scavenge	Percentage of diet composed of carrion
Fruits	Percentage of 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

699

700



## 701 Figures

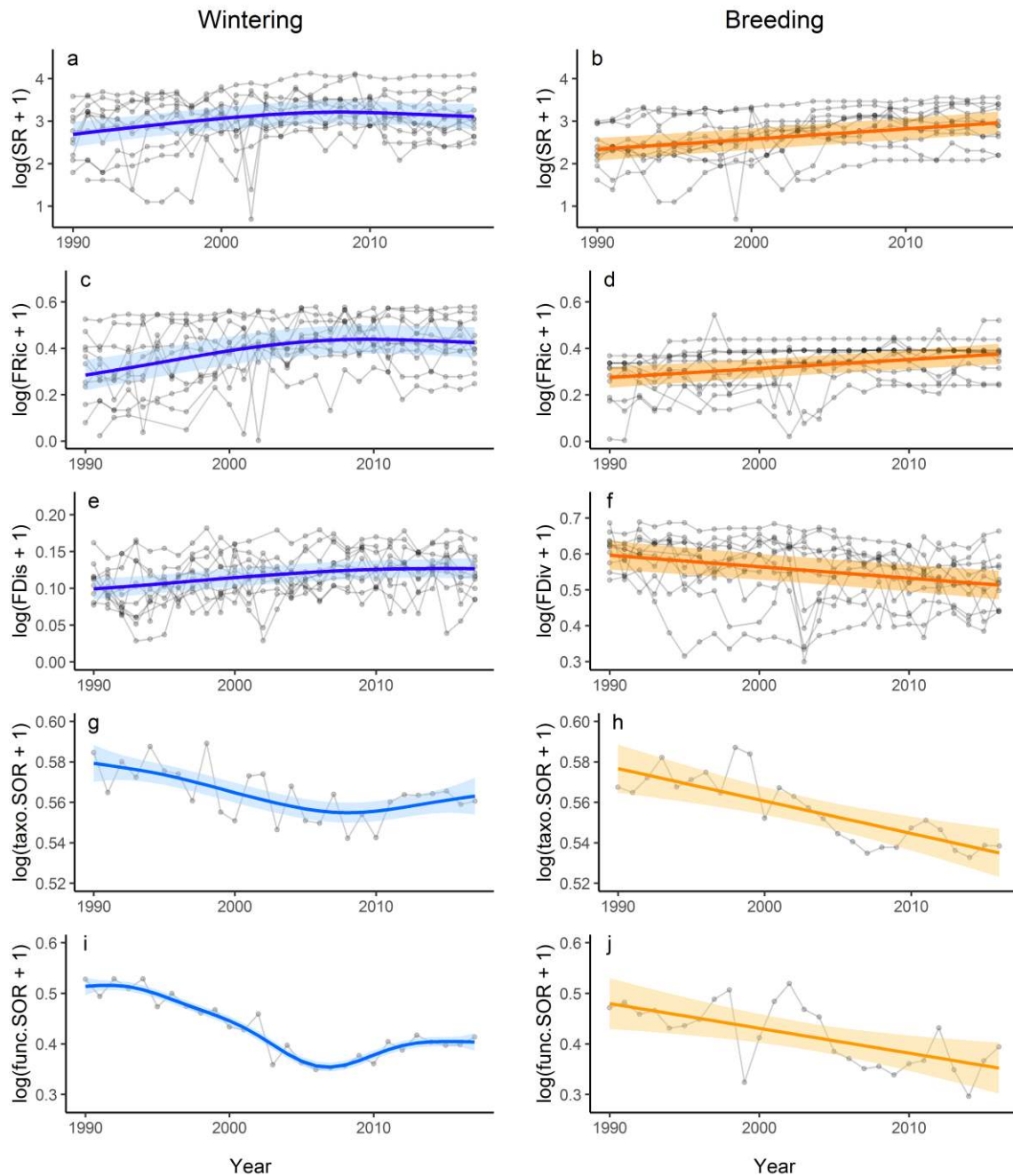


702

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.

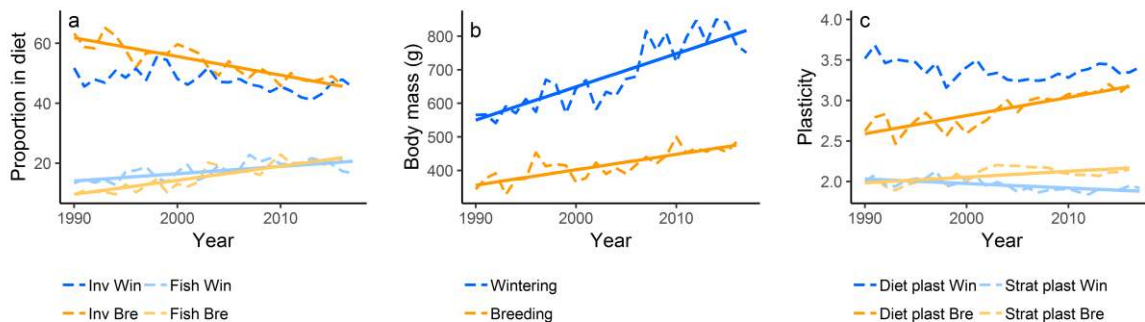
717



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

730

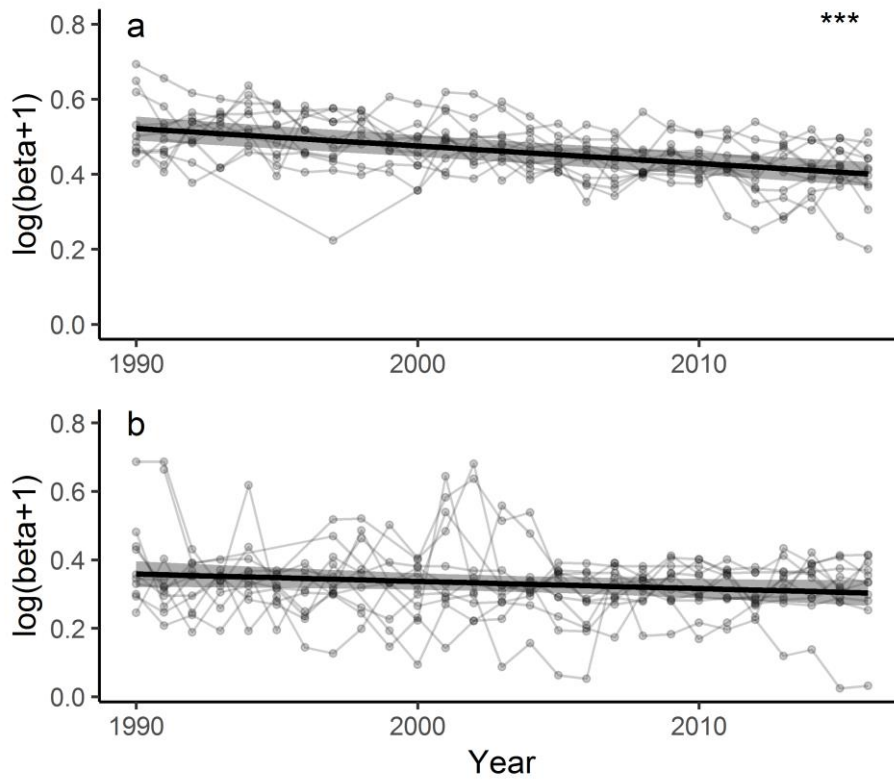
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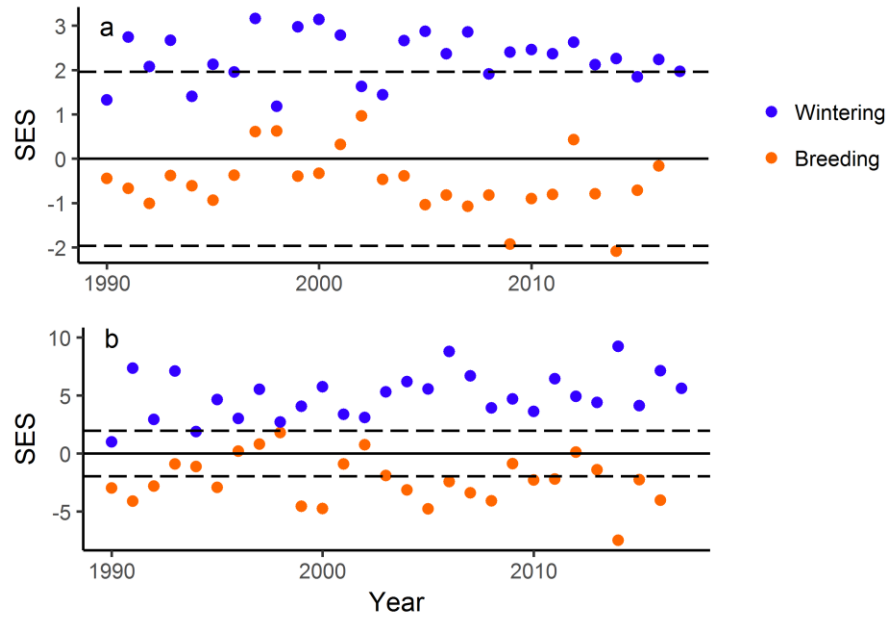
733 Fig. 3. Temporal trends of CWM values of (a) invertebrate and fish proportions in diet, (b)  
 734 body mass, and (c) diet and strata plasticity for wintering and breeding waterbird  
 735 communities in the Valencian wetlands. Dashed lines represent mean observed values. Solid  
 736 lines represent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

740



741

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



746

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.