

RESEARCH ARTICLE

Functional diversity of macroinvertebrates as a tool to evaluate wetland restoration

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Abstract

1. Ecological restoration of aquatic ecosystems has become widespread in recent decades. Although the recovery of biodiversity in restored wetlands has been studied from a taxonomic perspective, our knowledge of how functional biodiversity recovers remains poorly understood.
2. We studied the functional diversity of macroinvertebrate communities in 32 Mediterranean temporary ponds 6–7 years after their creation during a restoration in South-West Spain, and compared them with 10 natural reference sites during two consecutive hydroperiods. We compared alpha functional diversity indices, and the individual contributions of new ponds and reference sites to the regional functional beta diversity, as well as to its turnover and nestedness components. We also investigated the influence of environmental and spatial variables on the dissimilarities of functional beta diversity and its components between new ponds and reference sites.
3. Alpha functional diversity in new ponds was lower than in reference sites. Although the contribution of new ponds to the regional functional beta diversity was similar to that of reference sites, the latter contributed more to functional turnover while new ponds contributed more to functional nestedness.
4. Dispersal limitation coupled with environmental filtering structured the functional variation in communities between new ponds and reference sites, but their relative importance differed between beta components. New ponds can hold species with unique functional compositions, but their contribution to the regional functional beta diversity was mostly due to trait losses with respect to reference sites.
5. *Synthesis and applications.* Considering different aspects of functional diversity of invertebrate communities can help elucidate the processes and mechanisms through which ecosystems recover following restoration. We encourage the use of trait-based approaches to identify trends in processes and patterns that can guide future wetland restoration projects.

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KEYWORDS

beta diversity, functional diversity, macroinvertebrates, Mediterranean wetlands, nestedness, turnover, wetland restoration

1 | INTRODUCTION

Wetlands are critical ecosystems for sustaining biodiversity and ecosystem services to humans (Maltby & Acreman, 2011). Nonetheless, wetland loss and degradation continue to be a global problem. Mediterranean wetlands are particularly at risk, being threatened by, for example, land-use change, water overexploitation or climate change (Taylor et al., 2021). In recent decades, ecological restoration of aquatic ecosystems has become widespread in effort to reverse these losses, and is expected to increase during the current decade (An & Verhoeven, 2019). Integrative freshwater ecology and biodiversity conservation approaches are needed in wetland management (Geist, 2011). This requires understanding of functional diversity of biological communities in these systems to make conservation and restoration evidence based and effective (Geist, 2015; Geist & Hawkins, 2016). However, the outcomes of wetland restorations in many cases remain unclear (Zedler, 2000).

In general, restoration success focuses on the recovery of taxonomic biodiversity compared with reference sites, which in many cases has been slow and incomplete (Moreno-Mateos et al., 2012). Nevertheless, biodiversity includes other dimensions, for example, phylogenetic and functional diversity, which can provide complementary insights (Perez-Rocha et al., 2018). Functional diversity represents the variety of morphological, physiological and phenological measurable traits (e.g. body size, life-history characteristic, feeding habits) within communities. Since functional traits determine the response of organisms to environmental changes and their effects on the system, linking biodiversity, ecosystem functioning and environmental constraints, they are ideal for assessing the effects of restoration (Cadotte et al., 2011; Montoya et al., 2012). Nonetheless, functional diversity and its components have only rarely been considered to assess restoration success, mainly focusing on changes in alpha functional diversity through restoration (Español et al., 2015; Rumm et al., 2018).

Functional diversity can be described by its alpha (functional trait variation within an individual site [local]) and beta (functional variations between sites) components (Whittaker, 1960). Moreover, the beta component can also be partitioned into its nestedness (differences in trait richness between sites) and turnover (trait replacement between sites) subcomponents (Baselga, 2010; Villéger et al., 2013). Patterns of alpha and beta functional diversity can be used to infer the ecological processes structuring community re-assembly during restoration, such as environmental filtering, dispersal limitation and competition, as well as community effects on ecosystem functioning (Feit et al., 2019).

In general, newly created habitats have unoccupied niches that are quickly colonized by some pioneer macroinvertebrate species

from nearby natural wetlands (Bloechl et al., 2010). These colonizers possess traits that allow them to use a wide range of resources, disperse over long distances and reproduce quickly (i.e. short life cycle). As time after restoration increases, and in relation to increases in niche availability through time, generalist species are gradually replaced by specialists with narrower environmental tolerance, limited dispersal capacity and longer life cycles (Ruhí et al., 2013). In restored wetlands, pioneering communities dominated by active dispersers usually represent a nested subset of species present in older natural wetlands (Ruhí et al., 2013).

Aquatic macroinvertebrates participate in and regulate key ecological functions such as nutrient cycling and primary production (Batzer & Wissinger, 1996; Schmera et al., 2017). Macroinvertebrates are sensitive to ecological conditions, including habitat heterogeneity (Heino et al., 2003) and water quality (Soldner et al., 2004). In addition, they possess a broad range of functional traits, making them excellent models for functional-based studies.

Here, we evaluate the success of Mediterranean temporary ponds created during wetland restoration in supporting macroinvertebrate functional diversity. First, we compared alpha functional diversity between new ponds and reference sites during two consecutive hydroperiods. Second, we compared the contributions of new ponds and reference sites to the overall regional functional beta diversity and to its turnover and nestedness components, as well as the differences in the levels of beta diversity (and its components) within each wetland type. Finally, we investigated the influence of environmental and spatial variables on the functional beta diversity (and its components) calculated between new ponds and reference sites. Examining both functional alpha and beta diversity components may help to understand the outcomes of restoration at the local scale, and the processes that affect the restoration at the landscape level.

In a previous study of the same system, Coccia et al. (2016) showed that taxonomic diversity in new ponds matched or was even higher than that of reference sites, while their habitat heterogeneity was lower. Nonetheless, we expected that (a) alpha functional diversity would be higher in reference sites than in new ponds because their greater environmental heterogeneity may enable more varied trait compositions (Wilson, 1999). We also expected (b) to observe differences in the contributions to the overall regional functional beta diversity and its components (nestedness and turnover) between new ponds and reference sites because they should be influenced by differences in habitat heterogeneity and by dispersal limitation. Specifically, we expected that reference sites would contribute more to overall functional turnover because they support species that have less dispersal capacity and/or greater specialization to specific habitats. In contrast, new ponds should show strong

functional nestedness because they support pioneering communities (Coccia et al., 2016). Finally, based on other studies conducted on aquatic macroinvertebrates (Español et al., 2015; Hill et al., 2019), we expected that (c) the environmental differences between new ponds and reference sites would drive functional beta diversity and its components because traits should reflect adaptations to the environment.

2 | MATERIALS AND METHODS

2.1 | Study area and climate

This study was conducted within and around the Caracoles estate, at the northern edge of Doñana National Park (Southwest Spain; Figure 1). This estate of 27 km² was a former seasonally inundated marsh that was disconnected from the surrounding marshes and turned into arable farmland during the 1960s. During 2004–2005, due to a restoration plan aimed at re-establishing former connectivity with surrounding marshes, the agricultural drainage system was removed and a set of 96 elliptically shaped temporary ponds were created. The ponds were of three different sizes (with a long axis of 250, 125 and 60 m in 8, 24 and 64 ponds, respectively) and two excavation depths (30 and 60 cm). These ponds are distributed in two main blocks of 44 ponds each, plus 8 medium size, relatively isolated ponds distributed throughout the estate (Figure 1). The ponds are filled mainly by local precipitation, with important variation in water level according to season and year, occasionally overflowing and connecting after major rainfall events, and drying out completely during summer (Coccia et al., 2016). The colonization of these ponds by waterbirds, zooplankton and macroinvertebrates has been previously described (Coccia et al., 2016; Frisch et al., 2012; Sebastián-González & Green, 2014).

Doñana has a Mediterranean climate with Atlantic influence, determined by short, mild winters and dry, hot summers. Rainfall is variable and concentrated mainly between October and the beginning of April (wet season), with little precipitation and high temperatures causing rapid evaporation from April to September (dry season; Paredes et al., 2021). Caracoles ponds and surrounding waterbodies are usually flooded during the wet season and dry out in summer (Coccia et al., 2016). Dates of flooding and drying vary among years, as a result of different rainfall and evaporation patterns, which are quantified for hydrological years running from September to the following August. Total precipitation was 784 mm during the first study hydroperiod (between 2009 and 2010) and 712 mm for the second (2010–2011; Coccia et al., 2016).

2.2 | Study site characterization

We selected 32 new ponds in Caracoles representing all size and depth classes (Figure 1; Table S1 in Supporting Information),

including 24 within the two blocks and the 8 outside. In addition, we also sampled 10 nearby older, temporary, shallow waterbodies as reference sites (Figure 1; Table S1). These reference sites are similar to new ponds as they fill in response to rainfall and dry out during the dry summers. Occasionally, heavy flooding in the marshes can connect almost the whole area for several days, including some connections between new ponds and reference sites, as occurred during our two study hydroperiods (Coccia et al., 2016). Choice of reference sites was limited because the Caracoles estate is surrounded by drained farmland to the North and East, and a continuous and inaccessible marshland to the south and west. Owing to limited options for reference sites, they included a greater range in size and depth than the new ponds. However, this combination of new ponds and reference sites has previously been shown to be an adequate system to study restoration trajectories (Coccia et al., 2016; Frisch et al., 2012).

2.3 | Environmental and taxonomic data

Environmental and taxonomic data were collected in May, the month with the most extensive sampling during both hydroperiods (2009–2010 and 2010–2011, from Coccia et al., 2016). We excluded taxa for which taxonomic identification did not reach the family level (e.g. Nematoda and Oligochaeta). The final dataset included 70 taxa belonging to 19 families and 51 genera (Table S2); plus 10 environmental and 4 spatial variables (Table S3). Emergent vegetation coverage was only available for 2010.

Previous analyses in Coccia et al. (2016) found significant differences between new ponds and reference sites in some environmental variables, including pH, chlorophyll-a concentration, vegetation cover and fish (see Moreno-Valcarcel et al., 2013 for details of fish; Table S4).

2.4 | Functional traits

For the characterization of macroinvertebrates, we selected 14 functional traits related to morphology, physiology or behaviour. These included the following: Maximal potential body length, Life cycle duration, Potential number of cycles per year, Aquatic stages, Dispersal, Resistance forms, Locomotion and substrate relation, Food preference, Feeding habits, Adult life span, Female wing length, Wing pair type, Lifelong fecundity and Propensity to drift. These traits were selected because they describe the influence of macroinvertebrates on ecosystem processes, such as on nutrient cycling, secondary productivity and energetic transfer (see Table S5 for details on the relationships between each trait and functions). The affinity values of genera with the different trait categories were determined mainly using Tachet et al. (2002) and Sarremejane et al. (2020), but see Table S6 for exceptions. Affinity values at the family level were estimated as the average of affinity values of all the

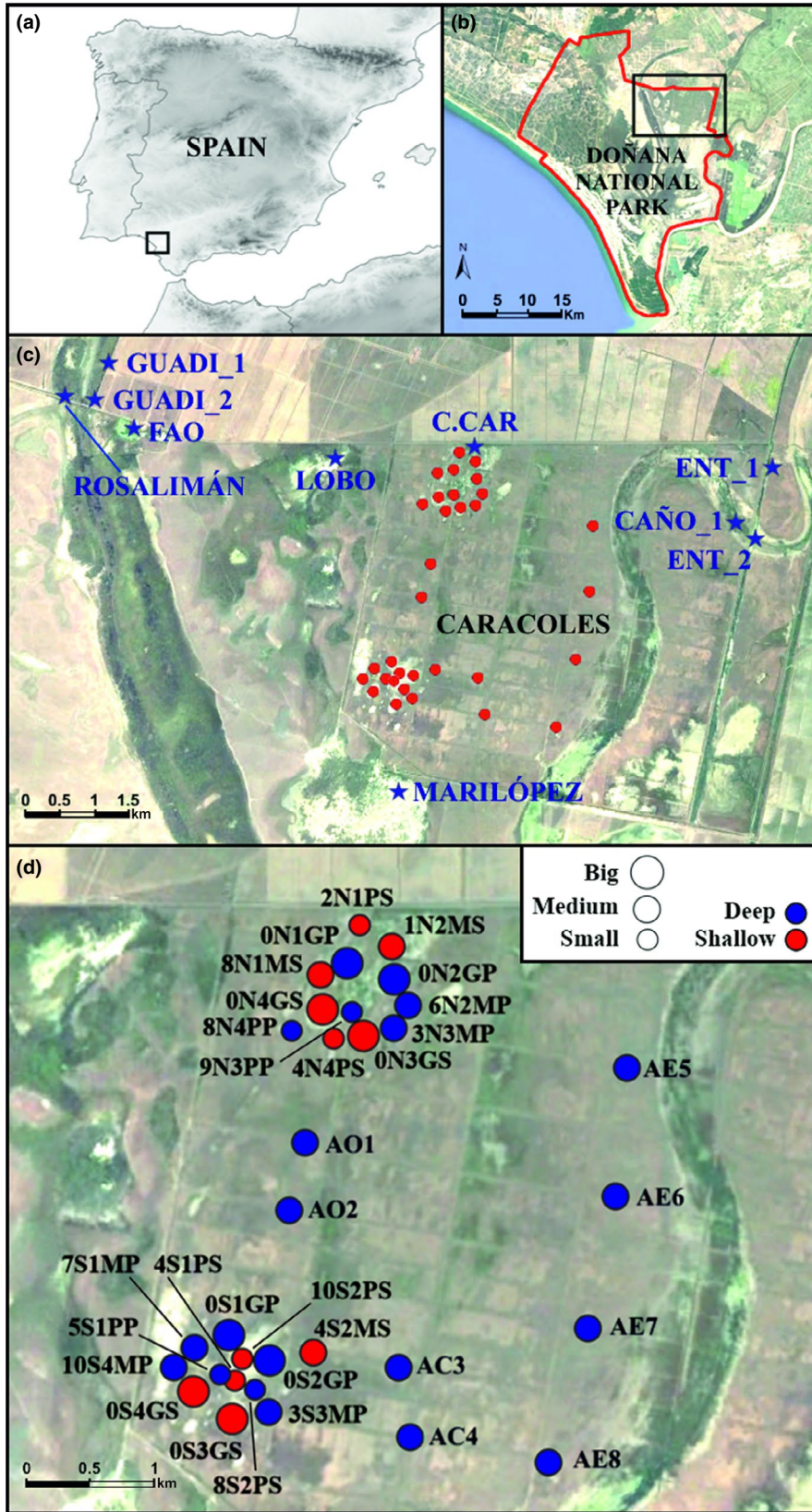


FIGURE 1 Map of the sampling sites in Doñana National Park. (a) Location of Doñana within Spain, (b) study area in Doñana, (c) Reference sites (blue stars) and new ponds (red circles) and (d) close-up of the new ponds

genera in that family (Sarremejane et al., 2017). If values for genera belonging to a family in our dataset were undescribed, we used affinity values for other genera from that family covered by the above references.

2.5 | Functional diversity

We calculated alpha and beta functional diversity for each wetland type (i.e. new ponds or reference sites) in each sampled year.

As software limitations prevent beta functional measurements to be calculated considering species abundances, we considered only presence-absence data in the calculation of both alpha and beta diversities. As measurements of alpha diversity, we calculated complementary functional diversity indices that together describe the community functional structure, that is, the distribution of species in the functional space built from trait values. We constructed the functional space by computing a principal coordinates analysis (PCoA; Gower, 1966) from trait values of all taxa present in our samples. First, we calculated functional distances among pairs of taxa using the Gower distance (Gower, 1966). Then, we performed a PCoA on the functional distance matrix and considered the PCoA axes as dimensions of the functional space. We removed sites with four or less taxa from all analyses so that we could use at least four axes to construct functional space. A total of three new ponds (2 in 2010 and 1 in 2011) and one reference site (2011) were removed.

From the scores of the taxa in the axes, we calculated functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) and functional dispersion (FDis; Laliberté & Legendre, 2010). FRic is the volume of the minimum convex hull of the community, where taxa with more extreme functional trait values are the vertices of the hull (Figure 2a). It represents the volume of the functional space occupied by each community, and varies when the composition of taxa with extreme traits changes. FEve is the minimum spanning tree among taxa, and describes how evenly taxa are distributed in the functional space, increasing when functional distances among them are more regular (Figure 2b). FDiv is the mean distance of all taxa present in a community to its centre of gravity. It represents the degree to which taxa are distributed towards the edges of the occupied functional volume, and increases when taxa in a community are more dissimilar (Figure 2c). Finally, FDis is the mean distance of taxa to the centroid of the community, and increases when taxa are more dispersed in the overall functional space (Figure 2d). To evaluate whether there were differences in values of specific functional traits between new ponds and reference sites, we evaluated Community-Weighted Means (CWM, Garnier et al., 2004) of each trait category. CWM is a community-level mean of the values that each taxon has for a given trait. First, we calculated CWMs for each trait category in each wetland type. Then, we correlated these values with the site scores in the four PCoA axes, to identify which traits were more responsible for the distribution of species in the functional space (considered to be those with $r > 0.6$). We calculated all indices with the dbFD function of the FD package (Laliberté & Legendre, 2010; Laliberté et al., 2014) within the R environment, v. 3.5.1 (R Core Team, 2018).

We calculated functional pairwise beta diversity among all wetland types, and its turnover and nestedness components (Baselga, 2010; Villéger et al., 2011). We calculated total functional beta diversity as the Sorensen dissimilarity index, representing total variation among communities. The turnover component (dissimilarity due to the replacement of some traits by others) was calculated as the Simpson dissimilarity index. Finally, the nestedness component (dissimilarity due to differences in functional richness among

communities) was quantified as the difference between total beta diversity and its turnover component. For each year, we generated a dissimilarity matrix for each of these components of beta. Then, we used these distance matrices in multivariate dispersion analyses (Anderson, 2006) in two ways: (1) to compare the contributions of new ponds and reference sites to overall (regional) beta diversity, we obtained distances of each wetland type to the median of all wetland types (combining both new ponds and reference sites) in the multivariate space (Figure 2e). Then, (2) to evaluate differences in beta diversity and its components when they were calculated separately for each wetland type, we obtained distances of each wetland to the median of all sites of that type (i.e. one median for new ponds, another median for reference sites; Figure 2f). We calculated pairwise functional beta diversity with the functional.beta.pair function of the BETAPART package (Baselga et al., 2017), and performed multivariate dispersion analyses with the function betadisper of the VEGAN package (Oksanen et al., 2018), in the R environment, v. 3.5.1 (R Core Team, 2018).

2.6 | Data analyses

To evaluate differences in functional alpha diversity between wetland types, we fitted linear mixed models (LMM) to the values of each functional diversity index (FRic, FEve, FDiv, FDis and CWMs highly correlated with PCoA axes) using wetland type as an explanatory variable and year as a random factor. We compared those models to null models constructed without the variable 'wetland type' and selected the model with lower Δ AIC in each case. To evaluate differences in the contribution of each wetland type to regional beta diversity (and its turnover and nestedness components), we fitted linear models to the distances for each individual wetland from the median for all sites generated by multivariate dispersion analyses, separately for each year. We checked assumptions for all models graphically. Models were fitted using the lmer and lm functions (package LME4, Bates et al., 2015), in the R environment v. 3.5.1 (R Core Team, 2018).

To evaluate differences in the levels of beta diversity among new ponds and among reference sites, we used a permutation-based test of multivariate homogeneity of group dispersions on the results from betadisper when calculated with medians for each group. This was done using the permutest function from the VEGAN package, in R, correcting for unequal number of samples between wetland types.

We also evaluated how environmental variables influenced dissimilarity among wetland types in beta diversity. In Mediterranean wetlands, most environmental variables (e.g. flooding area, depth) vary between years, so we analysed each year separately. To identify which connectivity and environmental variables were the best predictors of differences between new ponds and reference sites in regional functional beta diversity, turnover and nestedness, we used generalized dissimilarity modelling (GDM; Ferrier et al., 2007). We calculated GDMs for each beta diversity index in each year, using the dissimilarity matrices generated by the functional.beta.pair function

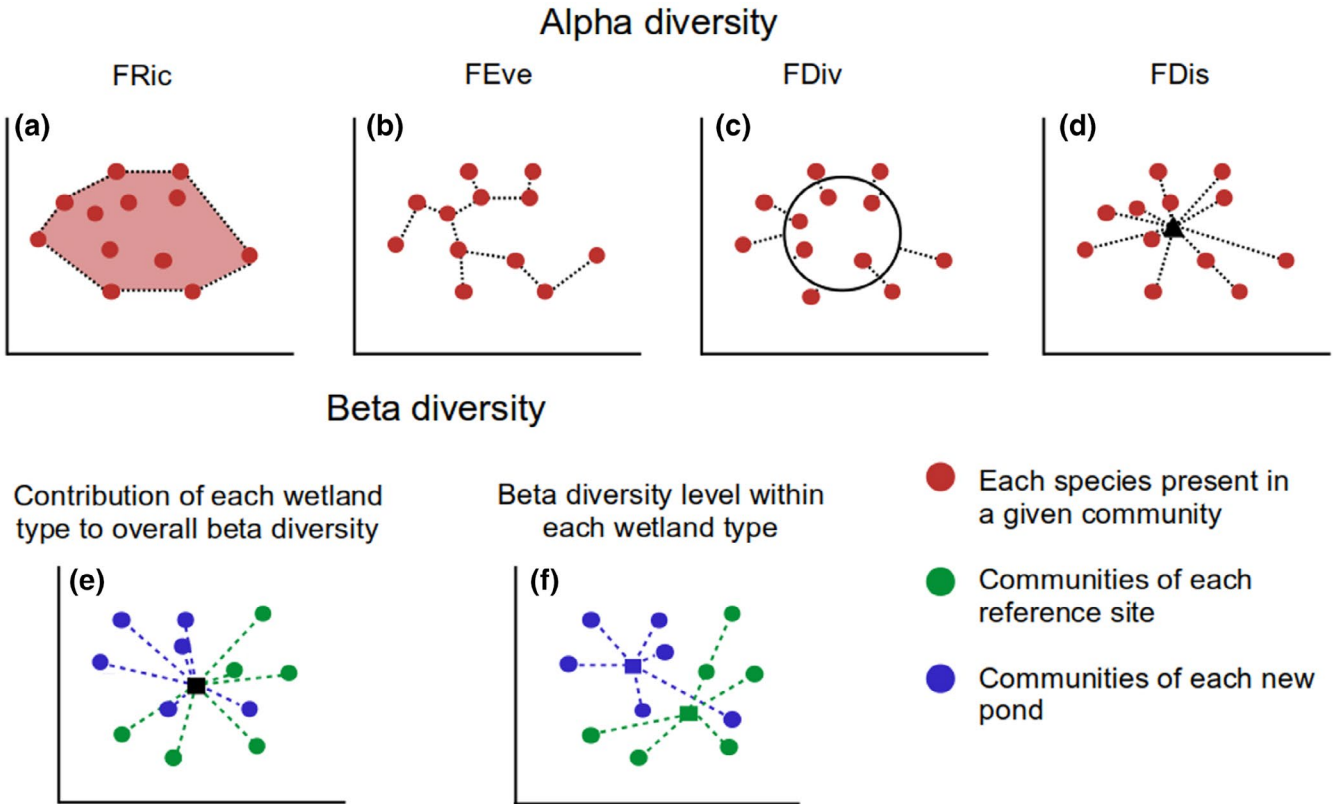


FIGURE 2 Representation of the alpha and beta functional diversity aspects used in this study in the functional space constructed for each scale. (a) FRic: Functional richness; (b) FEve: Functional evenness; (c) FDiv: Functional divergence; (d) FDis: Functional dispersion. Beta diversity functional spaces were built separately for total beta diversity and its turnover and nestedness components, and in two manners: (e) to compare the contributions of each wetland type to overall beta diversity and (f) to compare beta diversity when calculated separately for each wetland type

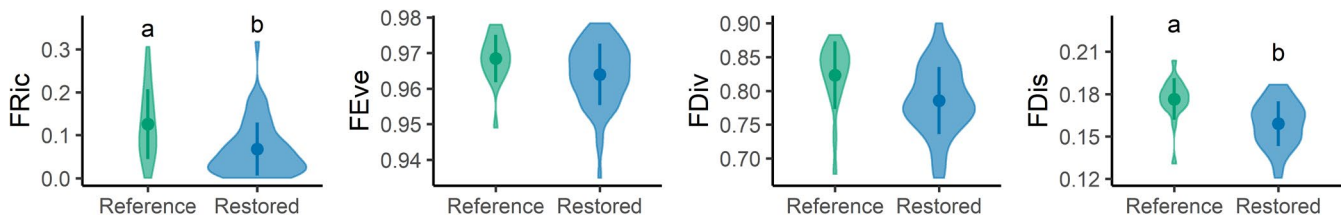


FIGURE 3 Violin plots showing the kernel probability density of alpha functional diversity indices (mean \pm SE) by wetland type. Points represent the mean of the data, and bars are equal to one standard error. Letters indicate significant differences between types according to linear mixed models. The functional space used to calculate all indices was built from the total pool of species

as a response variable, and a matrix of environmental variables and geographical distances among wetland types (calculated from geographical coordinates) as explanatory variables. To account only for the differences between wetland types, we only used the pairwise dissimilarities between reference sites and new ponds, removing new pond \times new pond and reference site \times reference site dissimilarities in the following steps. GDM makes no assumptions about the shape of distributions, and it assumes only that the relationship between variables increases (or decreases) monotonically. We used the default setting of three I-splines to define the flexibility of the fit. We started GDM fitting with all the available variables. Then,

we followed a permutation-based backward elimination procedure (Ferrier et al., 2007). In each step of this procedure, all environmental variables included in the model were permuted in turn, and the difference in explained deviance between the permuted model and the previous one was calculated. After 999 permutations, the variable with the least significant contribution to explained deviance was excluded. This procedure was repeated until all variables included in the model made significant contributions to explained deviance ($p < 0.05$). We fitted GDMs using the functions `gdm` and `gdm.varImp` from the `GDM` package (Fitzpatrick et al., 2020), in the R environment, v. 3.5.1 (R Core Team, 2018).

3 | RESULTS

3.1 | Alpha diversity

Linear mixed models indicated differences in alpha functional diversity indices between reference sites and new ponds while controlling for year. Specifically, reference sites had higher Functional Richness (FRic) and Functional Dispersion (FDIs) compared to new ponds (Figure 3; Table S7). We found 10 functional trait categories with CWM correlations to PCoA axes >0.6 (Table S8). Among these, new ponds showed higher CWMs than reference sites for 'aerial active' (within the Dispersal trait), 'flier' (Locomotion and Substrate Relation trait) and 'one pair of wings plus one pair of elytra/pseudoelytra' (Wing Pair Type trait; Figure 4; Table S9). Reference sites showed higher CWMs for 'predators' (Feeding Habit trait), 'no wings' and 'two pairs of wings' (Wing Pair Types trait; Figure 4; Table S9).

3.2 | Beta diversity

Differences in the contribution to regional functional turnover and nestedness between wetland types varied between years (Figure 5; Table S10). In both years, reference sites contributed more than new ponds to functional turnover, while in 2011 new ponds contributed more than reference sites to functional nestedness. The permutation test of multivariate homogeneity of group dispersions showed no significant differences in the level of beta diversity (intra-group differences) or its components between new ponds and reference sites (Figure 6; Table S11). However, multivariate dispersion analyses showed a clear separation between reference sites and new ponds for total beta diversity and turnover in 2011 (Figure 6).

Generalized dissimilarity modelling models showed that dissimilarities between wetland types in regional functional beta diversity, turnover and nestedness depended on different variables each year (Figure 7; Table 1). In 2010, no significant variables were found to affect total beta diversity and turnover, while nestedness increased steadily with emergent vegetation cover and values of total nitrogen >1.5 ppm (Figure 7). During 2011, total beta diversity increased with geographical distance and with values of turbidity above 60 NTU; turnover increased with geographical distance until around 0.025 decimal degrees, distance to the nearest pond, distance to the nearest reference site (especially in the first 1,000 m) and fish presence; and nestedness increased with pH, plateauing around a pH value of nine (Figure 7).

4 | DISCUSSION

We used a trait-based approach to evaluate the efficacy of wetland restoration in supporting macroinvertebrate functional diversity in South-West Spain. Functional traits have been used previously to measure restoration success in other aquatic systems and taxa (Español et al., 2015; Josué et al., 2021), but in our unique study of a Mediterranean restoration we partitioned total functional beta diversity into its turnover and nestedness components, and explored how environmental and spatial variables affected the dissimilarities of the restored area. We found some aspects of alpha functional diversity were still lower in new ponds than in reference sites 6–7 years after restoration, resulting in contrasting mechanisms affecting their contributions to the regional functional beta diversity. We also found that functional diversity among wetland types was driven by both dispersal-based processes (through trait replacements) and environmental filtering (through trait losses).

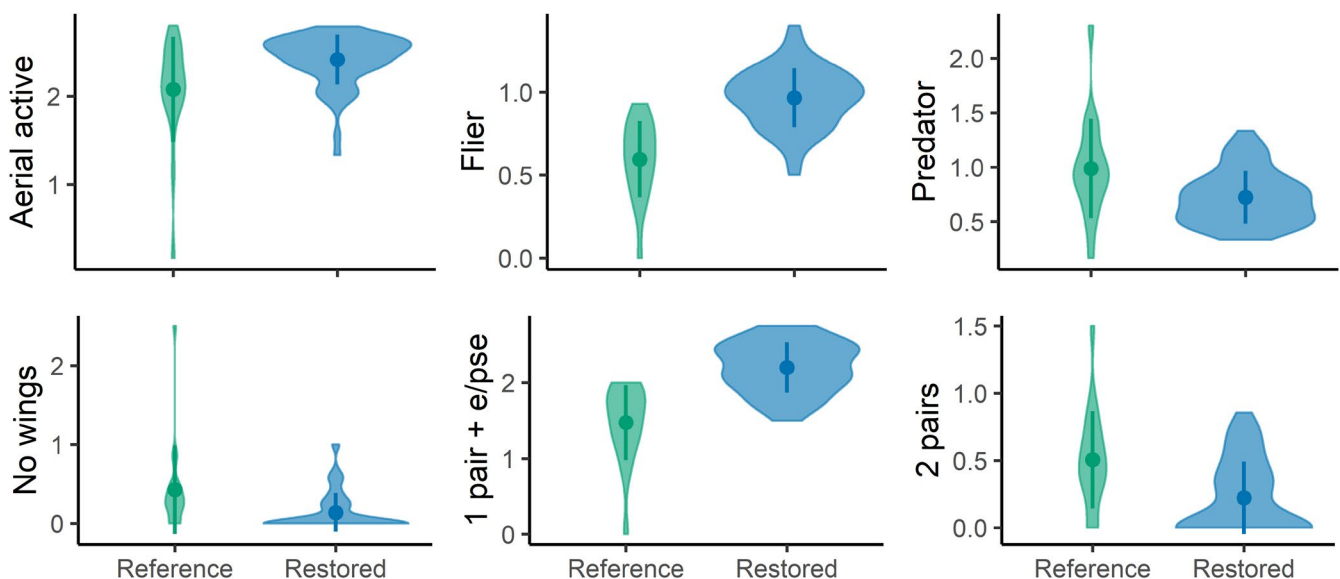


FIGURE 4 Violin plots of the raw Community-Weighted Means values (mean \pm SE) according to wetland type. CWMs are only shown for which linear mixed models indicated a significant difference between wetland types. 'Aerial active' (Dispersal trait); 'flier' (Locomotion and Substrate Relation trait); 'one pair of wings plus one pair of elytra/pseudoelytra' (Wing Pair Types trait); 'predators' (Feeding Habit trait), 'no wings' and 'two pairs of wings' (Wing Pair Types trait)

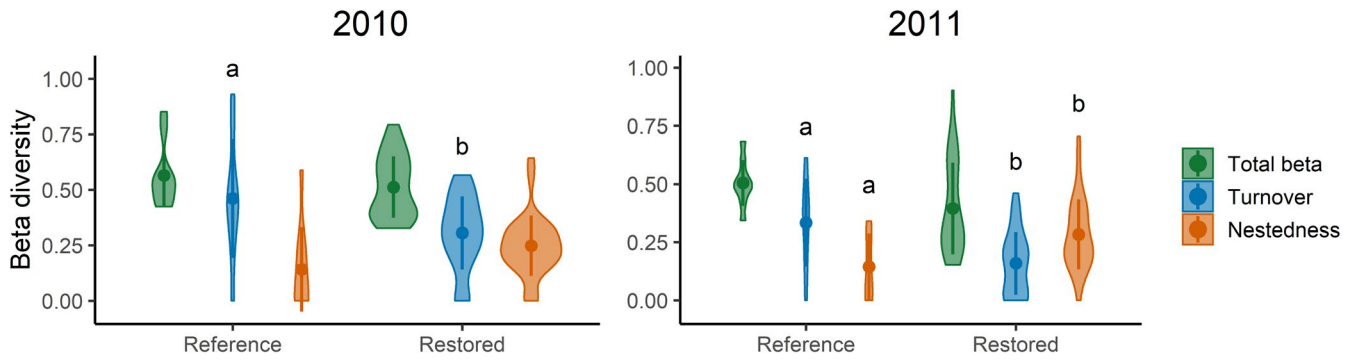


FIGURE 5 Violin plots of the distances (mean \pm SE) of each wetland type to the median of all sites (new ponds and reference sites combined) in the multivariate space for functional beta diversity and its two components in each year and pond type. These values represent the contributions of each wetland type to regional beta diversity (and regional turnover and nestedness). Letters indicate significant differences between types according to linear models

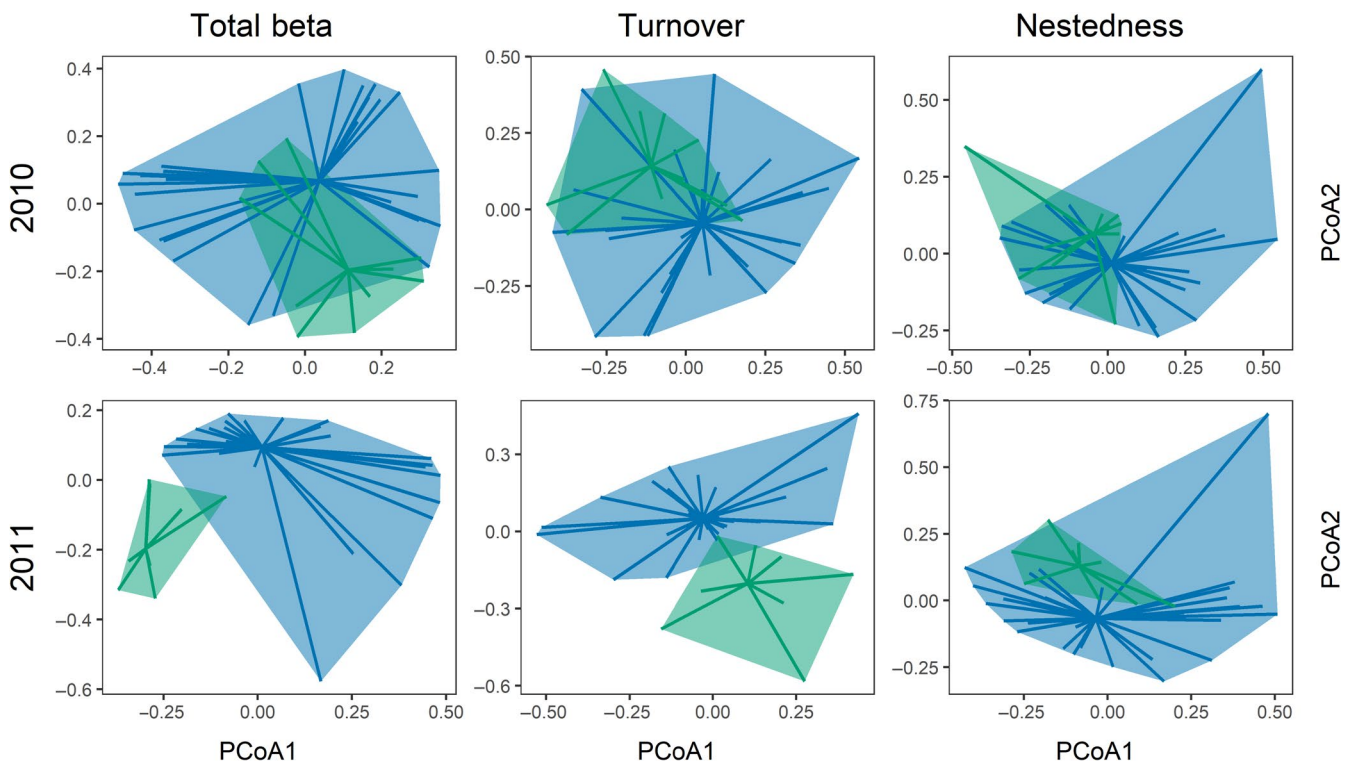


FIGURE 6 Multivariate dispersion analyses showing the distances between each reference site to the median position for all reference sites (green lines), and between each new pond and the median position for all new ponds (blue lines) for total beta diversity, turnover and nestedness during each year

4.1 | Differences in functional alpha diversity between new ponds and reference sites

As hypothesized, macroinvertebrates in new ponds showed lower functional richness (FRic) and dispersion (FDis) than in reference sites. Functional richness tends to be related to taxonomic richness (i.e. higher functional richness in taxonomically richer sites, see Mason et al., 2005), but taxonomic diversity in new ponds matched, or was even higher than that of reference sites (Coccia et al., 2016). This indicates that multiple species in new ponds possess similar trait

combinations, and thus do not occupy the functional space as efficiently as those in reference sites (Mason et al., 2005), suggesting functional redundancy (Lawton & Brown, 1993).

Functional redundancy can result from strong environmental filtering early after restoration, that is, abiotic conditions select for species according to their tolerance, filtering suitable traits (Helsen et al., 2012). However, the trait convergence found in this study was mainly related to dispersal-related traits (e.g. aerial dispersal, flier, winged organisms) affecting the capacity to colonize new habitats. Dispersal is expected to be high in early colonizers common in

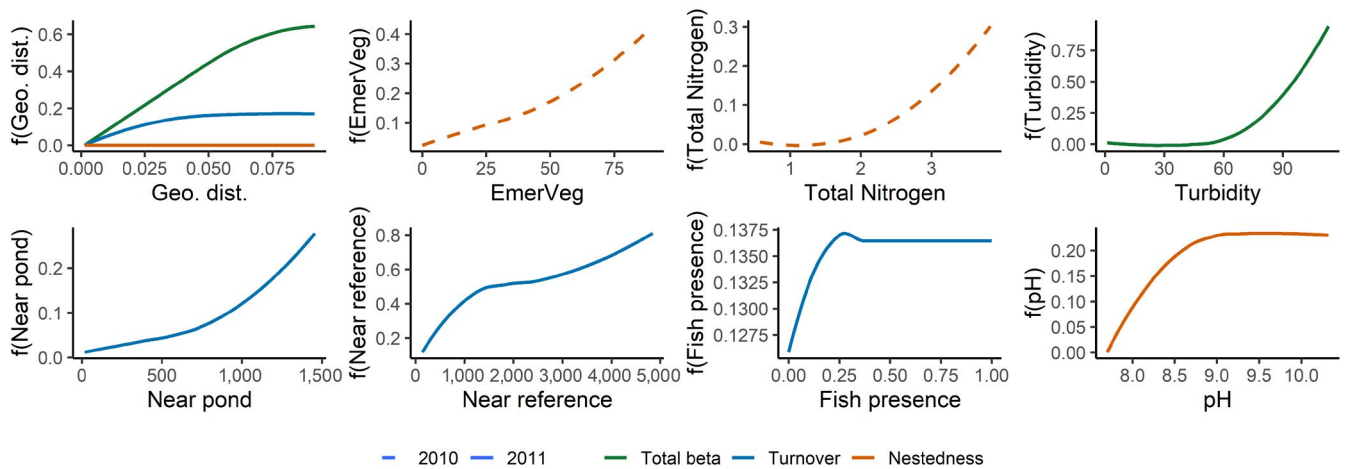


FIGURE 7 Partial regression fits of geographical distance and selected environmental variables as predictors of total functional beta diversity (green line), turnover (blue line) and nestedness (orange line) for reference and restored sites combined in 2010 (dashed line) and 2011 (solid line). The steeper the slope of the line, the greater the predicted beta diversity (or turnover/nestedness) on that section of the gradient. Geo. Dist., geographical distance; EmerVeg, emergent vegetation presence; Near pond, nearest new pond; Near ref, nearest reference

TABLE 1 Explained deviance and *p*-values from final generalized dissimilarity models (GDMs) of regional beta diversity, and information on their selected variables. Variable importance is measured as the percent change in deviance between the full model and a model fit with that variable permuted

	Explained deviance	Model <i>p</i> -value	Selected variables	Variable importance	Variable significance	Fitted permutations
2010						
Total beta	—	—	—	—	—	—
Turnover	—	—	—	—	—	—
Nestedness	21.65%	0.007	Geograph. distance	0%	0.006	967
			Emergent vegetation	36.1%	0.016	995
			Total nitrogen	35%	0.006	999
2011						
Total beta	24.1%	<0.001	Geograph. distance	39.7%	0.001	938
			Turbidity	52%	0.009	999
Turnover	27.4%	<0.001	Geograph. distance	4.5%	<0.001	986
			Nearest pond	10.8%	0.025	999
			Nearest reference	50.2%	0.005	999
			Fish presence	8.3%	0.011	999
Nestedness	6.5%	0.044	Geograph. distance	0%	0.038	909
			pH	94.6%	0.033	999

new ponds, such as Coleoptera and Hemiptera (which have 1 pair of wings + psuedoelytra), which are fast colonizers (Ruhí et al., 2013) that establish rapidly and then persist (Fairchild et al., 2000). In contrast, the greater association of species that lack wings (low propensity to dispersal; e.g. Crustacea and Gastropoda) or possess two pairs (e.g. Odonata) and are predators, with reference sites reflect their greater maturity and structural complexity (Coccia et al., 2016), providing more oviposition sites and prey. Other studies elsewhere showed predominance of high dispersal taxa in new restored ponds (Barnes, 1983; Kim et al., 2014; Lu et al., 2021;

Ruhí et al., 2013). Although communities in both wetland types are largely re-assembled through colonization from nearby permanent wetlands, new ponds are more dominated by early colonizers whose movement from one new pond to another could be enhanced either by their homogeneous environmental conditions or their spatial configuration. From a functional perspective, this suggests that the restoration remains in a pioneering phase, which could be expected since these are temporary wetlands and given the slow recovery of macroinvertebrate communities in general (Moreno-Mateos et al., 2012).

4.2 | Patterns of functional beta diversity

Contrary to our expectations, the individual contribution of new ponds and reference sites to the regional functional beta diversity was similar. Nevertheless, reference sites contributed more to regional functional turnover, whereas new ponds contributed more to regional functional nestedness. This may reflect the greater functional redundancy of new pond communities compared to reference sites, and their tendency to possess a subset of traits from more functionally diverse reference sites.

This result contrasts with the previous study based on taxonomic diversity (Coccia et al., 2016), in which new ponds were not found to be impoverished taxonomic subsets of reference sites. Mismatches between taxonomic and functional composition patterns have been reported in aquatic macroinvertebrates (Bevilacqua & Terlizzi, 2020; Heino & Tolonen, 2017), as a result of different processes operating on the multiple facets of biodiversity. Here, the elimination of some taxa may have also played a role. On the other hand, findings for functional macroinvertebrate diversity do not generally apply to other taxonomic groups, since they are not good surrogates, for example, for vertebrate communities (Guareschi et al., 2015). Neither do such functional results indicate value for specialized species, which may benefit, for example, from low connectivity (Pander et al., 2018).

Importantly, May communities in these Mediterranean wetlands consist mostly of macroinvertebrates that lack resistant stages to survive the long, dry summer, and that recolonize these sites each year. In such colonization-dominated systems, significant levels of nestedness are not unusual (Ruhí et al., 2013), as strong dispersers that dominate pioneering communities drive nested patterns (Flores et al., 2011). However, the varied contribution of functional nestedness and turnover across wetland types and time suggests that colonization changed between years, especially within new ponds. There are several factors, not included in this study, that can drive colonization patterns and processes. For example, intrinsic waterbody characteristics (e.g. water permanence) and specific species landscape perceptions (Cunillera-Montcusí et al., 2020; Pires et al., 2017) may have changed according to annual variation in precipitation while the colonization by invasive species increased during the second studied year (e.g. *Trichocorixa verticalis*, Coccia et al., 2016), perhaps accentuating the degree of nestedness in new ponds.

Further research is needed to investigate these factors and to assess whether the functional composition of new ponds will become more, or less, similar to that of reference sites over time.

4.3 | Processes affecting functional dissimilarities across the study area

We found that spatial and environmental variables had weak power in explaining the functional beta diversity between new ponds and reference sites. This result agrees with previous studies revealing

that functional beta diversity and its components were poorly predicted by environmental and spatial variables for aquatic macroinvertebrates (Heino & Tolonen, 2017; Hill et al., 2019; Perez-Rocha et al., 2018). However, unlike these studies, we found a relatively stronger spatial effect on functional turnover, whereas environmental variables exerted a stronger control on functional nestedness. These differences could reflect the different spatial extent of study areas (280, 170 and >100,000 km², respectively, in the above studies, vs. 27 km² in ours), as mechanisms driving biodiversity patterns are scale dependent (Heino et al., 2015).

Dissimilarities in functional composition between wetland types increased continuously as geographical distances between them increased (Figure 6). Interestingly, wetlands that were closer to each other exhibited lower functional turnover, which increased as the distances among them increased (Figure 6). Spatially close wetlands tend to be more similar environmentally, biologically and functionally (Leibold & Chase, 2018). Since this study included taxa with different dispersal abilities, over short distances species with similar functional traits likely replaced each other among adjacent new ponds and reference sites, producing low functional turnover between them (i.e. homogenization by dispersal). In contrast, incomplete colonization and/or limited dispersal across distant ponds and reference sites, which can occur even for stronger dispersers (Gálvez et al., 2020), could have increased their dissimilarities in functional composition. However, it remains possible that the significant spatial effect found in this study results from spatially structured environmental variables that were not measured (Legendre et al., 2005).

Environmental variables significantly explained both regional functional beta diversity and its components. Turbidity, fish, nutrient enrichment, pH and emergent vegetation were the most relevant predictors (Figure 6). All these variables are known to affect macroinvertebrate assemblages and functions (Forio et al., 2018; Hill et al., 2019; Perez-Rocha et al., 2018; Swartz et al., 2019) and some of them also induced taxonomic nested patterns in aquatic ecosystems (Gianuca et al., 2017). New ponds showed turbidity values below the threshold where most functional changes occur (Figure 6), contrary to the most isolated reference sites (i.e. Entremuros 1 and 2, Caño and Rosaliman, see Figure 1) being well above this threshold (Coccia et al., 2016). In addition, fish were detected in a lower proportion of new ponds than in reference sites (Table S4), and macroinvertebrate communities tend to be more dissimilar in functional composition when fish are present. New ponds appear to provide a refuge for macroinvertebrates against the strong effects of fish predation and/or perturbation (Maceda-Veiga et al., 2017), supporting communities that are functionally different from those in reference sites.

However, new ponds also possess lower vegetation cover and showed pH and nitrogen concentration values above the thresholds driving nested patterns (Table S4). Since nestedness can result from differences in environmental tolerance among species (Driscoll, 2008), some sets of functional traits related to environmental heterogeneity and sensitivity to stressors have likely not yet been

established in new ponds, producing assemblages with a nested subset of traits from reference sites.

On the other hand, different variables were important in each hydroperiod. The time and frequency of inundation changed between years (Coccia et al., 2016), and even small variations in hydroperiod length may change macroinvertebrate communities (Jeffries et al., 2016; Pires et al., 2021).

5 | CONCLUSIONS

New ponds are less functionally diverse than reference ponds, reflecting the dominance of pioneering species, but their contribution to the overall functional beta diversity was similar to reference sites, although each contributed more to one component of beta diversity. Environmental filtering and dispersal limitation are key drivers of changes in functional composition between new ponds and reference sites, but their importance changed between beta components. Overall, new ponds did not reach functional equivalency to natural wetlands within 7 years from restoration. However, their diverse spatial configuration and environmental characteristics allow them to support a different functional composition from reference sites. Nonetheless, their contribution to the regional functional diversity is mostly due to trait losses.

Wetlands are subjected to dynamic changes that can modify their spatial distribution (e.g. connectivity) and environmental conditions, which, in turn, affect how species move between sites. In the Mediterranean area, these dynamics will be further affected by climate change and by its interactions with local stressors such as salinity and nutrient loadings (Green et al., 2017). Our results suggest that future wetland restorations should consider both spatial and temporal landscape dynamics (e.g. through remote sensing) to predict potential restoration trajectories.

We showed that a trait-based approach reveals different and complementary insights compared to a taxonomic perspective, even over a short time frame. We recommend incorporating both taxonomic and functional diversity in post-restoration monitoring, to detect trajectories towards a comprehensive recovery of biodiversity following restoration. We also emphasize the value of the functional approach in inferring mechanisms behind community assembly, so facilitating the planning and implementation of management.

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CONFLICT OF INTEREST

The authors declare no conflict of interest with the publication of this article.

AUTHORS' CONTRIBUTIONS

C.C., B.A.A., A.J.G. and J.A.C. conceived the study; C.C. J.A.C. and A.B.G collected the data; B.A.A. analysed the data; C.C. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.z8w9ghxcn> (Coccia et al., 2021).

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