



Connection over creation: hydrological connectivity drives post-restoration community assembly in coastal ponds

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Abstract Evaluations of wetland restoration have often focussed on the role that dispersal, environmental filters and/or spatial features play in new habitats. Success has generally been measured by comparing new habitats with reference sites. However, in coastal ponds, hydrological connectivity can determine environmental constraints as it can influence salinity, nutrient concentration, and connectivity strength. Based on these premises, we expect that hydrological connectivity should be a stronger determinant of community assembly following restoration. To test this hypothesis, we took advantage of a restoration project carried out in La Pletera salt marsh (NE Iberian Peninsula) and compared the effects of hydrological connectivity and pond age on community composition and functioning after restoration. Macroinvertebrate communities of 13 ponds (10 new and 3 old) were

surveyed in 2016, 2017 and 2022. We analysed community changes over time by comparing nestedness, modularity, diversity, and similarity indices between pond categories and based on taxonomic and biological trait data. Our results showed that hydrological connectivity shaped two distinct communities. These findings underscore the central role of hydrology in community dynamics and highlight the importance of integrating hydrological connectivity into restoration strategies for coastal ponds.

Keywords Wetland restoration · Biological traits · Macroinvertebrates · Coastal ponds

Introduction

The growing concern for the conservation and recovery of aquatic habitats has led to the implementation of restoration projects in recent decades to maintain the ecological and socio-economic importance of these habitats (Meli et al., 2014; Pueyo-Ros et al., 2018; Pereira-Lindoso et al., 2025). In some of these projects, the creation of new ponds has been undertaken with the aim of increasing the functionality and biodiversity of the habitats, especially in those areas where they were desiccated some decades ago (Perennou et al., 2012; Ruhí et al., 2016). Such initiatives have provided an opportunity for ecologists to study community assembly and colonisation dynamics in newly created habitats (e.g. Coccia et al., 2016;

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Cabrera et al., 2019; Hernández-Carrasco et al., 2023).

Several ecological processes, at both regional and local scales, determine community assembly in time and space (De Bie et al., 2012; Sarremejane et al., 2017; García-Girón et al., 2020) in recently created habitats. These early stages of colonisation are determined by: (1) the egg banks present in the sediments (Cabrera et al., 2019) and (2) habitat connectivity, which is determined by both habitat spatial distribution and the dispersal capacity of species present in the region (Cañedo-Argüelles & Rieradevall, 2011), that together define a network of interconnected communities (Barnes, 1983; Cunillera-Montcusí et al., 2020). Therefore, nested communities will emerge at the outset of colonisation, as species in new habitats will represent a subset of the species present in the regional species pool (Ruhí et al., 2013). Later on, the abundance of fast colonisers is expected to progressively decline because of the arrival of passive dispersers, resulting in the homogenisation of the community with nearby habitats, concomitantly decreasing nestedness (Ruhí et al., 2012). However, the relative location within the landscape (i.e. centrality-isolation gradient) of the network of habitats may affect this process of homogenisation, making it stronger in more central locations which are more connected to surrounding neighbours (Cunillera-Montcusí et al., 2020). In contrast, isolated habitats would present a more heterogeneous assembly, composed of species with good dispersal abilities and more subjected to stochasticity and priority effects, which occur when a group of individuals establishes a new population in a new habitat, monopolising available resources at the early stages of colonisation (Fukami, 2015). Therefore, over time, the centrality-isolation gradient may lead to greater modularity at the metacommunity level. On the one hand, higher connectivity among more central locations would lead to a higher presence of the same set of species, which would define a group (i.e. module) of communities. In contrast, more isolated communities would tend to host more different sets of species (e.g. organisms with greater flight capacity), which in turn could also explain the formation of other modules comprising distinct communities (Economato & Keitt, 2010; Fletcher et al., 2013). Overall, the influence of the centrality-isolation gradient would result in more modular structures, where communities are grouped

into clusters that share more species within the group but diverge from other clusters. This contrasts with nested structures, where species found in more isolated communities represent subsets of those found in more central and connected communities (Borthagaray et al., 2014; 2015; Grilli et al., 2016). This stresses the necessity to account for the spatial structure in guiding biodiversity management strategies (Savary et al., 2024). Additionally, local processes such as biotic interactions and abiotic conditions also contribute to community changes during colonisation in both new and existing habitats (Waterkeyn et al., 2008; Florencio et al., 2014; Hernández-Carrasco et al., 2023). For example, newly created systems can increase habitat heterogeneity at regional scale, supporting new species and increasing the complexity of biotic interactions in existing communities (Hernández-Carrasco et al., 2023). Moreover, the abiotic characteristics of the habitat, such as conductivity and surface area, can also influence community composition and structure. Indeed, increased conductivity tends to simplify communities (e.g. decreasing species richness; Muresan et al., 2020), while surface area is usually positively correlated with species richness (Basset et al., 2007). The drivers described above are closely interconnected and influence key ecological mechanisms simultaneously, making it essential to consider them collectively (Leibold & Chase, 2018; Thompson et al., 2020).

Mediterranean coastal ponds are strongly determined by hydrological connectivity, which drive community assembly structure and composition because of the alternation of flooding-confinement periods (Badosa et al., 2006; Beklioglu et al., 2007; Cabrera et al., 2019). On the one hand, ponds can become superficially interconnected, forming a continuous aquatic network, as a consequence of flooding events (e.g. intense rainfall or occasional seawater input after sea storms), but after these events, they will progressively become isolated during confinement periods (i.e. summer dry months) with the concomitant effects on dispersal between ponds. On the other hand, hydrological connectivity affects abiotic conditions (e.g. nutrients, conductivity) enhancing environmental filtering and favouring species with specific traits (Townsend & Hildrew, 1994; Poff, 1997; Ruhí et al., 2014). Such recurrent disturbances may facilitate the arrival of species that are better adapted to these conditions and thus replace the existing ones

(Félix et al., 2015; Williams-Subiza et al., 2022). Therefore, hydrological connectivity may have the potential to be as relevant as other factors (e.g. pond age) when assessing post-restoration trends in coastal pond metacommunities.

Typically, restoration actions have been evaluated by comparing communities in new sites with existing ones (Coccia et al., 2016; 2021; Cabrera et al., 2019; de Donnová et al., 2022). However, in highly dynamic systems such as coastal ponds, hydrological connectivity should also be considered to fully account for all the factors driving restoration success. In this study, we assess the importance of hydrological connectivity after a restoration project conducted in several Mediterranean coastal ponds located in La Pletera salt marsh, in the NE Iberian Peninsula. This restoration project was undertaken to re-establish the coastal pond network and to restore its ecological function (Hernández et al., 2023). As part of it, several ponds were created, allowing us to simultaneously consider pond age (comparing old vs. new ponds) and hydrological connectivity (high-connected ponds vs. low-connected ponds). We monitored environmental parameters and changes in macroinvertebrate community diversity and composition. Additionally, we compared functional metrics across pond categories by considering species biological traits. Thus, we incorporated a complementary functional perspective providing new insights into restoration assessments (Antón-Pardo et al., 2025; Bonada et al., 2007; Cadotte et al., 2011; Coccia et al., 2024). We tested three hypotheses in this study. (H1) Communities in newly created ponds will represent a subset of the existing ones (i.e. higher nestedness metacommunity structure) at the beginning of the colonisation process (i.e. 2016), but they will progressively become modular (i.e. increasing clustering within the metacommunity network) responding to hydrological connectivity and environmental filters. When analysing the changes observed over time, we hypothesise (H2) that the rate of change in community composition will be greater in newly created ponds compared to existing ones as a consequence of colonisation. Furthermore, these temporal changes should also respond to differences in hydrological connectivity, with low-connected ponds becoming more heterogeneous over time, as they are less connected to the rest of the system (Jeffries, 2011). Finally, we also expect that (H3) hydrological connectivity will influence community diversity

and composition during the colonisation process. Consequently, we anticipate a decrease in the differences between new and existing ponds beyond the second year (i.e. from 2017 and onwards). However, we expect differences to emerge beyond this point between ponds due to their hydrological connectivity. Functional trait results should align with taxonomic community patterns, as hydrological connectivity is likely to create two distinct subsets of communities, each adapted to specific habitat conditions and characterised by different trait modalities.

Materials and methods

Study area

The studied Mediterranean salt marsh, called La Pletera, is located in the NE Iberian Peninsula, in Baix Ter Wetlands, between l'Estartit village and the mouth of the Ter River. Its frontline is about two kilometres parallel to the sea and a foredune. This study focuses on a group of temporary and permanent ponds within La Pletera salt marsh that are not directly connected to the sea via surface water (Fig. 1; Supplementary Material 1). This site constitutes a perfect candidate to test our hypotheses, since La Pletera landscape was degraded in 1987 due to an unfinished urbanistic project, which diminished its ecological value and functioning. Later, this area was protected and included in the Natura 2000 network. In 2002, a Life project (LIFE99NAT/E/006386) was implemented, creating three ponds to improve Iberian toothcarp [*Aphanius iberus* (Valenciennes, 1846)] populations, an endemic fish species that is in danger of extinction. A second Life project (LIFE13NAT/ES/001001) was conducted between 2014 and 2016 with the aim of restoring the ecological system and its functioning and enhancing the system's resilience to anticipated impacts of climate change. Through this project, the remnants of urbanisation were first removed, clearing the area of rubble and debris. Hydrological and geomorphological studies were conducted beforehand to evaluate the feasibility of pond creation. Subsequently, holes were dug in the cleared ground to form the structure of the ponds, which were naturally filled with rainwater and/or groundwater. These newly created ponds significantly enhanced the connectivity of the salt marsh.

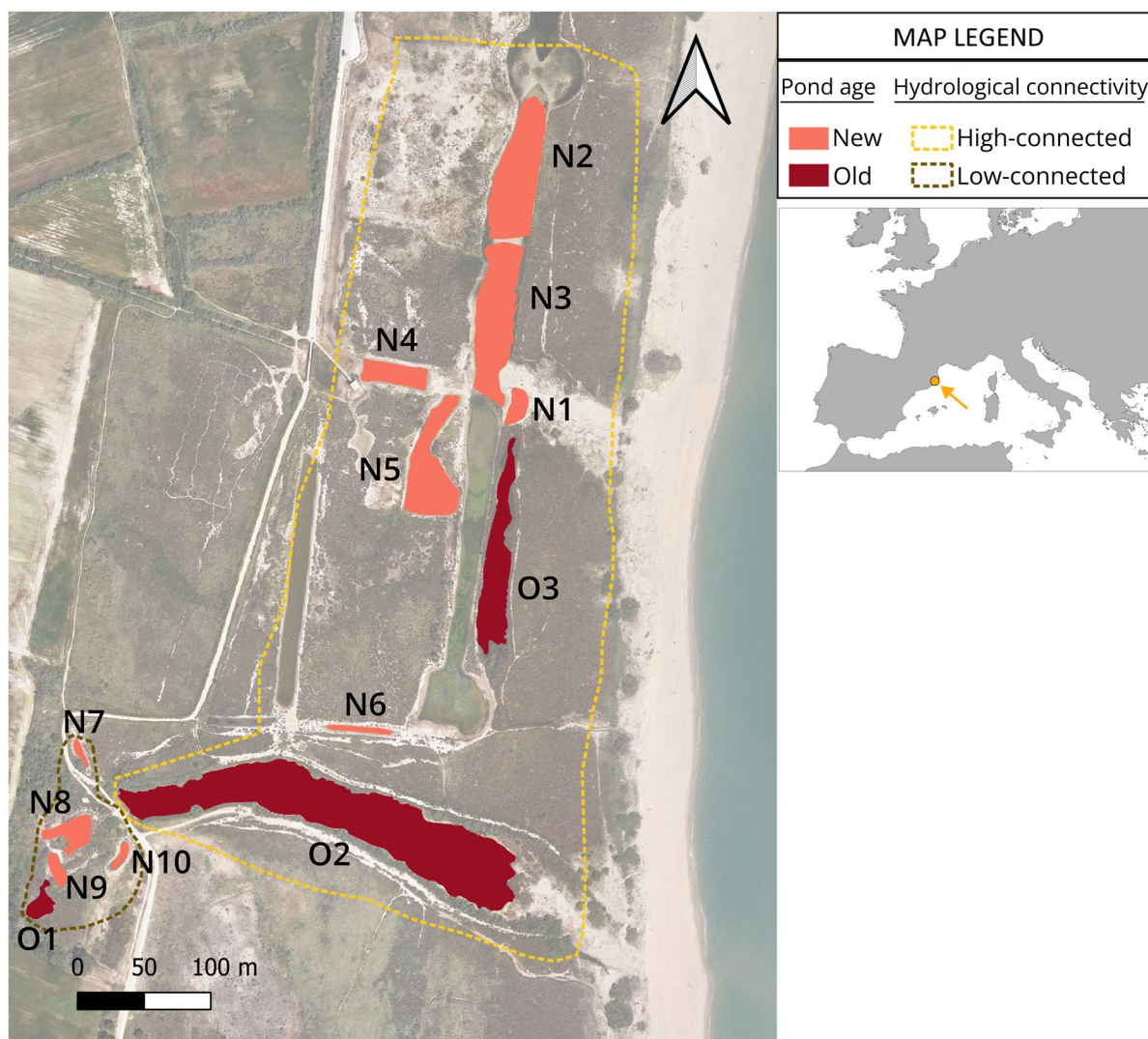


Fig. 1 Map of La Pletera salt marsh showing the location of the thirteen surveyed ponds

The hydrology of La Pletera salt marsh is characterised by flooding-confinement cycles. Flooding periods are driven by rainfall, sea storms, and groundwater inputs, whereas confinement periods can result in a high decrease of the water level and even desiccation in temporary ponds (Quintana et al., 1998; Menció et al., 2017). These fluctuations influence both abiotic conditions and hydrological connectivity among ponds (Quintana et al., 1998; Badosa et al., 2006). Following the creation of La Pletera ponds in 2016, significant floods occurred between December 2016 and February 2017, causing a water level rise above 1 m a.s.l (Pascual & Martinoy, 2018), and

connecting superficially all the ponds. Since hydrological connectivity depends on ground elevation, we classified ponds into two groups according to the probability of being connected after a flooding event: high-connected ponds, which connect even when the water level rises below 1 m a.s.l, and low-connected ponds, which only connect when water levels surpass 1 m a.s.l. (Pascual & Martinoy, 2018; Supplementary Material 2). Interestingly, this classification, based on the hydrological connectivity of ponds, does not correspond to their permanent or temporary nature. In this sense, when comparing between hydrological connectivity, both categories included all types of

ponds in terms of water permanence. It allows us to test how hydrological connectivity influences community structure and composition during the colonisation process.

Field sampling

For this study, we selected 13 ponds. Three of them, all permanent, were designated as “old” ponds, since they existed before the second restoration project. The other ten ponds, referred to as “new”, were created during the second restoration project, between October 2015 and March 2016. One of these is permanent, while the others are temporary (Fig. 1).

The selected ponds were surveyed on three occasions: the first year after restoration (2016), the following year (2017) and 6 years later (2022), always between April 15 and 20.

In each survey, temperature, conductivity, pH, and dissolved oxygen were measured in situ at 0.5 m depth with a Hach HQ30d portable multiparameter probe. The habitat quality was also evaluated using ECELS index (Conservation status of Shallow Lentic Ecosystems; Sala et al., 2004). This index allows us to assess habitat quality with a value ranging from 0 to 100, being 100 the highest expected quality of a pond. It considers five aspects: (I) pond morphology, (II) human activity around the pond, (III) aspects of pond water, (IV) emergent vegetation of the pond, and (V) hydrophytic vegetation of the pond. Macroinvertebrates samples were taken from each pond using a dip-net of 20 cm in diameter and a mesh size of 250 μm . We followed the official and standardised protocol to assess the ecological status of lentic Mediterranean ecosystems (Agència Catalana de l'Aigua, 2006; Boix et al., 2005). Thus, we did 20 dip-net sweeps of 1 m long in each pond. The dip-net sweeps were evenly distributed trying to cover all the present mesohabitats. The obtained samples were preserved in situ with 4% formalin.

Taxonomic and trait data

In the laboratory, taxa were identified at species level, when possible, except for some Diptera and Oligochaeta that were identified at subfamily and family level (mainly using Franciscolo, 1979; Jansson, 1986; Tachet et al., 2010; Queney & Prévost, 2021). Identification was carried out with a stereomicroscope.

Then, taxa abundance (number of individuals per sample) and biological trait abundance were estimated for each pond. Abundance was extrapolated per unit of sampling effort (number of individuals in 20 dip-net sweeps) across the different samples to compare abundance values. We selected seven functional traits related to morphology and physiology (maximal potential body length and respiration), trophic characteristics (feeding habits and food preferences), resistance potential (dispersal ability, locomotion and substrate relation) and life history (aquatic stages). We selected these traits because they are directly linked to key ecological processes such as species dispersal and mobility (e.g. colonisation of new habitats), and species relationship with the environment (e.g. resistance to harsher conditions; Español et al., 2014; Coccia et al., 2021; Martini et al., 2021). Tachet et al. (2010) was used to assign affinities to the different trait modalities. Additionally, we used Budd (2008), Faulwetter et al. (2014) and polytraits database to assign Polychaeta trait modalities. When taxonomic classification in our data was at family or class level, we used the mean of all genera affinities corresponding to each group. Affinities were converted to fuzzy codes (following Chevene et al., 1994) and weighted by the corresponding sample taxa abundance (number of individuals per sampling effort).

Data analysis

Two factors were included in our analyses: hydrological connectivity (i.e. high-connected vs. low-connected) and pond age (i.e. old vs. new). Additionally, to assess changes in environmental conditions over the study period, we conducted a principal component analysis (PCA) using z-score normalisation for the variables. Samples were grouped by surveyed years and by the factors under investigation to facilitate comparison.

To test our first hypothesis, we calculated metacommunity nestedness and modularity for each studied year using bipartite networks. In total, we constructed six bipartite networks as a result of combining data types (trait or taxonomic) and studied years (2016, 2017 and 2022). These networks define the site-species interactions and provide information about the structural properties of the metacommunity at each particular moment of the colonisation process: just after restoration (2016),

a year after restoration (2017), and six years after restoration (2022). Therefore, we have two different types of nodes, one corresponding to ponds and the other corresponding to taxa or traits in each case. Network links correspond to the presence of a particular species or trait in a pond. Abundance was also used to weight network links. Then, to assess the structural properties of the resulting networks, we computed network indices of nestedness NODF (Almeida-Neto et al., 2008) and weighted NODF (wNODF) (Almeida-Neto & Ulrich, 2011), as well as Modularity-Q (Dormann & Strauss, 2014). The NODF and its weighted equivalent, wNODF, are metrics directly based on the concept of nestedness that assess this property by comparing the degree of nestedness for each pair of rows and columns in the site \times species matrix. wNODF incorporates species or trait abundances, providing a weighted version of this metric. In contrast, Modularity Q quantifies the degree to which the sampled communities are structured into different clusters of more similar communities, by identifying subsets of nodes (modules) that are more strongly connected among themselves than with the rest of the network. We used these metrics to directly quantify these patterns, expecting higher nestedness at the beginning of the colonisation process, followed by an increase in modularity over time, as differences in hydrological connectivity will promote divergence among communities. Null models (500 per network using swap method) were carried out to obtain standardised values (z-values) of network parameters NODF, wNODF and Modularity-Q. These null models were constructed to conserve marginal totals of the matrix (i.e. species or trait richness) and connectance of the observed network (i.e. number of links). We used bipartite package v. 2.18 for the network analyses (Dormann et al., 2008; 2009, 2011).

To test our second hypothesis, we analysed the magnitude of community composition changes over time using community trajectory analyses (CTA). Prior to analysis, the data were transformed using the Hellinger method, and Bray–Curtis distances were calculated based on abundance data. The rate of community change for the two periods, from 2016 to 2017 and from 2017 to 2022, was determined by dividing the trajectory length of each period by the number of years it spanned (i.e. 1 and 5, respectively). Additionally, we calculated the trajectory net change by

considering the change along the whole study period, from 2016 to 2022. Ecological trajectories were calculated using the package *ecotraj* v. 0.1.1 (De Cáceres et al. 2019; Sturbois et al. 2021, 2023). Differences in trajectories between old and new ponds and high-connected and low-connected ponds were assessed with nonparametric Wilcoxon tests.

Our third hypothesis aimed to evaluate the impact of hydrological connectivity on community assembly. To achieve this, we assessed various metrics of taxonomic and functional diversity. On the one hand, we used two measures of taxonomic diversity (species richness and Shannon–Wiener diversity) which were obtained using Hill numbers (Hill, 1973), calculated through coverage-based integrations of rarefaction and extrapolation. For this, we used the *iNEXT* package v. 3.0.0 (Chao et al., 2014; Hsieh et al., 2016). We used four indices to characterise functional diversity, each capturing different aspect of trait distribution in communities: Functional Richness (FRic), which is the volume of trait space occupied by the community; functional Dispersion (FDis), the average distance of species to the trait space centroid; functional Divergence (FDiv), the spread of abundances towards extreme trait values; and functional Evenness (FEve), the regularity of abundance distribution within the trait space (Villéger et al., 2008; Laliberté & Legendre, 2010). To calculate functional diversity indices, we first computed a Gower dissimilarity matrix (de Bello et al., 2020) between pairs of species traits. This distance matrix was used to perform a Principal Coordinate Analysis (PCoA) where six axes were considered as dimensions of functional space. Finally, functional diversity indices were calculated from the position of samples in this functional space with package *FD* v. 1.0.12.1 (Laliberté and Legendre, 2010; Laliberté et al., 2014). Linear mixed models, including pond identity as a random intercept, were used to test the differences in taxonomic and functional metrics (response variables), among levels of the two analysed factors (pond age and hydrological connectivity). Samples with only one or two taxa were excluded from trait analysis. Thus, two samples taken in 2016 in new ponds were excluded. To assess community and modality-trait composition, non-metric multidimensional scaling (NMDS) was performed on taxonomic and on trait category matrices separately. Abundance data were log-transformed, and each trait matrix was transformed with centred

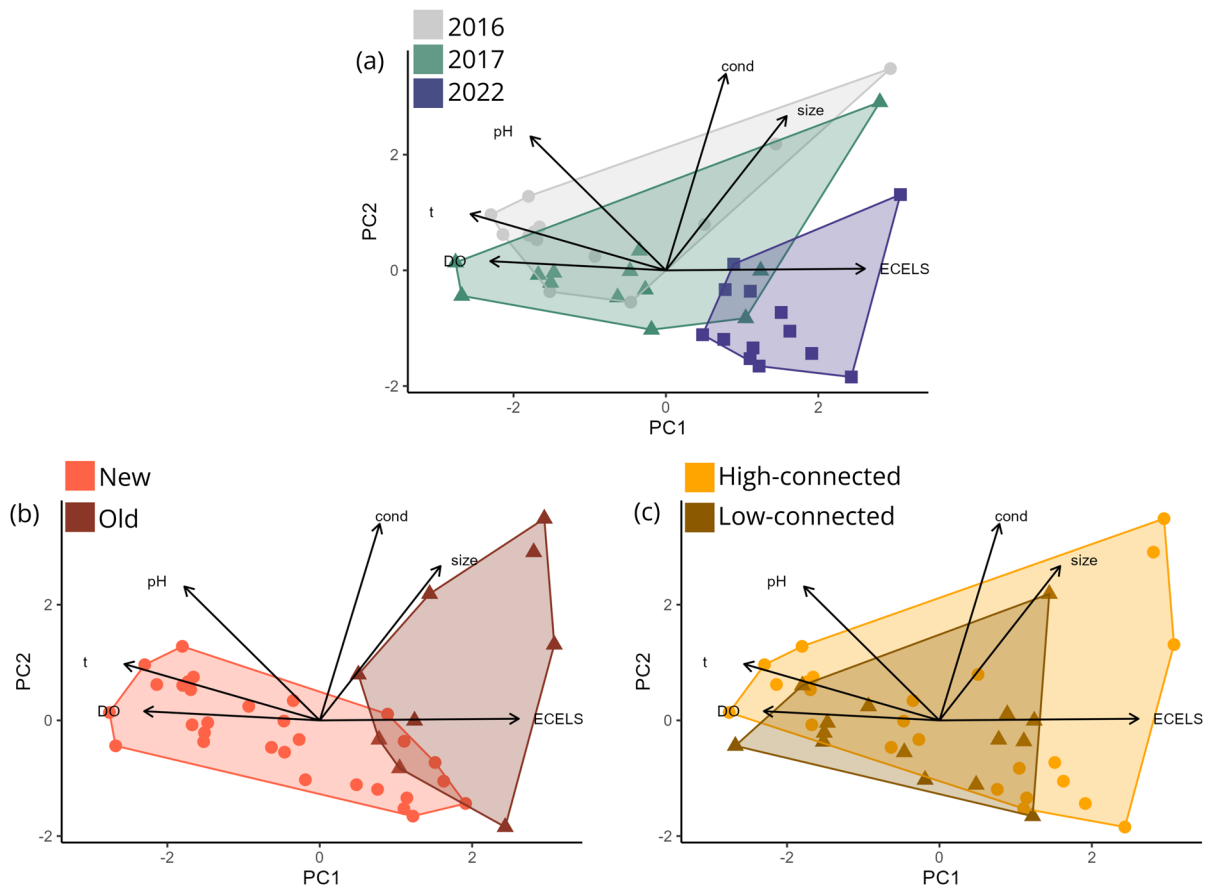


Fig. 2 PCA of environmental variables with distribution of samples. Polygons: **(a)** years, **(b)** pond age (New/Old), **(c)** hydrological connectivity (High-connected/Low-connected).

Variables: “cond”, conductivity; “DO”, dissolved oxygen; “ECELS”, habitat quality; “size”, pond size; “t”, temperature)

log-ratio (as these are compositional data), prior to obtaining the Euclidean distance matrices. To assess community composition and trait differences between factors we used Permutational multivariate analyses of variance (PERMANOVA) (using PRIMER v.6 version 6.1.11 with the PERMANOVA+ add-on v.1.0.1) with the year as a random variable and factors nested within years. This was coupled with a similarity of percentages analysis (SIMPER) to identify which taxa and trait modalities contributed to the observed differences in significant results. Additionally, we used multivariate homogeneity of variances (BETADISPER) to assess variance homogeneity between groups defined by the two factors studied (pond age and hydrological connectivity), to confirm the reliability of the significant results from the PERMANOVA analyses, since our design is not balanced

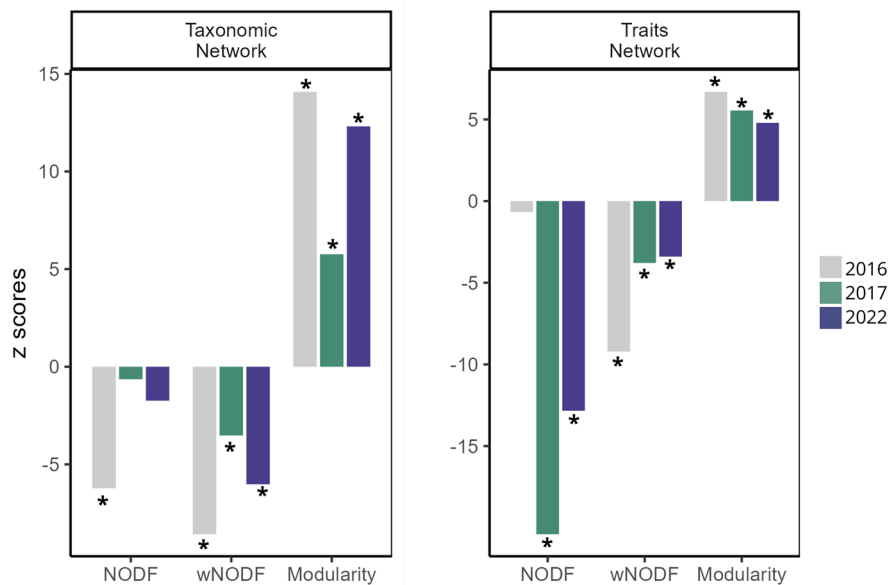
(Anderson and Walsh, 2013). These analyses were carried out with the vegan package v. 2.6.4 (Oksanen et al., 2022). All analyses and graphics were performed using the R language, version 4.3.0. (R Core Team, 2023).

Results

Environmental variables

The first two axes of PCA explained 68.61% of the total variance (Fig. 2). The first axis (45.7%) was positively related to habitat quality (ECELS index) and negatively related to dissolved oxygen and water temperature. The second axis (22.9%) was positively related to conductivity, pond size and pH.

Fig. 3 Z scores of the metrics calculated in bipartite networks (NODF, wNODF and Modularity Q). Taxonomic network refers to species abundance network, and traits network, to species biological traits. Significant values compared to null models ($P < 0.05$) are indicated with an asterisk



The distribution of samples in the space and groups defined by years showed a decrease in pH, dissolved oxygen and conductivity during the surveys (Fig. 2a). The factor pond age had a significant effect on habitat quality and conductivity, with higher values observed in old ponds (Fig. 2b). However, by 2022, new ponds had similar habitat quality values to those of old ponds, indicating that just six years after restoration, new ponds had become comparable to old ones (Supplementary Material 3). In contrast, the factor hydrological connectivity showed a strong overlap between high-connected and low-connected ponds, with high-connected ponds exhibiting greater variability (Fig. 2c).

Nestedness and modularity

When taxonomic data were used to calculate nestedness values, no nested structure was observed in any of the years. Instead, we identified anti-nested structures, where the species composition of less rich ponds did not represent a subset of the species found in richer ponds. The observed nestedness values for NODF in 2016 and wNODF in 2016, 2017, and 2022 were significantly lower than those predicted by the null models. In contrast, we did observe significant modularity values for the three surveyed years, with values higher than those of the null models,

indicating the existence of a more modular metacommunity structure. When we analysed biological traits, we also found anti-nested structures. In this case, significant results were observed for NODF in 2017 and 2022, and for wNODF in all years. Modularity-Q also showed significant results for the three years in functional networks with higher modularity than the null models (Fig. 3).

Temporal trajectories

Community trajectory analyses (CTA) of ponds showed that communities changed significantly from 2016 to 2017 (P1) in all ponds, even in the old ones (Fig. 4; Supplementary Material 4). In contrast, for the period from 2017 to 2022 (P2), the results showed a small amount of change per year. When comparing pond age, Wilcoxon analyses showed greater trajectory lengths in new ponds than in old ones for the P1 ($W=30$, $P=0.01$), as well as higher net change ($W=29$, $P=0.02$; Fig. 4a). When analysing hydrological connectivity, differences were only observed for P2, in which high-connected ponds showed shorter trajectory lengths than low-connected ones ($W=6$, $P=0.045$; Fig. 4b).

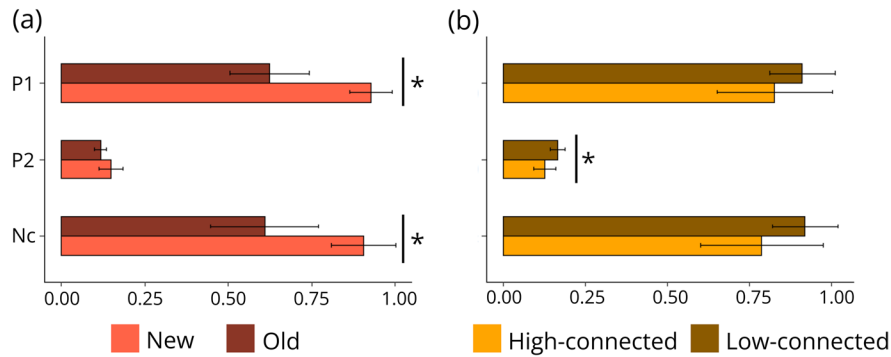
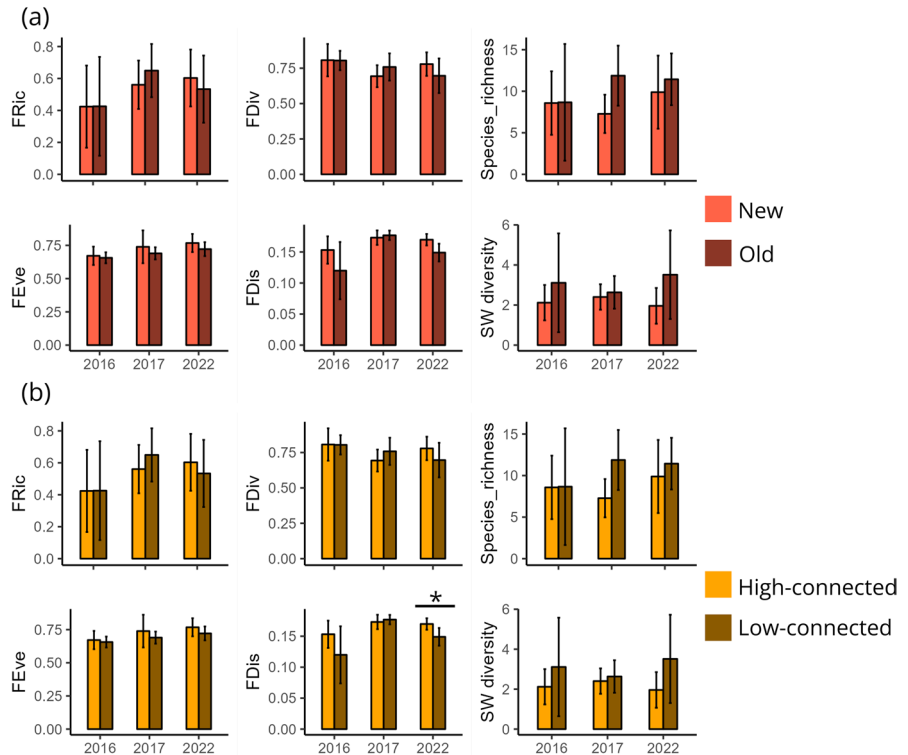


Fig. 4 Ecological trajectory lengths based on changes in community composition of two studied periods: P1 (2016–2017) and P2 (2017–2022) and net change of trajectories (Nc).

Grouped by (a) pond age (New/Old) and (b) hydrological connectivity (High-connected/Low-connected). Significant differences ($P < 0.05$) are indicated with an asterisk

Fig. 5 ANOVA results of taxonomic diversity indices (Species richness; Shannon–Wiener diversity, “SW diversity”) and functional diversity indices (Functional richness, FRic; functional dispersion, FDis; functional divergence, FDiv; and functional evenness, FEve) comparing (a) pond age (Old/New) and (b) hydrological connectivity (High-connected/Low-connected). Significant differences ($P < 0.05$) are indicated with an asterisk



Local community diversity and composition

Taxonomic and functional diversity indices (i.e. species richness, Shannon–Wiener diversity, FRic, FDiv, FDis and FEve) did not show differences between pond age categories (i.e. old and new ponds) for any of the surveyed years (Fig. 5a). In contrast, hydrological connectivity showed significantly lower

FDis (Fig. 5b) in low-connected ponds in 2022 ($F_{1,10} = 8.04$, $P = 0.05$; Supplementary Material 5).

Taxonomic results

In total, we found 38 different taxa throughout the study, but only 15 of these were found from the beginning to the end of the study, indicating a high

Table 1 Results of BETADISPER and PERMANOVA analyses comparing (a) pond age (Old/New) and (b) hydrological connectivity (High-connected/Low-connected) for each year sampled

	year	Old/New				High-connected/Low-connected			
		BETADISPER		PERMANOVA		BETADISPER		PERMANOVA	
		F(1,11)	P	t(1,11)	P	F(1,11)	P	t(1,11)	P
<i>Taxonomic</i>									
	2016	3.87	0.07	2.5	0.003*	0.22	0.64	1.44	0.058
	2017	0.77	0.39	0.89	0.5	3.33	0.09	1.61	0.01*
	2022	1.8	0.2	0.93	0.53	0.05	0.82	2.17	0.001*
<i>Traits</i>									
Maximal potential body length	2016	0.03	0.86	1.21	0.24	0.24	0.63	1.05	0.29
	2017	1.72	0.21	0.71	0.53	2	0.17	1.41	0.17
	2022	0.003	0.95	0.54	0.83	0.03	0.85	0.58	0.77
Aquatic stages	2016	1.09	0.31	2.49	0.03*	0.18	0.67	0.35	0.86
	2017	1.04	0.32	1.97	0.07	0.12	0.72	0.66	0.63
	2022	1.36	0.26	1.2	0.26	0.97	0.34	2.31	0.01*
Dispersal ability	2016	0.85	0.37	2.8	0.02*	0.22	0.64	2.07	0.03*
	2017	1.86	0.19	0.83	0.43	0.32	0.57	2.34	0.03*
	2022	0.24	0.63	0.36	0.83	0.59	0.45	5.05	0.002*
Respiration	2016	0.004	0.94	1.93	0.07	0.1	0.74	3.51	0.001*
	2017	0.004	0.94	0.23	0.81	1.2	0.29	3.93	0.01*
	2022	0.18	0.67	0.44	0.69	0.44	0.51	4.29	0.003*
Locomotion/ substrate relation	2016	0.02	0.86	1.75	0.07	0.14	0.7	2.21	0.01*
	2017	0.73	0.4	0.73	0.58	0.52	0.48	3.14	0.008*
	2022	0.03	0.85	0.74	0.55	1.06	0.32	4.31	0.002*
Food preferences	2016	0.72	0.41	2.75	0.004*	0.01	0.9	0.63	0.07
	2017	0.002	0.96	1.09	2.78	0.001	0.96	1.07	0.3
	2022	0.24	0.63	0.82	0.58	6	0.03*	1.97	0.01*
Feeding habits	2016	0.02	0.88	2.29	0.007*	0.02	0.87	1.35	0.1
	2017	0.09	0.76	1.08	0.28	0.65	0.43	1.9	0.046*
	2022	0.01	0.91	1.04	0.33	0.08	0.77	2.9	0.003*

Significant values ($P < 0.05$) are indicated in bold and with an asterisk

temporal replacement (Supplementary Material 6). We did not find significant differences in the variability of taxonomic composition between levels of pond age or hydrological connectivity (Table 1; Supplementary Material 7). Differences in taxonomic composition between pond age categories were only observed in 2016, the first year after restoration (Table 1). Taxa that contributed to these differences were the gastropod *Ecrobia ventrosa* (Montagu, 1803), dominating old ponds, and dipterans and hemipterans that dominated new ponds (Table 2). In 2017, when all ponds became superficially connected due to flooding, the relative abundance of gastropods, polychaetes, and amphipods increased across

all ponds (Supplementary Material 8), and no further age-related differences were detected afterwards. In contrast, differences in taxonomic composition associated with hydrological connectivity were only observed in 2017 and 2022 (Table 1). High-connected ponds were characterised by *E. ventrosa* and *Hediste diversicolor* (O.F. Müller, 1776), while *Sigara selecta* (Fieber, 1848) was more abundant in low-connected ponds (Table 2).

Biological traits results

When examining trait composition, no differences in variability were observed between pond age and

Table 2 SIMPER results of significant PERMANOVA comparisons between pond age (Old/New), and hydrological connectivity (High-connected (HC)/Low-connected (LC)) of the taxonomic data, showing contribution of taxa to total dissimilarities between factors (Cont. (%)). The contributions listed

Taxa	Pond age		2016						
	Old	New	Cont. (%)						
<i>Ecobia ventrosa</i> (Montagu, 1803) (G)			23.39						
<i>Hediste diversicolor</i> (O.F. Müller, 1776) (P)			11.54						
Chironominae (D)			8.42						
<i>Gammarus aequicauda</i> (Martynov, 1931) (A)			8.12						
Orthoclaadiinae (D)			7.41						
<i>Ficopomatus enigmaticus</i> (Fauvel, 1923) (P)			4.98						
<i>Culicoides</i> sp. (D)			4.65						
<i>Sigara selecta</i> (Fieber, 1848) (H)			4.49						
Taxa	Hydrological connectivity			2017			2022		
	HC	LC	Cont. (%)	HC	LC	Cont. (%)	HC	LC	Cont. (%)
<i>Sigara selecta</i> (H)			16.28			10.5			
<i>Ecobia ventrosa</i> (G)			12.28			12.83			
<i>Hediste diversicolor</i> (P)			11.2			4.24			
Tubificidae (O)			7.79			-			
Chironominae (D)			6.66			5.54			
<i>Gammarus aequicauda</i> (A)			5.87			8.54			
<i>Hydroporus pubescens</i> (Gyllenhal, 1808) (C)			5.22			5.4			
<i>Berosus hispanicus</i> (Küster, 1847) (C)			-			8.15			
<i>Enochrus bicolor</i> (Fabricius, 1792) (C)			-			6.35			
Orthoclaadiinae (D)			-			5.55			

^aA: Amphipoda; C: Coleoptera; D: Diptera; G: Gastropoda; H: Hemiptera; O: Oligochaeta; P: Polychaeta

hydrological connectivity categories, with the only exception of food preference trait, which showed higher variability in high-connected ponds in the year 2022 (Table 1; Supplementary Material 7). When comparing pond age across years, differences were observed in some trait composition only in 2016, with no differences observed in 2017 or 2022, in line with the taxonomic results. These traits were aquatic stages, dispersal ability, food preferences, and feeding habits (Table 1). The trait modalities that contributed more to these differences were markedly different between old and new ponds (Table 3). Hydrological connectivity showed an increase in compositional differences over the study period. Therefore, in the first year (2016), we observed differences in the composition of three traits: dispersal ability, locomotion and substrate relation, and respiration. One year later (2017), there were four (those observed in 2016 plus feeding habits). Six years after restoration (2022), there were six (those observed in 2017 plus aquatic stages and food preferences; Table 1). Broadly, high-connected ponds exhibited communities with higher abundances of aquatic dispersers with macrophytes

account for at least 65% of the total dissimilarity. Shaded squares indicate which group has the highest mean abundance. The capital letter next to each species name represents its taxonomic group^a. Note that only the significant PERMANOVA results are indicated

as a food preference, while low-connected ponds had greater abundances of aerial dispersers with living macroinvertebrates as a food preference (Table 3).

Discussion

In this study, we described changes in macroinvertebrate communities during the colonisation process following the creation of new ponds in a salt marsh, where hydrological connectivity is expected to be a key driver of community assembly. Environmental variables indicated higher habitat quality (Sala et al., 2004) in old ponds compared to newly created ones. However, over time, environmental conditions converged, suggesting that new ponds were becoming increasingly similar to existing habitats. Despite this trend towards ecosystem homogenisation, macroinvertebrate communities diverged both taxonomically and functionally due to hydrological connectivity, as hypothesised.

Table 3 SIMPER results of significant PERMANOVA comparisons between pond age (Old/New), and hydrological connectivity (High-connected (HC)/ Low-connected (LC)) of the traits data, showing contribution of trait modalities to total dissimilarities between factors (Cont. (%)). The contributions listed account for at least 65% of the total dissimilarity. Shaded squares indicate which group has the highest mean abundance. Note that only the significant PERMANOVA results are indicated

		Pond age		2016		Cont. (%)			
Traits	Modalities	Old	New						
Aquatic stages	nymph					30.36			
	adult					25.99			
	larva					24.21			
Dispersal ability	aerial active					42			
	aquatic passive					36.6			
Food preference	dead plant>=1mm					23.15			
	living microphytes					18			
	living macrophytes					18			
	detritus < 1mm					14			
Feeding habits	scraper					29.96			
	shredder					18.39			
	deposit feeder					14.55			
	parasite					11.16			
Hydrological connectivity		2016		2017		2022		Cont. (%)	
Traits	Modalities	HC	LC	HC	LC	HC	LC		
Aquatic stages	larva							-	36.5
	adult							-	29.4
Dispersal ability	aerial active							28	39.3
	aquatic passive							41.5	47.4
Respiration	spiracle							23.2	27.6
	gill							46.2	45.5
Locomotion and substrate relation	burrower							8.9	11
	full water swimmer							34.8	38
	Interstitial crawler							-	-
Food preference	living macrophytes							-	24.6
	living microinv.							-	21.4
	dead plant>=1mm							-	19.4
	living microphytes							-	11.3
Feeding habits	scraper							34.4	36.7
	shredder							19.2	15
	piercer							18	17.9

Community dynamics in time and space

The period analysed in this study allowed us to distinguish different community phases. Initially, during the early stages of the colonisation process, newly created habitats, presented different communities from those of the existing habitats, dominated by active dispersers (Ruhí et al., 2012). Subsequently, a flooding event connected all ponds superficially within the salt marsh, leading to community homogenisation between existing and newly created ponds. From that point onward, communities diverged only as a response to hydrological connectivity. These findings support the importance of long-term ecosystem monitoring to detect changes in communities (Chase, 2007; Jeffries, 2011).

At the beginning of the colonisation process, contrary to our first hypothesis, we did not observe a nested structure in La Pletera as observed in other

studies (i.e. Ruhí et al., 2013; Coccia et al., 2016). Instead, we observed an anti-nested structure, suggesting that a high number of taxa colonising new ponds were actually not present in old ponds. This idea is reinforced by the observed modular structures, with newly created and old ponds presenting two different communities, or modules, at both taxonomic and functional levels.

In a later phase of the colonisation, we expected communities to become more similar, as habitats tend to become environmentally homogeneous. We also expected that this process would be faster if ponds are closer or periodically connected hydrologically, for example, because of extreme inundation events (Meutter et al., 2007). Indeed, this happened in La Pletera during our study with an intense storm event right after the restoration (between 2016 and 2017), which raised the water level above 1 m a.s.l. Consequently, the salt marsh became

superficially connected and dispersal among ponds was feasible even for strictly aquatic dispersers. Accordingly, dominant taxa in old ponds (i.e. gastropods and amphipods) colonised some of the newly created ones. This aligns with the anti-nested structure observed in 2017, as all communities became very similar. However, the modular structure remained, but with a lower clustering coefficient (i.e. less strong), which indicated that communities maintained some intrinsic differences. These remaining differences appear to be more closely linked to hydrological connectivity than to the age of pond creation, as the composition of taxa and traits was significantly different only in response to hydrological connectivity. These compositional differences became even more evident six years later (i.e. 2022), with the persistence of anti-nested and modular structures. While restoration should lead to community convergence between old and new ponds over time, our study supports the idea of divergent trajectories of communities (Chase, 2007). This divergence observed in La Pletera can be explained by the presence of distinct communities at the outset, along with differing hydrological connectivity that created two groups of ponds. By 2022, high-connected ponds hosted species with weak dispersal abilities (i.e. aquatic passive dispersers), such as gastropods and amphipods, whereas low-connected ponds were dominated by aerial active dispersers, such as hemipterans and coleopterans. Overall, we observed similar changes in community for both taxonomic and functional analyses, suggesting that, in our case, taxa and functional traits are strongly correlated (Cadotte et al., 2013).

The reported trends in communities over time were reinforced by the ecological trajectory analysis, which showed that new ponds experienced greater changes in community composition than old ponds at the early stages of the colonisation, as we hypothesised (i.e. H2) coinciding with the findings made by Coccia et al. (2016). The most important change was observed during the period from 2016 to 2017 (P1), which coincided with the flooding event that connected superficially all ponds. This implied a marked change from the recently colonised communities to more homogeneous communities that shared more species with old ponds. During the second period, from 2017 to 2022 (P2), changes in community composition did not differ between old

and new ponds. However, compositional changes between high-connected and low-connected ponds did show significant differences for that period, coinciding with our second hypothesis. This was likely explained by the divergence of communities in low-connected ponds, which remained hydrologically isolated along that period. Nonetheless, the absence of regular surveys between 2017 and 2022 hinders our capacity to reliably attribute these compositional trajectories only to these factors.

The importance of hydrological connectivity

Most studies based on monitoring after a restoration project evaluate the community maturity of newly created habitats or the success of restoration by assessing the similarities between communities of new ponds and existing ones (Moreno-Mateos et al., 2012; 2015; Ruhí et al., 2016). In some studies, macroinvertebrate (Español et al., 2014) and plankton communities (Cabrera et al., 2019), achieve similar community composition between old and new ponds during the colonisation process. In our study, only one year was necessary to achieve it. Thus, taxonomic and functional differences between old and new ponds were observed only in the first survey, just after restoration (i.e. 2016), in which active dispersers were occupying the newly created ponds. However, coinciding with our third hypothesis, differences were observed when comparing ponds regarding their hydrological connectivity from 2017 and onwards.

In contrast to existing studies that only found a partial effect of hydrological connectivity on community assemblages (Kang & King, 2013), our results suggest that hydrological connectivity is the main driver of community composition. Consistent with our hypothesis, active dispersers remain important in the later colonisation phase (i.e. 2022). This suggests that the isolation, during the first phase of colonisation, of low-connected ponds supports different assemblages, providing the opportunity for pioneering species to establish there in the long term. Thus, differences in hydrological connectivity, particularly the isolation of some ponds, promote community heterogeneity despite the fact that we observed similar environmental conditions. Moreover, low-connected ponds presented differences in functional diversity indices in 2022, with higher functional redundancy (indicated by a lower FDis), suggesting that species

in these ponds shared similar functional roles. Nonetheless, there were no more diversity indices showing differences, indicating that the divergence of these communities was, mainly, at the compositional level. In this sense, high-connected and low-connected communities contained different species associated with different traits. Thus, in the first year, only traits related to the mobility of organisms and their respiration differed between high-connected and low-connected ponds. However, differences in feeding habits were added to the previous differences in the second year, and food preferences and aquatic stages in the last year of the study, overly suggesting that these two subsets of communities were diverging over time. Unfortunately, we did not measure some water variables, such as available organic matter, that might also influence community composition (Kang et al., 2007). In addition, more extensive monitoring would help determine whether community differences between high-connected and low-connected ponds persist over time or are eventually homogenised by recurrent flooding events. It would also provide insights into community establishment and the role of hydrological connectivity, especially given that the recovery of ecological functionality in restored habitats may take more than 5 years (Moreno-Mateos et al., 2012; 2015).

Conclusion

In conclusion, our results highlight that hydrological connectivity could be crucial in shaping community composition after restoration. Therefore, it should be considered in post-restoration evaluation since it might drive differences among communities that, otherwise, could be attributed erroneously to a failure of restoration success. By considering spatial factors, restoration strategies can be refined to enhance biodiversity at a regional level and achieve more resilient ecosystems, as also suggested by Visconti & Elkin (2009). Recognising hydrological connectivity as a key driver not only provides a deeper understanding of the ecological processes but also emphasises the need to adapt restoration efforts to the inherent properties of each habitat. This approach could be vital for ensuring the long-term success of restoration projects

by better aligning management actions with the natural dynamics of the system.

Author contributions A.E. conceived and drafted the manuscript. A.E., D.B., D.C.M., X.Q., J.S., and S.G. reviewed and revised the manuscript. D.B., X.Q., J.S., and D.C.M. conducted the surveys. A.E., D.B., and J.S. processed the samples. A.E., D.C.M., and S.G. curated the data and performed the analysis.

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Data availability The data will be openly accessible and freely downloadable. Upon acceptance of the manuscript, these materials will be assigned a handle identifier and archived in our institutional repository: <https://dataverse.csuc.cat>.

Declarations

Conflict of interest The authors have no conflicts of interest.

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