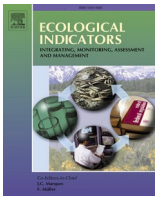
Ecological Indicators 159 (2024) 111632

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind



Hydroperiod length, not pond age, determines zooplankton taxonomic and functional diversity in temporary ponds

C. Coccia [a,b,c,d,1,*], B.A. Almeida [a,1], A. Badosa [e], L.P. Diniz [f], L. Brendonck [g,h], D. Frisch [i], A.J. Green [a]

[a] Department of Conservation Biology and Global Change, Estación Biológica de Doñana, EBD-CSIC, Américo Vespucio 26, 41092 Sevilla, Spain
[b] Department of Sciences, University of Roma Tre, Viale G. Marconi 446, 00146 Rome, Italy
[c] NBFC - National Biodiversity Future Center, 90133 Palermo, Italy
[d] Bahía Lomas Research Center, Universidad Santo Tomás, Santiago, Chile
[e] Aquatic Ecology Group, University of Vic-Central University of Catalonia, 08500 Vic, Spain
[f] Universidade Federal de Ouro Preto (UFOP), Departamento de Biodiversidade, Evolução e Meio Ambiente, Laboratório de Ecologia Aquática, Evolução e Conservação (LAECO), CEP: 35400-000, Campus Morro do Cruzeiro, Ouro Preto, Minas Gerais, Brazil
[g] Laboratory of Animal Ecology, Global Change and Sustainable Development, KU Leuven, Leuven, Belgium
[h] Water Research Group, Unit for Environmental Sciences, and Management, North-West University, Private Bag X6001, Potchefstroom 2520, South Africa
[i] Department of Evolutionary and Integrative Ecology, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany

ARTICLE INFO

Keywords:
Mediterranean temporary ponds
Zooplankton
Functional diversity
Hydroperiod
Wetland restoration
Turnover

ABSTRACT

Mediterranean Temporary ponds (MTPs) are suffering severe alterations in their hydrological and salinity regime through global change, and restoration or conservation of these habitats is a priority. However, there is little information that can be used as a scientific basis for restoration.

We studied the taxonomic and functional diversity of zooplankton communities in a set of 96 ponds in Doñana, Spain during four consecutive hydroperiods after their creation. We examined the differences across hydroperiods in alpha and beta diversity (and its turnover and nestedness components) of the rotifer, cladoceran and copepod community, as well as the influence of local environmental variables including the proximity to natural wetlands.

There was no general increase in diversity indices after the first two hydroperiods. We found that shorter hydroperiods significantly reduced taxonomic diversity, but increased the contribution to functional beta diversity through turnover. Shorter hydroperiods also reduced community complexity, with long-term effects. Conductivity was the most important predictor of zooplankton alpha and beta diversity, but the direction of its effects changed between hydroperiods. The distance from a natural source of colonists, and pond depth, were key during the early stage of community assembly and after a hydrological perturbation.

Our results suggest that new restoration projects for MTPs should focus on increasing local environmental heterogeneity and on reducing vulnerability to salinization.

The use of functional approaches in monitoring studies can improve our understanding of mechanisms and processes affecting zooplankton community assembly under dynamic hydrological regimes. This in turn can help us predict the consequences of management and restoration policies for biodiversity conservation in MTPs.

1. Introduction

Temporary ponds are small, seasonally inundated aquatic systems (*sensu* Hunter et al., 2017) with major ecological and economical roles. They are habitats of high diversity (Zacharias and Zamparas, 2010; Céréghino et al., 2014) and provide important ecosystem functions (e.g., stepping stones) and services (e.g., nutrient retention, hydrological regulation) (Céréghino et al., 2014; van Meter and Basu, 2015). Nonetheless, they are disappearing worldwide, owing to increasing human-driven pressures, including climate change (Rhazi et al., 2012;

* Corresponding author at: Department of Sciences, University of Roma Tre, Viale G. Marconi 446, 00146 Rome, Italy.
E-mail address: cristina.coccia@uniroma3.it (C. Coccia).
[1] Both authors contributed equally to the manuscript.

https://doi.org/10.1016/j.ecolind.2024.111632
Received 18 October 2023; Received in revised form 19 January 2024; Accepted 20 January 2024
Available online 24 January 2024

Calhoun et al., 2017; Oertli, 2018; Lefebvre et al., 2019; Parra et al., 2021).

In the Mediterranean region, temporary ponds (hereafter MTPs) are threatened ecosystems (Waterkeyn et al., 2008; Zacharias and Zamparas, 2010; Rhazi et al., 2012), despite receiving protection through the EU Habitats Directive (92/43/CEE). MTPs are characterized by high inter-annual variation in timing and duration of water retention, which is largely unpredictable (Zacharias and Zamparas, 2010). Climate change and increasing water demand for human use (Reid et al., 2019; Strachan et al., 2015; Dimitriou et al., 2017) are causing severe alterations in their hydrological regime, delaying pond filling and reducing water retention time. Many temporary ponds in the Mediterranean have already experienced a reduction in their inundation period or an increase in the number of years in which they remained completely dry (Díaz-Paniagua and Aragonés, 2015; Olmo et al., 2016; de Felipe et al., 2023). For these reasons, the restoration or conservation of these habitats is considered a priority (European Commission, 2022), but there is limited information that can be used as a scientific basis for restoration.

Hydroperiod changes can be particularly relevant for zooplankton communities (Boven and Brendonck, 2009) despite prevalent life history traits such as dormancy, fast reproduction rate, and active or passive dispersal that allow them to survive the dry phase, and re-establish and reproduce quickly after filling (Brendonck and De Meester, 2003; Brendonck et al., 2017). In newly created habitats, first colonizers are pioneer species with small body size, fast reproduction and quick hatching (Brendonck and De Meester, 2003). As ponds age and vegetation develops, pioneer species become less important while more efficient, larger competitors are likely to occur. Successful establishment after pond filling depends either on the emergence from egg banks determined by e.g. salinity and temperature (Jiménez-Melero et al., 2023), or on propagule dispersal into ponds from nearby aquatic habitats (e.g., by waterbirds, Green et al., 2023; or via pond connectivity, Michels et al., 2001), as well on the colonizer's capacity to grow and reproduce fast to maintain stable populations in the environmental conditions during each wet phase.

Hydroperiod length variation or changes in the timing of inundation impact zooplankton community structure and composition, modifying life history traits or/and dispersal dynamics (Quintana et al., 1998; Kneitel, 2014; Zokan and Drake, 2015; Olmo et al., 2016; Pinceel et al., 2016; Brendonck et al., 2017; Florencio et al., 2020). Variation in hydroperiods can also increase spatial beta diversity and generate nested communities (Florencio et al., 2011; Lopes et al., 2014). In general, shorter hydroperiods limit the time available for growth and reproduction (Pinceel et al., 2018), reduce hydrological connections among habitats that facilitate dispersal, and result in reduced water quantity and increased water salinity (Fernández-Aláez and Fernández-Aláez, 2010), thus imposing stronger pressure on pond inhabitants. From a taxonomic perspective, shorter hydroperiods and increasing water salinity, associated with increased isolation of aquatic habitats and reduced water depths, can reduce both alpha and beta diversity in freshwater organisms (Ripley and Simovich, 2009; Cañedo-Argüelles et al., 2013; Fernández-Aláez et al., 2020; Diniz et al., 2021). On the other hand, from a functional perspective, shorter hydroperiods and linked environmental changes can filter out intolerant species or those with a long development time, while promoting traits that can provide resistance and resilience to drought (Schriever and Lytle, 2016) such as a small body size, dormancy with drought resistant stages, and a multivoltine life cycle.

Functional traits (including either behavioural or morphological aspects) complement the classical, taxonomic approach to the ecology of freshwater communities, and provide novel insights into the relationships between environment, community structure and ecosystem processes. Recent studies demonstrated the utility of functional traits to infer patterns and processes through which aquatic communities recover after restoration (Coccia et al., 2021; Josué et al., 2021). However, the effect of hydrological alterations (e.g., prolonged drought or atypical hydroperiods) on zooplankton functional diversity and the nature of these effects (i.e., gain and loss of traits) has so far been poorly investigated (Galir Balkić et al., 2018). As the creation of ponds and pondscapes has been recommended as a Nature Based Solution to cope with climate change (Cuenca-Cambronero et al., 2023), it is crucial to understand how new communities develop both taxonomically and functionally, and how they respond to variation in disturbance regime. This is especially relevant for MTPs, where changes in water level and salinity associated with climate change are expected to affect community structure and dynamics (Jeppesen et al., 2015; Parra et al., 2021).

Here we took advantage of a large wetland restoration project conducted in Doñana (SW Spain) in the Mediterranean climate region, where a set of experimental temporary ponds were created in 2005 and monitored then for four consecutive hydroperiods. This allowed investigation of temporal patterns of colonization and how hydroperiod and related environmental variables affect the assembly of zooplankton communities from a taxonomic and functional perspective. We had the following working hypotheses:

Hyp 1) alpha diversity (taxonomic and functional), and community mean body size would be lower in ponds during shorter hydroperiods, because drought conditions act as an environmental filter, excluding those species which need longer hydroperiods for establishment (Chase, 2007). For the same reasons, we expected that Hyp 2) ponds experiencing shorter hydroperiods would contribute less to beta taxonomic and functional diversity, because only a few species with specific trait combinations can cope with high stress. Furthermore, Hyp 3) environmental differences between ponds were expected to explain more variation in beta taxonomic and functional diversity (and its components) during shorter hydroperiods, when ponds were expected to become more dissimilar (Cardoso et al., 2022).

Lastly, Hyp 4) we expected that the last hydroperiod of our study period would contribute most to overall beta diversity (both taxonomic and functional) and its turnover and nestedness components (as observed by Anton-Pardo et al., 2016). This is because ponds are generally expected to become more complex over time through increased habitat structure and ecological succession, accompanied by a higher abundance and species richness of dormant eggs in the egg bank (Vandekerkhove et al., 2005).

2. Material and methods

2.1. Study area

Doñana National Park (SW- Spain) has a Mediterranean climate with Atlantic influence. This leads to short and relatively mild winters, and long, dry and hot summers. Rainfall is concentrated mainly between October and April (Green et al., 2018). Caracoles estate, situated at the northern edge of the park, is a former temporary marshland area of 27 km^2 converted into arable land in the 1960 s. In 2004–2005, the drainage system was removed and hydrological connectivity with the surrounding marshes was reestablished as part of a restoration plan. At this point, 96 temporary ponds were excavated in the area (Badosa et al., 2010, Coccia et al., 2016). Eight isolated ponds were distributed across the estate, and the rest were aggregated in two blocks of 44 ponds each (Fig. 1). These temporary ponds are filled by precipitation, with large interannual variation in hydroperiod length and flooded surface (Fig. 1). During major rainfall events, the ponds overflow and can connect to one another, forming large temporary water bodies (Frisch et al., 2012). Their hydroperiod can begin in the fall, or winter, depending on precipitation patterns, and ponds dry up completely at the end of spring or beginning of summer. During the time of this study, filling dates and hydroperiod lengths varied between years. The latter was much shorter in H3 (Fig. 1 and Table A.1), when fewer ponds could be sampled. All necessary permits to enter Doñana National Park were obtained from the Consejería de Medioambiente, Junta de Andalucia.

Previously in these ponds, a taxonomic approach was used to study

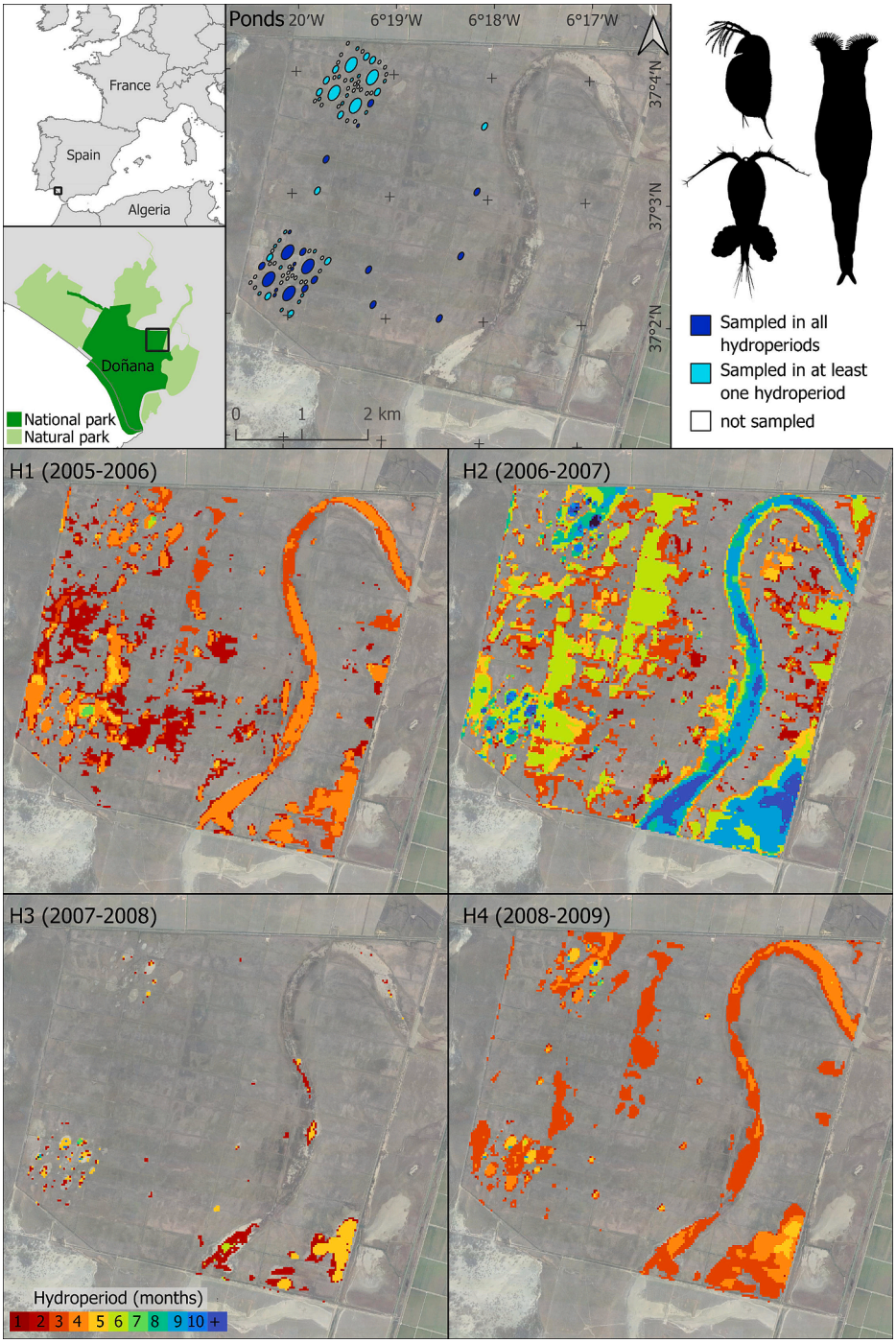


Fig. 1. Map of the sampled ponds in Doñana (upper part of the figure) and maps of the same area showing the full duration in months of the four studied hydroperiods (lower part of the figure). In the upper figure, dark blue identifies ponds sampled during all hydroperiods (from H1 to H4); light blue identifies ponds sampled in at least one hydroperiod; white identifies ponds that were never sampled. Hydroperiods begin in September. Based on monthly Landsat satellite images. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

changes in the zooplankton communities immediately after pond restoration in (H0), H1 and H2 (Frisch and Green, 2007, Badosa et al., 2010, Frisch et al., 2012), and a genetic study addressed colonization dynamics by the rotifer *Brachionus plicatilis* (Badosa et al., 2017).

2.2. Zooplankton sampling and analyses

Samples included in this study were from April 2006 (n = 48), 2007 (n = 50), 2008 (n = 31) and 2009 (n = 43), hereafter called hydroperiods H1, H2, H3 and H4, respectively. April was the month with the highest number of ponds sampled for all hydroperiods. A total of 172 pond samples were collected across these 4 hydroperiods, but only a subset of 21 ponds was common to all hydroperiods. To overcome the expected patchy distribution of zooplankton, 500-ml plastic jug subsamples were randomly collected along a transect from the margin to the center of each pond, and then mixed. A total of 20 L of the collected water was then filtered through a 64 μm nylon mesh, and zooplankton preserved in 70 % ethanol. Conductivity (mS/cm^{-1}) was measured *in situ* during zooplankton sampling with a WTW 340i multiprobe, and water depth (cm) was measured with a calibrated stick from five points

within each pond. No fish were observed in the ponds while samples were being taken.

Individual copepods, cladocerans and large rotifers were counted and identified to species level in most cases (Table A.2) under inverted microscope (Utermöhl method). At higher densities, subsampling was performed and at least 200 individuals of the most abundant species taxa were counted. Then, the entire sample was screened for rare taxa. Samples with less than 400 individuals were analyzed entirely. All non-adult individuals were excluded from further analyses. For more details on zooplankton sampling and analyses, as well as details of natural wetlands in surrounding areas, see Badosa et al. (2010) and Frisch et al. (2012).

2.3. Species traits

To calculate alpha and beta functional diversity indices we used five zooplankton functional traits assigned to each species: mean body length (continuous), feeding type (categorical with five levels: filter feeder, predator, raptorial, scraper and sucking), habitat type (categorical with three levels: littoral, pelagic and epibenthic), life span (binomial: long or short) and predatory escape response (ordinal with four levels: low, medium, high and maximum) (Table A.2). All traits are connected to the role of zooplankton species in the food web, and thus to secondary productivity and energy transfer in aquatic ecosystems (Litchman et al., 2013), and also respond to changing environmental conditions (Barnett et al., 2007). Individual body length was measured directly from the zooplankton samples for 26 % of the species. For the other species, body length was obtained from the literature (51 %, Table A.2) or estimated as means of values of other species belonging to the same genus (23 %), following Coccia et al. (2021) for other taxa. Values for the other traits were retrieved at subclass level from various literature sources (see Table A.2).

2.4. Diversity at the alpha scale

To describe the structure of the communities (each sampled pond in each sampled hydroperiod) we used three indices representing different aspects of alpha diversity: species richness, the Shannon diversity index and functional dispersion (FDis, Laliberté and Legendre, 2010), plus the community weighted mean of body length (CWM, Garnier et al., 2004). These metrics were calculated for all 172 pond samples ("communities" from here on) through the 4 hydroperiods. Functional dispersion represents the breadth of functional roles across species, so higher dispersion indicates greater functional diversity (i.e. no or less functional overlap between species). This index was calculated from a functional space constructed with a principal coordinates analysis (PCoA, Gower, 1966) composed by axes derived from the functional traits of all species in all years. For the PCoA construction, we first computed the functional distances between species using the Gower distance (Gower, 1966) and then performed a PCoA on the distance matrix. Thus, FDis represents the mean functional distance of each species to the centroid of the community multivariate functional space, weighted by species abundances (Laliberté and Legendre, 2010). To evaluate how the size dominance changed across hydroperiods, we estimated the community weighted mean (CWM) of the body length in each community (Garnier et al., 2004). CWM measures the overall community-level value of a trait while accounting for abundance values of species in the community. We calculated FDis with the function *dbFD* and body length CWM with the *functcomp* function, both from the package 'FD' (Laliberté and Legendre, 2010; Laliberté et al., 2014), in the R environment, version 4.1.2 (R Core Team, 2021). We conducted all subsequent calculations and analyses using R.

2.5. Diversity at the beta scale

To measure the contribution of each pond community in each hydroperiod to the overall (i.e. combining four hydroperiods) beta diversity of species (taxonomic, as proposed by Baselga, 2010) and species' traits (functional, as proposed by Villéger et al., 2011), we considered only the communities of those ponds (21) that were sampled in all four hydroperiods (21 ponds x 4 hydroperiods = 84 communities).

To do this, first we calculated the pairwise dissimilarity matrices representing total beta diversity and its components turnover and nestedness for species and trait composition. Total beta diversity refers to the overall difference in composition (of species or traits) between these 84 communities. Turnover represents the amount of dissimilarity between communities owing to the replacement of some species (or traits) by others, while nestedness represents dissimilarity due to differences in richness (of species or traits). As proposed by Baselga (2010), the total beta diversity between ponds was calculated as the Sørensen dissimilarity index, the turnover component was calculated as the Simpson index, and the nestedness was calculated as the difference between the Sørensen and the Simpson dissimilarities in each case. We calculated taxonomic and functional dissimilarity matrices using the functions *beta.pair* and *functional.beta.pair* of the 'betapart' package (Baselga et al., 2021).

Then, from each dissimilarity matrix, we calculated a multivariate space represented in a PCoA. The positions of each of the 84 communities in this space represent their (species or traits) composition. For a measure of the contribution of each community to overall beta diversity (or turnover or nestedness), we used the distance in the multivariate space between this community and the centroid of all communities. We calculated such distances using the function *betadisper* from the package 'vegan' (Oksanen et al., 2020), as proposed by Anderson et al. (2006).

2.6. Data analysis

To evaluate how community structure at alpha and beta scales changed between hydroperiods, and whether this was related to the distance to the nearest natural wetland, mean depth and conductivity of the ponds, we fitted models to alpha diversity metrics (species richness, Shannon diversity index, FDis) and body length CWM (using all the 172 samples: all ponds sampled in all four years) and to the contributions of communities to species and functional beta diversity and its components (using the 84 samples in which the same pond was sampled in all four years). We used distance to the nearest natural wetland as a proxy for dispersal potential from the already established communities that surround the restored ponds. We used mean depth of the pond as an indicator of environmental stress, as shallower ponds can have higher daily maximum temperature and low oxygen concentration when close to desiccation. We used conductivity because it is highly correlated with salinity, a key stressor in MTPs. Thus, our global models included these four predictor variables plus three pairwise interactions: 1) hydroperiod (categorical) x distance to a natural wetland (continuous); 2) hydroperiod x mean depth (continuous), and 3) hydroperiod x conductivity (continuous), to evaluate if the importance of the different variables changes through time between hydroperiods. We used variance inflation factors (VIF) to detect model multicollinearity. Since all VIF values between predictors were ≤ 3, we did not detect any collinearity issue (Zuur et al., 2010).

We first fitted global generalized linear mixed-effects models (GLMMs) to each response variable, using the function *glmer* of the 'lme4' package (Bates et al., 2015). In these models, we used pond identity as a random factor to control for dependence among samples. However, when inspecting the variance of the residuals for each model, most showed strong heterogeneity which required correction. At the same time, GLMMs showed singular fit for many of our response variables, indicating that the small number of observations for some subjects (many ponds were only sampled once or twice in the case of the alpha metrics) did not allow the fit of the mixed effect model. We thus continued model fitting using generalized least square models (GLS), which allow the inclusion of both variance structures to correct variance

heterogeneity, and correlation structures to account for independence among samples. GLSs with Gaussian distributions were used to fit models for all response variables except for species richness, which showed no heterogeneity of variances, and for which GLMM revealed a singular fit. For species richness we therefore used generalized linear models (GLM) with the Poisson distribution using the function *glm* of the 'stats' package (R Core Team, 2021).

We fitted GLSs using the *gls* function of the package 'nlme' (Pinheiro et al., 2021) and added variance structures to the models until homogeneity of variance was met. We also compared GLSs fitted with and without a correlation structure to further investigate, and possibly account for, lack of independence among samples taken from different hydroperiods in the same pond. We fitted each global model with different variance structure options and selected the most appropriate fit through AIC, as suggested by Zuur et al. (2009). Once the adequate variance structure was selected for each response variable, we proceeded to model selection. We used the *dredge* function of the package 'MuMIn' (Barton, 2020) to compare all combinations of variables. In those cases where a variance structure was needed, we kept this term in all compared models. For each response variable, to prevent multiple, related variables from entering the final models ('pretending variable' problem, Anderson, 2008), we selected as best model the one containing the lowest number of explanatory variables among those having a $\Delta AIC < 4$.

We then ran post-hoc tests on the predicted values of the models using the package 'emmeans' (Lenth, 2022). For the models in which an interaction term was present, we evaluated which were the hydroperiods for which the slopes of the continuous variables were considered significant, using the function *emtrends*. For all models in which hydroperiod was selected, we verified if differences between hydroperiods were significant using functions *ref_grid* and *contrast*.

3. Results

Over the four hydroperiods, we identified a total of 51 taxa (40 identified to species level), of which 9 taxa belonged to Copepoda; 14 to Cladocera and 28 to Rotifera (Table A.2). Among them, 10 taxa (19 % of total) (2 copepods, 3 cladocerans and 5 rotifers), were common to all hydroperiods, while 7 (13 %), 9 (17 %) and 3 taxa (6 %) were found exclusively during H1, H2 and H3, respectively. No taxa were found exclusively during H4 (Table A.2). Mean taxonomic richness per pond varied between 8.5 in H2 and 4.2 in H3 (Table A.3). Rotifers had the highest values, followed by cladocerans and copepods (Table A.3). Except in H2, Rotifera was the dominant group by taxonomic richness (Table A.3).

Across all ponds, mean conductivity ranged from 6.8 to 16.5 mS^{-1} in H1 and H3, respectively. Mean depth varied between 18.9 and 28.1 cm in H1 and H4, respectively (Table A.3). When considering only the 21 ponds sampled in all hydroperiods, mean conductivity was much higher in H3 (15.6 mS^{-1}) than other hydroperiods (ranging between 6.6 in H2 and 9.5 in H4, Fig. A.1). In contrast, mean depth was much higher in H4 (29.6 cm) than in other hydroperiods (ranging between 22.0 in H1 and 23.3 cm H2, Fig. A.1). Both these variables varied considerably within each pond between hydroperiods (Fig. A.2).

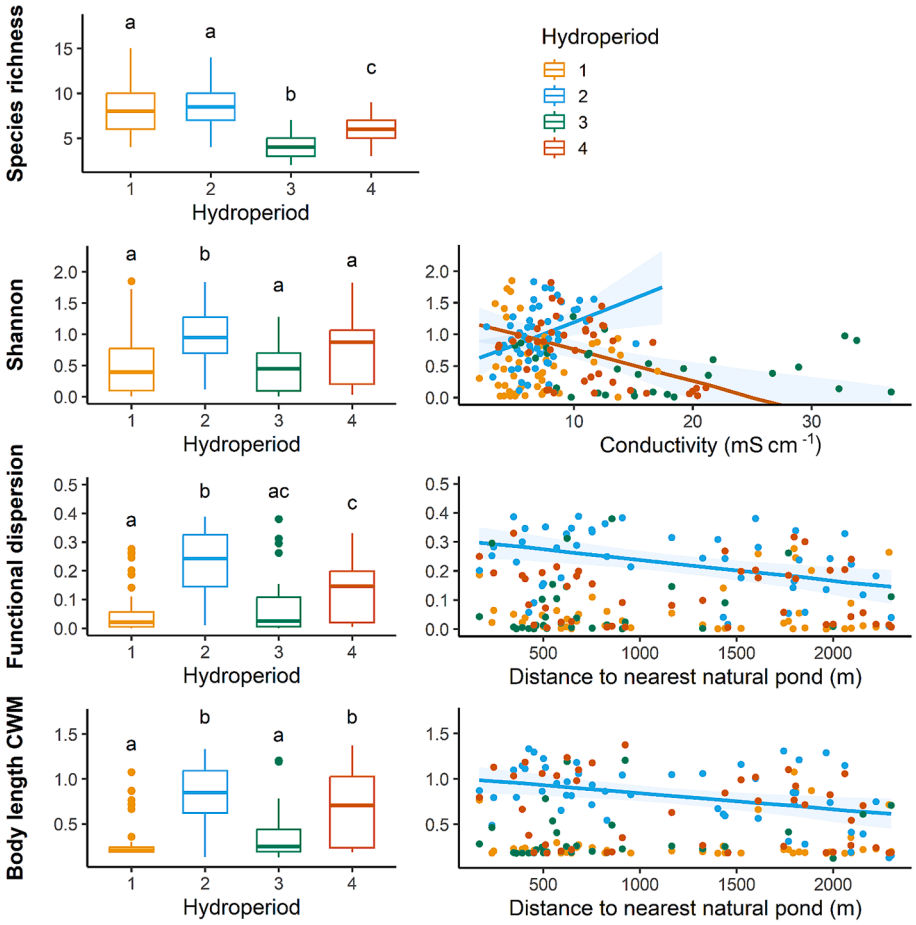


Fig. 2. Observed values of alpha diversity metrics and body length community weighted means (CWM) for zooplankton communities. Boxplots show median and quartiles and outliers are shown as points. Different letters above boxplots represent differences considered significant between hydroperiods, according to pairwise post-hoc tests. Fitted lines are shown on the right side for relationships with environmental variables considered significant according to best-fitted models.

3.1. Community structure at the alpha scale

Species richness did not differ between the first two hydroperiods, but it decreased strikingly and significantly in H3 with respect to H1 and H2, and then recovered partially to intermediate levels in H4 (Fig. 2, Tables 1 and A.4). The Shannon index was significantly higher during H2 with respect to the other three hydroperiods, which did not differ significantly between each other (Fig. 2, Tables 1 and A.4). Functional dispersion (FDis) was significantly higher in H2 with respect to the other three hydroperiods, and H4 was also significantly higher than H1 (Fig. 2, Tables 1 and A.4). Community Weighted Mean (CWM) body length was significantly higher during H2 and H4 with respect to H1 and H3 (Fig. 2, Tables 1 and A.4).

Model selection showed that, besides hydroperiod, other variables were also significant predictors of alpha diversity and CWM body length, but in a manner that varied between hydroperiods (i.e., interaction terms were significant). The Shannon index was positively related to conductivity in H2 but negatively related in H4, while FDis and CWM body length were negatively related to distance to the nearest natural wetland in H2 (Fig. 2, Tables 1 and A.5).

3.2. Community structure at the beta scale

For species composition, model selection showed that the contribution to total beta diversity was best explained by hydroperiod, conductivity and by the interactions between hydroperiod x conductivity and by hydroperiod x distance from the nearest natural pond (Table 1). In contrast, the contribution to taxonomic turnover was best explained by the hydroperiod x depth interaction (Table 1). For both taxonomic beta diversity and turnover, H2 and H3 contributed significantly more than H1 and H4, and H2 also contributed significantly more than H3 to taxonomic turnover (Fig. 3). However, since taxonomic compositions in H2 and H3 barely overlap (Fig. 4), they contribute with different species to the overall beta diversity and turnover. Conductivity was negatively correlated with a given pond's contribution to species beta diversity in H2, but positively correlated in H3, and also with a pond's contribution to taxonomic turnover overall. The contribution to taxonomic beta diversity was negatively correlated with distance to the nearest natural pond in H2 and in H4. Furthermore, the contribution to taxonomic turnover was negatively correlated with mean depth in H1 (Fig. 3, Tables 1 and A.5).

In contrast, for functional composition, model selection showed that the contributions to beta diversity and turnover were only significantly explained by hydroperiod (Table 1). In both cases, H3 contributed more than H2 and H4, while H1 did not differ from other hydroperiods (Fig. 5). We did not find any variable explaining a community's contribution to nestedness, whether for taxonomic or functional composition (Table A.6).

4. Discussion

In this study we used newly created Mediterranean temporary ponds (MTPs) within a restoration project to test for the effect of hydroperiod and related environmental (e.g., conductivity and water depth) variables on zooplankton taxonomic and functional diversity in MTPs. Support for our initial hypotheses was mixed. The shortest (H3) of four hydroperiods had the lowest taxonomic richness, but the highest contribution to functional turnover, while the longest hydroperiod (H2) had the highest taxonomic diversity and functional dispersion. Conductivity was the most important driver affecting alpha and beta taxonomic diversity, but with opposing effects in different hydroperiods. Our results demonstrate the key importance of nearby sources of colonists for community assembly, both taxonomically and functionally.

Table 1
Estimates, standard errors, t (or z) values and *p-values* for the best model for each diversity component for zooplankton communities. The intercept corresponds to hydroperiod 1. H: hydroperiod; Cond: conductivity (mS·cm^{-1}); Dpond: distance to the nearest natural wetland (m), Depth: mean depth of the pond (cm); CWM: community weighted mean. *For species richness, z values are presented.

Diversity components		Estimate	Std. Error	t-value*	*p-value*
Species richness	(Intercept)	2.1052	0.0503	41.786	0
	H2	0.0373	0.0699	0.5332	0.5939
	H3	−0.6793	0.1014	−6.6968	**<0.0001**
	H4	−0.2605	0.0788	−3.3051	**0.0009**
Shannon Index	(Intercept)	0.5404	0.0821	6.5782	**<0.0001**
	Cond	0.0237	0.1132	0.2095	0.8343
	H2	0.6217	0.1190	5.2242	**<0.0001**
	H3	−0.0361	0.1245	−0.2902	0.7720
	H4	0.2418	0.1009	2.3956	**0.0177**
	Cond: H2	0.4237	0.1995	2.1240	**0.0352**
	Cond: H3	−0.0566	0.1229	−0.4601	0.6460
	Cond: H4	−0.3288	0.1393	−2.3609	**0.0194**
Functional dispersion	(Intercept)	0.0383	0.0087	4.3926	**<0.0001**
	Dpond	0.0101	0.0085	1.1847	0.2378
	H2	0.1900	0.0175	10.8760	**<0.0001**
	H3	0.0332	0.0165	2.0139	**0.0457**
	H4	0.0892	0.0181	4.9160	**<0.0001**
	Dpond: H2	−0.0588	0.0173	−3.3974	**0.0008**
	Dpond: H3	0.0165	0.0189	0.8735	0.3837
	Dpond: H4	−0.0195	0.0178	−1.0981	0.2738
Body length CWM	(Intercept)	0.2145	0.0079	27.3051	**<0.0001**
	Dpond	0.0064	0.0090	0.7124	0.4772
	H2	0.6039	0.0422	14.2930	**<0.0001**
	H3	0.1590	0.0710	2.2409	**0.0264**
	H4	0.4391	0.0542	8.1044	**<0.0001**
	Dpond: H2	−0.1256	0.0428	−2.9312	**0.0039**
	Dpond: H3	0.0616	0.0724	0.8497	0.3967
	Dpond: H4	−0.0926	0.0532	−1.7417	0.0834
Contribution to taxonomic beta diversity	(Intercept)	0.2973	0.0128	23.2110	**<0.0001**
	H2	0.1731	0.0309	5.5968	**<0.0001**
	H3	0.1091	0.0310	3.5244	**0.0007**
	H4	−0.0202	0.0180	−1.1250	0.2644
	Cond	−0.0127	0.0158	−0.8054	0.4233
	Dpond	0.0147	0.0092	1.5941	0.1153
	H2: Cond	−0.0913	0.0506	−1.8033	0.0756
	H3: Cond	0.0791	0.0217	3.6475	**0.0005**
	H4: Cond	−0.0126	0.0244	−0.5189	0.6055
	H2: Dpond	−0.0460	0.0136	−3.3782	**0.0012**
	H3: Dpond	−0.0088	0.0224	−0.3916	0.6965
	H4: Dpond	−0.0385	0.0136	−2.8319	**0.0060**
Contribution to species turnover	(Intercept)	0.2100	0.0203	10.3386	**<0.0001**
	Cond	0.0491	0.0137	3.5710	**0.0006**
	H2	0.2966	0.0278	10.6710	**<0.0001**
	H3	0.1333	0.0342	3.8969	**0.0002**
	H4	−0.0173	0.0250	−0.6934	0.4902
	Depth	−0.0773	0.0359	−2.1562	**0.0343**
	H2: Depth	0.1406	0.0501	2.8087	**0.0064**
	H3: Depth	0.0263	0.0462	0.5686	0.5714
	H4: Depth	0.1138	0.0433	2.6267	**0.0105**
Contribution to functional beta diversity	(Intercept)	0.3836	0.0461	8.3112	**<0.0001**
	H2	−0.0627	0.0502	−1.2479	0.2158
	H3	0.0907	0.0645	1.4066	0.1635
	H4	−0.1350	0.0518	−2.6091	**0.0108**
Contribution to functional turnover	(Intercept)	0.2117	0.0305	6.9378	**<0.0001**
	H2	−0.0406	0.0432	−0.9398	0.3502
	H3	0.1110	0.0437	2.5399	**0.0130**
	H4	−0.0989	0.0432	−2.2922	**0.0246**

4.1. Community structure at the alpha scale

We predicted (Hyp 1) that the community weighted mean (CWM) of body length and alpha diversity would be lower in shorter hydroperiods (i.e. H3). While we found a hydroperiod effect on all metrics, it was only species richness that showed the lowest values in H3 with respect to the other hydroperiods. Ponds in H3 were smaller in surface area, higher in conductivity and with fewer hydrological connections between each other (Figs. 1 and A.1), all of which might have reduced the rate of

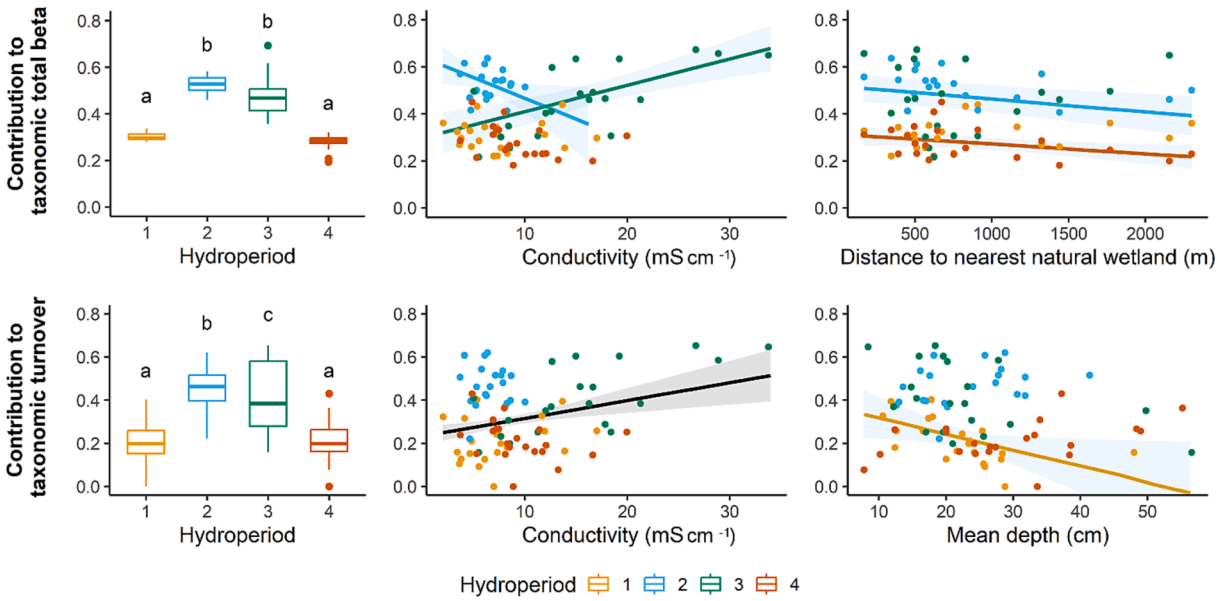


Fig. 3. Observed values of contributions to taxonomic total beta diversity and turnover. Boxplots show quartiles with outliers shown as points. Different letters above boxplots represent significant differences between hydroperiods according to pairwise post-hoc tests. Fitted lines are shown for relationships with environmental variables considered significant according to best fitted models. The black line represents a significant trend found for all four hydroperiods combined.

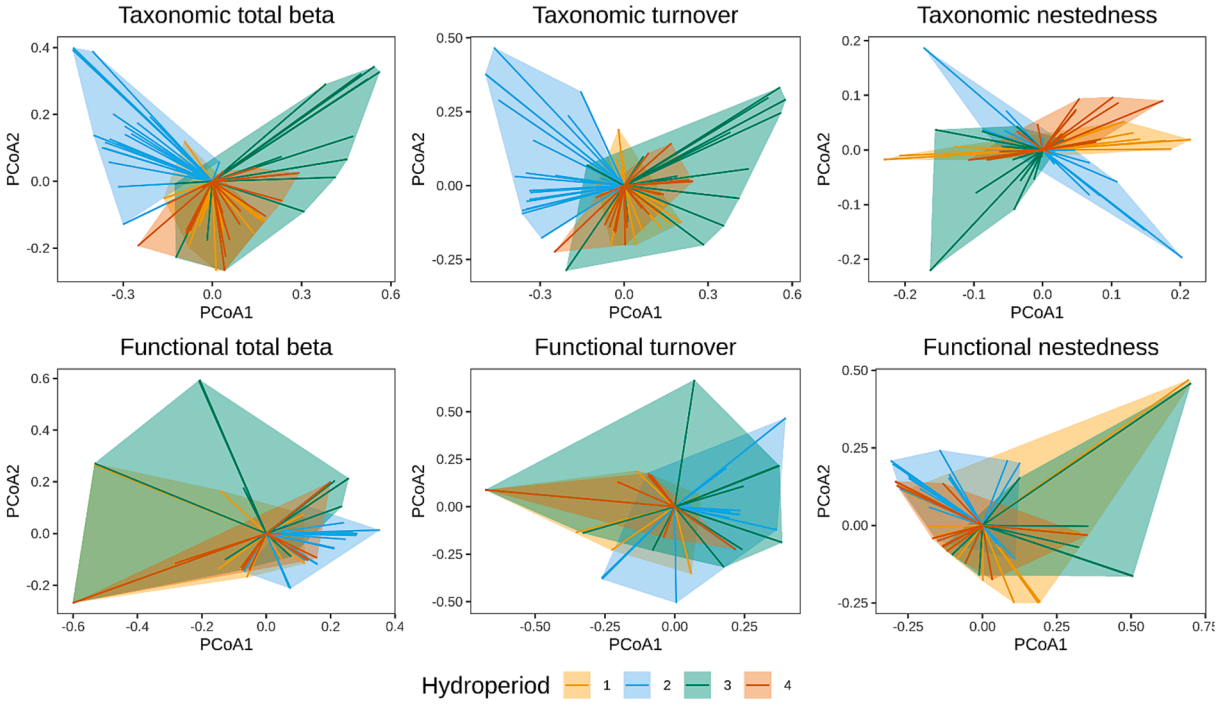


Fig. 4. Contribution of each sampling event to taxonomic and functional total beta diversity, turnover and nestedness for zooplankton communities, represented as distances between each sampling unit and the centroid for all sampling events in a multivariate dispersion analysis. Distances and polygons for each hydroperiod are represented in different colors. Polygons allow visualization of differences in taxonomic and functional composition between hydroperiods.

species colonization (Frisch et al., 2006). Overall, after an increase from H1 to H2 for all metrics (statistically significant except for richness), these decreased in H3, recovering partially in H4 but without reaching the higher values of H1 or H2 (Fig. 2).

These results are in line with previous studies showing fast richness saturation in newly created ponds and unpredictable community assembly in highly dynamic temporary systems driven by variation in hydroperiod length (Caramujo and Boavida, 2010; Louette et al., 2008; Frisch et al., 2006; Cáceres and Soluk, 2002; Olmo et al., 2016). In general, more diverse zooplankton communities can develop during longer hydroperiods, as a result of longer habitat availability and colonization time, and more time for vegetation development (Schneider and Frost, 1996). New and larger zooplankton species were indeed found by Badosa et al. (2010) in our study area during the second, longer hydroperiod (H2) when compared to H1. Similarly, we also found higher CWM and functional dispersion (FDis) in H2 than in H1. However, the decrease in the CWM observed in H3 (passing from 823.45 to 363.47 μm, Table A.3) indicates that some larger taxa found in H2 failed to

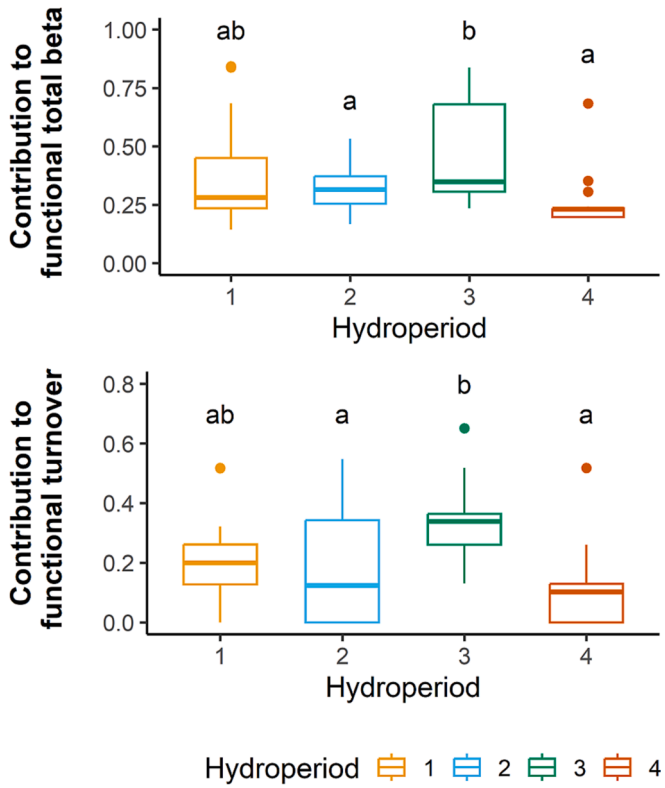


Fig. 5. Observed values of contributions to overall functional beta diversity and functional turnover in zooplankton communities from different hydroperiods. Boxplots show median and quartiles and outliers are shown as points. Different letters above boxplots represent significant differences between hydroperiods according to pairwise post-hoc tests.

successfully mature and reproduce in very short hydroperiods, while developing again in the next one. Changes in temperature, oxygen concentration, food quality and quantity (among others) during shorter hydroperiods can influence traits linked to body size such as longevity, reproduction and feeding, affecting zooplankton body size at the community level (Brans et al., 2017; Hart and Bychek, 2011). This in turn may decrease FDis (i.e., increasing functional redundancy), with potential implications for productivity, as more functionally diverse communities are often more productive (Setubal et al., 2020).

Besides the hydroperiod effect, other factors were also influencing zooplankton diversity. For example, during H2 CWM and FDis decreased as the distance to a natural wetland increased. This indicates that new ponds that were far away from natural habitats were easily colonized by smaller propagules of smaller taxa with similar functional roles (i.e., rotifers) but not by larger taxa that differed in their functional traits (e.g., cladocerans and copepods). These results point to differences in the potential for dispersal between zooplankton taxa, which are in line with previous findings (Vanschoenwinkel et al., 2009; Frisch et al., 2012; Pinceel et al., 2016). We also found that species diversity increased with conductivity during H2, but decreased in H4 (see Table A.5). Depending on their tolerance to salinity, certain zooplankton taxa can be favoured by salinity increases until a threshold (Grindley, 1981), while increases beyond that value can reduce diversity, abundance and size (Jeppesen et al., 2007, Brucet et al., 2009; Gutierrez et al., 2018). This suggests that there was variation in the proportion of less halotolerant taxa (i.e., cladocerans) compared to more halotolerant taxa (rotifers, e.g., *Hexarthra* sp.) between H2 and H4, as observed in other studies (Gutierrez et al., 2018; Jiménez-Melero et al., 2023). However, we did not find any conductivity effect on CWM of body length nor on FDis, suggesting that conductivity affects the addition or removal of species independently of body size, without affecting zooplankton functional diversity. This may reflect high functional redundancy in variable environments that increases the resilience of the communities.

4.2. Community structure at the beta scale

We did not find a negative impact of a shorter hydroperiod (H3) on beta diversity, in contrast to our prediction (Hyp 2) made because we expected it to filter out species unable to cope with stressful conditions (e.g., copepods with long life cycles). Likewise we predicted a greater contribution of the last hydroperiod H4 to beta diversity (Hyp 4) due to an expected increase in pond complexity as ponds aged, but we found no support for this (Fig. 3).

Instead, H3 had a similarly high contribution to total beta diversity as H2, which was due to different taxonomic compositions, while H3 had also the greatest contribution to functional beta diversity (Fig. 5). Previous studies showed that droughts increased beta diversity in aquatic taxa, increasing environmental divergence across sites (Simões et al., 2022; Cardoso et al., 2022). Here, the higher environmental heterogeneity between ponds in H3 (e.g., conductivity, Figs. 3 and A.1) may have increased beta diversity through turnover. Thus, we suggest that very short hydroperiods like H3 can reorganize communities, favouring fewer new species that differently colonize ponds (i.e., increasing dissimilarity) according to their tolerance to conductivity and perhaps temperatures. These species possess different sets of traits (Fig. 4) that best fit the environmental heterogeneity, increasing the contribution of H3 to functional beta diversity. For example, small body size, asexual reproduction, fast escape response and short generation time are favourable traits under environmental stress (De Melo et al., 2022). Species with these traits are also less affected by dispersal limitation, but are more influenced by local conditions (Leibold et al., 2004).

A higher contribution to taxonomic beta diversity of the longer hydroperiod H2 (Fig. 3) is not surprising since taxonomic dissimilarity often increases with hydroperiod length (Chase, 2003, 2007; Zokan and Drake, 2015). Here, compositional variation between ponds was likely related to species turnover. Previous studies have reported that turnover can be dominant when local diversity is low with respect to regional diversity (Corti and Datry, 2015), and as a result of dispersal or niche processes (Anton-Pardo et al., 2019). Nonetheless, Badosa et al. (2010) did not find any significant difference in the diversity supported by these new ponds and natural sites in the surrounding area during H1 and H2. Likewise, we did not find any effects of distance to nearby natural wetlands (a proxy for dispersal rate) nor environmental effects (niche process) on species turnover. This suggests that other variables not included in this study may have played a role and should be further investigated. For example, heterogeneous vegetation across new ponds started to develop in H2 (Badosa et al., 2010), which may have caused differences in available niches for zooplankton, leading to species replacement (Deosti et al., 2021). This could explain the differences in community composition in H2 with respect to the other hydroperiods (Fig. 4).

On the other hand, the large overlap in the multivariate total beta dispersion between H1, H3 and H4 (Fig. 4), suggests that in-pond (taxonomic and functional) composition was similar across these hydroperiods. Significant egg banks were probably produced during the first year after new habitat colonization (Vandekerkhove et al., 2005; Olmo et al., 2016; Badosa et al., 2017), suggesting that some species were able to accumulate a buffer of resting eggs that contributed to the active population across hydroperiods. This could also explain the similar values between H1 and H3 in diversity, FDis and CWM, and the overall lack of nestedness. Further, the lower contribution to beta diversity and turnover in H1 may reflect a pioneer phase of the community assemblages, i.e. communities composed of more efficient dispersers (Badosa et al., 2010; Frisch et al., 2012). For instance, turnover can decrease under unlimited dispersal (Mouquet and Loreau, 2003) and high similarity has already been reported in pioneer communities (Louette and De Meester, 2005; Allen et al., 2011). Hence, shorter

hydroperiods reduced community complexity and this effect lasted across years.

Lastly, taxonomic beta diversity was structured either by the pond environment or by the distance from nearby natural wetlands, but with variable importance across hydroperiods. Conductivity was the only driver of taxonomic changes in H3, supporting our expectation (Hyp. 3), probably because changes in these ponds during shorter hydroperiods are influenced by differences in pond size and depth of excavation (Fig. A.3). However, the fact that conductivity showed contrasting effects on beta diversity in H2 and H3 (i.e. positive or negative relationships), but had no effects in H1 and H4, suggests that the zooplankton response to conductivity was idiosyncratic and thus difficult to predict in such variable systems. Conductivity effects on zooplankton are complex and may be affected by other factors such as the nutrient status of the pond (Ersoy et al., 2022). In all cases, conductivity acted mainly *via* species replacement, supporting species sorting. We also found that water depth had a negative effect on species turnover, suggesting that shallower ponds can experience more variable environmental conditions (e.g. temperature, salinity, oxygen, nutrients, vegetation structure) than deeper sites, thus providing more niches to zooplankton species.

In contrast, the effect of distance to nearby natural habitats found in H2 and H4 suggested that zooplankton communities in these hydroperiods had dispersal-limited distributions. According to De Bie et al. (2012) larger taxa are more limited by dispersal than smaller size invertebrates, and Frisch et al. (2012) found evidence that rotifers were less dispersal limited than cladocerans and copepods in our study system. We also showed that taxa with larger body size were likely to occur in H2 and H4. Larger species should rely more on egg banks, and on the presence of animal vectors (e.g., waterbirds) to establish their communities (Sebastián-González and Green, 2014; Lopes et al., 2016). The negative effect of distance to the natural ponds on body size in H2 suggests that, by that time, large zooplankton species had not yet developed rich egg banks, making them more dependent on the proximity of a natural source of colonizers.

Surprisingly, we did not find any effect of conductivity, water depth or distance from natural habitat on functional beta diversity and its turnover component. This may be due to the functional complementarity of the community inhabiting these highly dynamic systems, as species losses due to environmental variables may be compensated by species with similar traits e.g. *Scapholeberis ramneris* replaced by *Moina salina* (i.e. functional redundancy). Nonetheless, we cannot exclude the possibility that some key environmental variables (e.g., nutrient concentrations) were missed in our study, or that the limited number of traits we used influenced the results. We used the only traits available from the literature, and further studies of zooplankton traits are needed to.

4.3. Implications for monitoring and restoration

Our results show how taxonomic and functional approaches provide different but complementary results to understand zooplankton assembly in relation to hydroperiod variations in MTPs, thus providing further support to the inclusion of functional diversity (at alpha and beta scale) in restoration monitoring as previously suggested for aquatic macroinvertebrates (Coccia et al., 2021).

At the alpha scale, taxonomic indices were more sensitive to environmental stressors, whereas functional indices revealed the role of nearby natural wetlands in maintaining functional diversity. At the beta scale, species turnover was the most important component for taxonomic diversity, and it was driven by environmental variables, whereas functional diversity revealed that hydrological disturbance changes functional composition even in pioneer (i.e., functionally redundant) communities.

Our results suggest that future restorations of MTPs should aim to increase pond heterogeneity in order to maintain zooplankton diversity, and also to benefit other aquatic taxa (Sebastián-González and Green, 2014, Coccia et al., 2021). To maintain and restore adequate hydroperiods in the face of climate change, water supplies to ponds should be guaranteed by restoring their catchment areas and preventing groundwater overexploitation (Green et al., 2017, 2024). For new ponds, greater depth will increase hydroperiods (only 30 cm or 60 cm were dug out in our ponds). Importantly, the effects of wetland restoration and associated patterns in hydrology on functional diversity of zooplankton may not be congruent with effects on functional diversity of other groups such as macroinvertebrates (Coccia et al., 2021) or waterbirds (Almeida et al., 2020).

5. Conclusions

Zooplankton communities in newly created MTPs followed over different seasons were subjected to idiosyncratic changes in response to hydroperiod duration, both taxonomically and functionally. Shorter hydroperiods significantly reduced taxonomic diversity, but increased the contribution to functional beta diversity through turnover. Conductivity emerged as a key driver of zooplankton alpha and beta diversity, with differing effects according to hydroperiod. Zooplankton communities in MTPs do not experience a clear trajectory across years as may be expected in permanent ponds or those in temperate zones.

Our results suggest that a core of small zooplankton species better able to cope with high salinity and short hydroperiods recolonise MTPs after rehydration (with lasting effect through hydroperiods). These species may become dominant in shortened hydroperiods, as larger species with specific requirements for hydroperiod duration and nearby sources of colonists are unable to hatch and restock their egg-bank. However, if shorter hydroperiods become the new “normal”, emergence from dormant eggs after rehydration can become risky even for small taxa, and thus hatching can be reduced or even avoided, with potential consequences for their persistence over the long-term (Pinceel et al., 2018). Future studies should address how zooplankton can adapt to more frequent desiccation and shorter hydroperiods under ongoing climate change.

The use of functional approaches revealed mechanisms and processes affecting zooplankton community assembly under changing hydroperiods and environmental conditions that were not detected by traditional taxonomic indices. We advocate incorporating functional traits in pond research and monitoring studies, as this will better inform management and conservation strategies than when relying on taxonomic methods alone.

CRediT authorship contribution statement

C. Coccia: Conceptualization, Data curation, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. **B.A. Almeida:** Conceptualization, Data curation, Formal analysis, Methodology, Visualization, Writing – review & editing. **A. Badosa:** Writing – review & editing, Methodology, Investigation, Data curation. **L.P. Diniz:** Data curation, Writing – review & editing. **L. Brendonck:** Writing – review & editing. **D. Frisch:** Writing – review & editing, Funding acquisition, Data curation, Conceptualization. **A.J. Green:** Conceptualization, Funding acquisition, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

This research was funded by the Spanish Ministerio de Medio Ambiente Doñana 2005 restoration project, by the Junta de Andalucía (project P06-RNM-02431), by CSIC (project PIE 202030E247), by a postdoctoral contract from Junta de Andalucía (DOC_00215) and by NBFC, funded by the Italian Ministry of University and Research, PNRR, Missione 4 Componente 2, "Dalla ricerca all'impresa", Investimento 1.4, Project CN00000033. We are grateful to David Aragonés Borrego for preparing the maps of the study area. We also thank Arantza Arechederra, Sarah Rousseaux, Raquel Ortells, Pieter Vanormelingen, María José Villena, Ernesto García, and Raquel López for fieldwork assistance. Arantza Arechederra and Mayca Lozano assisted in the zooplankton analysis. We are also grateful to three anonymous referees for their helpful comments.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2024.111632.

References

Allen, M.R., VanDyke, J.N., Cáceres, C.E., 2011. Metacommunity assembly and sorting in newly formed lake communities. Ecology 92 (2), 269–275.

Almeida, B.A., Sebastián-González, E., dos Anjos, L., Green, A.J., 2020. Comparing the diversity and composition of waterbird functional traits between natural, restored and artificial wetlands. Freshwater Biol. 65, 2196–2210. https://doi.org/10.1111/fwb.13618.

Anderson, D.R., 2008. Model Based Inference in the Life Sciences: a Primer on Evidence, Vol. 31. Springer, New York.

Anderson, M., Ellingsen, K.E., McArdle, B.H., 2006. Multivariate dispersion as a measure of beta diversity. Ecol. Lett. 9 (6), 683–693.

Anton-Pardo, M., Armengol, X., Ortells, R., 2016. Zooplankton biodiversity and community structure vary along spatiotemporal environmental gradients in restored peridunal ponds. J. Limnol. 75 (1).

Anton-Pardo, M., Ortega, J.C., Melo, A.S., Bini, L.M., 2019. Global meta-analysis reveals that invertebrate diversity is higher in permanent than in temporary lentic water bodies. Freshwater Biol. 64 (12), 2234–2246.

Badosa, A., Frisch, D., Arechederra, A., Serrano, L., Green, A.J., 2010. Recovery of zooplankton diversity in a restored Mediterranean temporary marsh in Doñana National Park (SW Spain). Hydrobiologia 654, 67–82.

Badosa, A., Frisch, D., Green, A.J., Rico, C., Gómez, A., 2017. Isolation mediates persistent founder effects on zooplankton colonisation in new temporary ponds. Sci. Rep. 7 (1), 43983.

Barnett, A.J., Finlay, K., Beisner, B.E., 2007. Functional diversity of crustacean zooplankton communities: Towards a trait-based classification. Freshwater Biol. 52, 796–813.

Barton, K., 2020. MuMIn: Multi-Model Inference. R package version 1.43.17. https://CRAN.R-project.org/package=MuMIn.

Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. Glob. Ecol. Biogeogr. 19, 134–143.

Baselga, A., Orme, D., Villéger, S., De Bortoli, J., Leprieur, F. Logez, M., 2021. betapart: Partitioning Beta Diversity into Turnover and Nestedness Components. R package version 1.5.4. https://CRAN.R-project.org/package=betapart.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. J. Stat. Soft. 67 (1), 1–48. https://doi.org/10.18637/jss.v067.i01.

Boven, L., Brendonck, L., 2009. Impact of hydroperiod on seasonal dynamics in temporary pool cladoceran communities. Fund. Appl. Limnol. 174, 147–157.

Brans, K.I., Govaert, L., Engelen, J.M., Gianuca, A.T., Souffreau, C., De Meester, L., 2017. Eco-evolutionary dynamics in urbanized landscapes: evolution, species sorting and the change in zooplankton body size along urbanization gradients. Philos. Trans. r. Soc. B Biol. Sci. 372 (1712), 20160030.

Brendonck, L., De Meester, L., 2003. Egg banks in freshwater zooplankton: evolutionary and ecological archives in the sediment. Hydrobiologia 491 (1), 65–84.

Brendonck, L., Pinceel, T., Ortells, R., 2017. Dormancy and dispersal as mediators of zooplankton population and community dynamics along a hydrological disturbance gradient in inland temporary pools. Hydrobiologia 796 (1), 201–222.

Brucet, S., Boix, D., Gascón, S., Sala, J., Quintana, X.D., Badosa, A., Søndergaard, M., Torben, L., Lauridsen, L., Jeppesen, E., 2009. Species richness of crustacean zooplankton and trophic structure of brackish lagoons in contrasting climate zones: north temperate Denmark and Mediterranean Catalonia (Spain). Ecography 32 (4), 692–702.

Cáceres, C.E., Soluk, D.A., 2002. Blowing in the wind: a field test of overland dispersal and colonization by aquatic invertebrates. Oecologia 131, 402–408.

Calhoun, A.J., Mushet, D.M., Bell, K.P., Boix, D., Fitzsimons, J.A., Isselin-Nondedeu, F., 2017. Temporary wetlands: challenges and solutions to conserving a 'disappearing'ecosystem. Biol. Conserv. 211, 3–11.

Cañedo-Argüelles, M., Kefford, B.J., Piscart, C., Prat, N., Schäfer, R.B., Schulz, C.J., 2013. Salinisation of rivers: an urgent ecological issue. Environ. Pollut. 173, 157–167.

Caramujo, M.J., Boavida, M.J., 2010. Biological diversity of copepods and cladocerans in Mediterranean temporary ponds under periods of contrasting rainfall. J. Limnol. 69 (1), 64.

Cardoso, M.M.L., Sousa, W., Brasil, J., Costa, M.R.A., Becker, V., Attayde, J.L., Menezes, R.F., 2022. Prolonged drought increases environmental heterogeneity and plankton dissimilarity between and within two semiarid shallow lakes over time. Hydrobiologia 849 (17–18), 3995–4014.

Céréghino, R., Boix, D., Cauchie, H.M., Martens, K., Oertli, B., 2014. The ecological role of ponds in a changing world. Hydrobiologia 723 (1), 1–6.

Chase, J.M., 2003. Community assembly: when should history matter? Oecologia 136, 489–498.

Chase, J.M., 2007. Drought mediates the importance of stochastic community assembly. Proc. Nat. Ac. Sci. 104, 17430–17434.

Coccia, C., Vanschoenwinkel, B., Brendonck, L., Boyero, L., Green, A.J., 2016. Newly created ponds complement natural water bodies for restoration of macroinvertebrate assemblages. Freshwater Biol. 61, 1640–1654. https://doi.org/10.1111/fwb.12804.

Coccia, C., Almeida, B.A., Green, A.J., Gutiérrez, A.B., Carbonell, J.A., 2021. Functional diversity of macroinvertebrates as a tool to evaluate wetland restoration. J. Appl. Ecol. 58 (12), 2999–3011.

European Commission, 2022. Proposal for a Regulation on nature restoration. https://eur-lex.europa.eu/legal-content/EN/ALL/?uri=CELEX:52022PC0304.

Corti, R., Datry, T., 2015. Terrestrial and aquatic invertebrates in the riverbed of an intermittent river: parallels and contrasts in community organisation. Freshwater Biol. 61, 1308–1320.

Cuenca-Cambronero, M., Blicharska, M., Perrin, J.A., Davidson, T.A., Oertli, B., Lago, M., Beklioğlu, M., Meerhoff, M., Arim, M., Teixera, J., De Meester, L., Biggs, J., Robin, J., Martin, B., Greaves, H.M., Sayer, C.D., Lemmens, P., Boix, D., Mehner, T., Bartrons, M., Brucet, S., 2023. Challenges and opportunities in the use of ponds and pondscapes as Nature-based Solutions. Hydrobiologia 1–15.

De Bie, T., De Meester, L., Brendonck, L., Martens, K., Goddeeris, B., Ercken, D., Hampel, H., Denys, L., Vanhecke, L., Van der Gucht, K., Van Wichelen, J., Vyverman, W., Declerck, S., 2012. Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. Ecol. Lett. 15 (7), 740–747.

de Felipe, M., Aragonés, D., Díaz-Paniagua, C., 2023. Thirty-four years of Landsat monitoring reveal long-term effects of groundwater abstractions on a World Heritage Site wetland. Sci. Total Environ., 163329

de Melo, D.B., Dolbeth, M., Paiva, F.F., Molozzi, J., 2022. Extreme drought scenario shapes different patterns of Chironomid coexistence in reservoirs in a semi-arid region. Sci. Total Environ. 821, 153053.

Deosti, S., de Fátima Bomfim, F., Lansac-Tôha, F.M., Quirino, B.A., Bonecker, C.C., Lansac-Tôha, F.A., 2021. Zooplankton taxonomic and functional structure is determined by macrophytes and fish predation in a Neotropical river. Hydrobiologia 848, 1475–1490.

Díaz-Paniagua, C., Aragonés, D., 2015. Permanent and temporary ponds in Doñana National Park (SW Spain) are threatened by desiccation. Limnetica 34 (2), 407–424.

Dimitriou, E., Moussoulis, E., Díaz-Paniagua, C., Serrano, L., 2017. Hydrodynamic numerical modelling of the water level decline in four temporary ponds of the Doñana National Park (SW Spain). J. Arid Environ. 147, 90–102.

Diniz, L.P., Braghin, L.D.S.M., Pinheiro, T.S.A., Melo, P.A.M.D.C., Bonecker, C.C., Melo Junior, M.D., 2021. Environmental filter drives the taxonomic and functional β-diversity of zooplankton in tropical shallow lakes. Hydrobiologia 848, 1881–1895.

Ersoy, Z., Abril, M., Cañedo-Argüelles, M., Espinosa, C., Vendrell-Puigmitja, L., Proia, L., 2022. Experimental assessment of salinization effects on freshwater zooplankton communities and their trophic interactions under eutrophic conditions. Environ. Pollut. 313, 120127.

Fernández-Aláez, M., Fernández-Aláez, M.D.C., 2010. Effects of the intense summer desiccation and the autumn filling on the water chemistry in some Mediterranean ponds. Limnetica 29 (1), 0059–0074.

Fernández-Aláez, M., García-Criado, F., García-Girón, J., Santiago, F., Fernández-Aláez, C., 2020. Environmental heterogeneity drives macrophyte beta diversity patterns in permanent and temporary ponds in an agricultural landscape. Aquat. Sci. 82 (2), 20.

Florencio, M., Díaz-Paniagua, C., Serrano, L., Bilton, D.T., 2011. Spatio-temporal nested patterns in macroinvertebrate assemblages across a pond network with a wide hydroperiod range. Oecologia 166 (2), 469–483.

Florencio, M., Fernández-Zamudio, R., Lozano, M., Díaz-Paniagua, C., 2020. Interannual variation in filling season affects zooplankton diversity in Mediterranean temporary ponds. Hydrobiologia 847 (5), 1195–1205.

Frisch, D., Green, A.J., 2007. Copepods come first: rapid colonization of new temporary ponds. Fund. App. Limnol. - Archiv Für Hydrobiologie 1 68 (4), 289–297.

Frisch, D., Moreno-Ostos, E., Green, A.J., 2006. Species richness and distribution of copepods and cladocerans in relation to hydroperiod and other environmental variables in Doñana, south-west Spain. Hydrobiologia 556, 327–340.

Frisch, D., Cottenie, K., Badosa, A., Green, A.J., 2012. Strong spatial influence on colonization rates in a pioneer zooplankton metacommunity. PLoS ONE 7 (7), e40205.

Galir Balkić, A., Ternjej, I., Špoljar, M., 2018. Hydrology driven changes in the rotifer trophic structure and implications for food web interactions. Ecohydrology 11 (1), e1917.

Garnier, E., Cortez, J., Billès, G., Navas, M.L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Bellmann, A., Neill, C., Toussaint, J.P., 2004. Plant functional markers capture ecosystem properties during secondary succession. Ecology 85, 2630–2637.

Gower, J.C., 1966. Some distance properties of latent root and vector methods used in multivariate analysis. Biometrika 53, 325–338.
Green, A.J., Alcorlo, P., Peeters, E.T.H.M., Morris, E.P., Espinar, J.L., Bravo, M.A., Bustamante, J., Díaz-Delgado, R., Koelmans, A.A., Mateo, R., Mooij, W.M., Rodríguez-Rodríguez, M., van Nes, E.H., Scheffer, M., 2017. Creating a safe operating space for wetlands in a changing climate. Front. Ecol. Environ. 15, 99–107.
Green, A.J., Bustamante, J., Janss, G.F.E., Fernández-Zamudio, R., Díaz-Paniagua C., 2018. Doñana Wetlands (Spain). In: Finlayson, C.M., Milton, G.R., Prentice, R.C., Davidson N.C. (Eds.), The Wetland Book: II: Distribution, Description and Conservation. Springer, pp. 1123-1136. DOI 10.1007/978-94-007-4001-3_139.
Green, A.J., Lovas-Kiss, Á., Reynolds, C., Sebastián-González, E., Silva, G.G., van Leeuwen, C.H.A., Wilkinson, D.M., 2023. Dispersal of aquatic and terrestrial organisms by waterbirds: a review of current knowledge and future priorities. Freshwater Biol. 68, 173–190. https://doi.org/10.1111/fwb.14038.
Green, A.J., Guardiola-Albert, C., Bravo-Utrera, M.Á., Bustamante, J., Camacho, A., Camacho, C., Contreras-Arribas, E., Gil-Gil, T., Gomez-Mestre, I., Heredia-Díaz, J., Kohfahl, C., Negro, J.J., Olías, M., Rodríguez-González, P.M., Rodríguez-Rodríguez, M., Ruíz-Bermudo, F., Santamaría, L., Schmidt, G., Serrano-Reina, J.A., Díaz-Delgado, R., 2024. Groundwater abstraction has caused extensive ecological damage to the Doñana World Heritage Site, Spain. Wetlands.
Grindley, J.R., 1981. Estuarine plankton. In: Day, J.H., Balkema, A.A. (Eds.), Estuarine Ecology with Particular Reference to South Africa. Rotterdam, pp. 117–146.
Gutierrez, M.F., Tavşanoğlu, Ü.N., Vidal, N., Yu, J., Teixeira-de Mello, F., Çakiroglu, A.I., Zu, H., Liu, Z., Jeppesen, E., 2018. Salinity shapes zooplankton communities and functional diversity and has complex effects on size structure in lakes. Hydrobiologia 813, 237–255.
Hart, R.C., Bychek, E.A., 2011. Body size in freshwater planktonic crustaceans: an overview of extrinsic determinants and modifying influences of biotic interactions. Hydrobiologia 668, 61–108.
Hunter, M.L., Acuña, V., Bauer, D.M., Bell, K.P., Calhoun, A.J.K., Felipe-Lucia, M.R., Fitzsimons, J.A., González, E., Kinnison, M., Lindenmayer, D., Lundquist, C., Medellin, R.A., Nelson, E.J., Poschlod, P., 2017. Conserving small natural features with large ecological roles: a synthetic overview. Biol. Conserv. 211, 88–95.
Jeppesen, E., Søndergaard, M., Pedersen, A.R., Jürgens, K., Strzelczak, A., Lauridsen, T. L., Johansson, L.S., 2007. Salinity induced regime shift in shallow brackish lagoons. Ecosystems 10 (1), 48–58.
Jeppesen, E., Brucet, S., Naselli-Flores, L., Papastergiadou, E., Stefanidis, K., Nõges, T., Attayde, J.L., Zohary, T., Coppens, J., Bucak, T., Menesez, R.F., Sousa Freita, F.R., Kernan, M., Søndergaard, M., Beklioğlu, M., 2015. Ecological impacts of global warming and water abstraction on lakes and reservoirs due to changes in water level and related changes in salinity. Hydrobiologia 750, 201–227.
Jiménez-Melero, R., Jarma, D., Gilbert, J.D., Ramírez-Pardo, J.M., Guerrero, F.G., 2023. Cryptic diversity in a saline Mediterranean pond: the role of salinity and temperature in the emergence of zooplankton egg banks. Hydrobiologia 850, 3013–3029.
Josué, I.I., Sodré, E.O., Setubal, R.B., Cardoso, S.J., Roland, F., Figueiredo-Barros, M.P., Bozelli, R.L., 2021. Zooplankton functional diversity as an indicator of a long-term aquatic restoration in an Amazonian lake. Rest. Ecol. 29 (5), e13365.
Kneitel, J.M., 2014. Inundation timing, more than duration, affects the community structure of California vernal pool mesocosms. Hydrobiologia 732 (1), 71–83.
Laliberté, E., Legendre, P., Shipley, B., 2014. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. – R package ver. 1.0-12, <http://CRAN.R-project.org/package=FD>.
Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91, 299–305.
Lefebvre, G., Redmond, L., Germain, C., Palazzi, E., Terzago, S., Willm, L., Poulin, B., 2019. Predicting the vulnerability of seasonally-flooded wetlands to climate change across the Mediterranean Basin. Sci. Total Environ. 692, 546–555.
Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Gonzalez, A., 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecol. Lett. 7 (7), 601–613.
Lenth, R.V., 2022. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.7.2. https://CRAN.R-project.org/package=emmeans.
Litchman, E., Ohman, M.D., Kiørboe, T., 2013. Trait-based approaches to zooplankton communities. J. Plankton Res. 35, 473–484. https://doi.org/10.1093/plankt/fbt019.
Lopes, P.M., Bini, L.M., Declerck, S.A., Farjalla, V.F., Vieira, L.C., Bonecker, C.C., Bozelli, R.L., 2014. Correlates of zooplankton beta diversity in tropical lake systems. PloS ONE 9 (10), e109581.
Lopes, P.M., Bozelli, R., Bini, L.M., Santangelo, J.M., Declerck, S.A., 2016. Contributions of airborne dispersal and dormant propagule recruitment to the assembly of rotifer and crustacean zooplankton communities in temporary ponds. Freshwater Biol. 61 (5), 658–669.
Louette, G., De Meester, L., 2005. High dispersal capacity of cladoceran zooplankton in newly founded communities. Ecology 86 (2), 353–359.
Louette, G., De Meester, L., Declerck, S., 2008. Assembly of zooplankton communities in newly created ponds. Freshwater Biol. 53 (11), 2309–2320.
Michels, E., Cottenie, K., Neys, L., De Meester, L., 2001. Zooplankton on the move: first results on the quantification of dispersal of zooplankton in a set of interconnected ponds. Hydrobiologia 442, 117–126.
Mouquet, N., Loreau, M., 2003. Community patterns in source-sink metacommunities. Am. Nat. 162 (5), 544–557.
Oertli, B., 2018. Freshwater biodiversity conservation: The role of artificial ponds in the 21st century. Aquat. Conserv. Mar. Freshwater Ecosyst. 28 (2), 264–269.
Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., and Wagner, H., 2020. vegan: Community Ecology Package. R package version 2.5-7. <URL: https://CRAN.R-project.org/package=vegan>.
Olmo, C., Armengol, X., Antón-Pardo, M., Ortells, R., 2016. The environmental and zooplankton community changes in restored ponds over 4 years. J. Plankton Res. 38 (3), 490–501.
Parra, G., Guerrero, F., Armengol, J., Brendonck, L., Brucet, S., Finlayson, C.M., Zohary, T., 2021. The future of temporary wetlands in drylands under global change. Inland Waters 11 (4), 445–456.
Pinceel, T., Brendonck, L., Vanschoenwinkel, B., 2016. Propagule size and shape may promote local wind dispersal in freshwater zooplankton—a wind tunnel experiment. Limnol. Oceanogr. 61 (1), 122–131.
Pinceel, T., Buschke, F., Weckx, M., Brendonck, L., Vanschoenwinkel, B., 2018. Climate change jeopardizes the persistence of freshwater zooplankton by reducing both habitat suitability and demographic resilience. BMC Ecology 18 (1), 1–9.
Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team, 2021. nlme: Linear and Nonlinear Mixed Effects Models_. R package version 3.1-153, <URL: https://CRAN.R-project.org/package=nlme>.
Quintana, X.D., Comiín, F.A., Moreno-Amich, R., 1998. Nutrient and plankton dynamics in a Mediterranean salt marsh dominated by incidents of flooding. Part 2: Response of the zooplankton community to disturbances. J. Plankton Res. 20 (11), 2109–2127.
R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.
Reid, A.J., Carlson, A.K., Creed, I.F., Eliason, E.J., Gell, P.A., Johnson, P.T., Cooke, S.J., 2019. Emerging threats and persistent conservation challenges for freshwater biodiversity. Biol. Rev. 94 (3), 849–873.
Rhazi, L., Grillas, P., Saber, E.R., Rhazi, M., Brendonck, L., Waterkeyn, A., 2012. Vegetation of Mediterranean temporary pools: a fading jewel? Hydrobiologia 689 (1), 23–36.
Ripley, B.J., Simovich, M.A., 2009. Species richness on islands in time: variation in ephemeral pond crustacean communities in relation to habitat duration and size. Hydrobiologia 617, 181–196.
Schneider, D.W., Frost, T.M., 1996. Habitat duration and community structure in temporary ponds. J. North Am. Benthol. Soc. 15, 64–86.
Schriever, T.A., Lytle, D.A., 2016. Convergent diversity and trait composition in temporary streams and ponds. Ecosphere 7 (5), e01350.
Sebastián-González, E., Green, A.J., 2014. Habitat use by waterbirds in relation to pond size, water depth and isolation: lessons from a restoration in Southern Spain. Rest Ecol. 22, 311–318.
Setubal, R.B., Sodré, E.O., Martins, T., Bozelli, R.L., 2020. Effects of functional diversity and salinization on zooplankton productivity: an experimental approach. Hydrobiologia 847, 2845–2862.
Simões, N.R., Dias, J.D., Meerhoff, M., Lansac-Tôha, F.A., Bini, L.M., Bonecker, C.C., 2022. Drivers of zooplankton beta diversity in natural shallow lakes and artificial reservoirs in the Neotropics. Hydrobiologia 849 (17–18), 3705–3717.
Strachan, S.R., Chester, E.T., Robson, B.J., 2015. Freshwater invertebrate life history strategies for surviving desiccation. Springer Sci. Rev. 3, 57–75.
Van Meter, K.J., Basu, N.B., 2015. Signatures of human impact: size distributions and spatial organization of wetlands in the Prairie Pothole landscape. Ecol. Appl. 25 (2), 451–465.
Vandekerkhove, J., Declerck, S., Brendonck, L., Conde-Porcuna, J.M., Jeppesen, E., Johansson, L.S., De Meester, L., 2005. Uncovering hidden species: hatching diapausing eggs for the analysis of cladoceran species richness. Limnol. Oceanogr.: Meth. 3 (9), 399–407.
Vanschoenwinkel, B., Gielen, S., Seaman, M., Brendonck, L., 2009. Wind mediated dispersal of freshwater invertebrates in a rock pool metacommunity: differences in dispersal capacities and modes. Hydrobiologia 635 (1), 363–372.
Villéger, S., Novack-Gottshall, P.M., Mouillot, D., 2011. The multidimensionality of the niche reveals functional diversity changes in benthic marine biotas across geological time. Ecol. Lett. 14 (6), 561–568.
Waterkeyn, A., Grillas, P., Vanschoenwinkel, B., Brendonck, L., 2008. Invertebrate community patterns in Mediterranean temporary wetlands along hydroperiod and salinity gradients. Freshwater Biol. 53, 1808–1822.
Zacharias, I., Zamparas, M., 2010. Mediterranean temporary ponds. A Disappearing Ecosystem. Biod. Conserv. 19 (14), 3827–3834.
Zokan, M., Drake, J.M., 2015. The effect of hydroperiod and predation on the diversity of temporary pond zooplankton communities. Ecol. Evol. 5 (15), 3066–3074.
Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R, Vol. 574. Springer, New York.
Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Meth. Ecol. Evol. 1, 3–14.