Received: 10 January 2022 | Revised: 31 October 2022 | Accepted: 21 November 2022

DOI: 10.1111/fwb.14032

Freshwater Biology WILEY

ORIGINAL ARTICLE

An evaluation of crustacean and rotifer diversity and composition in a temporary pond metacommunity: Comparing results from field samples and a hatching experiment

Maria Bisquert-Ribes[1] | Alex Martínez[1] | Andreu Castillo-Escrivà[1] | Ángel Gálvez[1] | Sanda Iepure[1,2] | Berenice de Manuel[1] | Maria Marinho[3] | Fabio Martins[3] | Carla Olmo[4] | Francesc Mesquita-Joanes[1] | Xavier Armengol[1]

[1]Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, Valencia, Spain

[2]Emil Racoviță, Institute of Speleology, Cluj Napoca, Romania

[3]Department of Biology, Faculty of Sciences, University of Porto, Oporto, Portugal

[4]Centro GEMA – Genómica, Ecología & Medio Ambiente, Facultad de Estudios Interdisciplinarios, Universidad Mayor, Huechuraba, Santiago, Chile

Correspondence
Xavier Armengol, Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, Valencia, Spain.
Email: javier.armengol@uv.es

Funding information
Ministerio de Economía, Industria y Competitividad, Gobierno de España

Abstract

1. Many aquatic invertebrates that inhabit temporary ponds produce resting forms to overcome the dry period, building up the egg bank. When the wet phase returns, the resting forms hatch and the community is restored, and then pioneer species may have a major influence on how the pond community will assemble. We aimed to evaluate the diversity of an initial pond metacommunity by comparing the early active metacommunity collected in the field and the egg bank metacommunity (by carrying out a hatching experiment) of 32 Mediterranean temporary ponds. We hypothesised that both metacommunities would be similar but also that species turnover may play an important role, and that γ diversity would be similar with both approaches.
2. After the identification and counting of rotifers and crustaceans in both metacommunities (i.e. the field vs. the experiment) we performed a Partial Triadic Analysis comparing the field metacommunity with those corresponding to each of the eight times the hatching experiment was checked for hatchlings. Furthermore, we compared the field and experimental metacommunities with a PROTEST analysis and identified the taxa responsible for differences between metacommunities with a SIMPER analysis. We assessed γ diversity using a size-based rarefaction curve and an evenness profile and explored β diversity and its components (turnover and nestedness) for the two metacommunities.
3. Our experimental results showed differences in the temporal pattern of emergence between groups of organisms, with copepods, rotifers, and anostracans appearing first, but ostracods and rotifers reaching the highest diversity at the end of the experiment. The active and experimental pioneer metacommunities were similar according to a Procrustes analysis. Nevertheless, β diversity was high in both metacommunities and the differences among ponds and between both assemblages were mostly explained by species turnover.

4. Both the active and experimental pond metacommunities showed some exclusive species that may be more difficult to uncover with only one type of approach. Furthermore, the high β diversity observed indicates that each temporary pond is an important contributor to γ diversity in the metacommunity.
5. These results show that hatching experiments provide information that is complementary to standard sampling of the active community, and consequently is a useful tool to uncover pond biodiversity.

KEYWORDS
beta diversity, egg bank, gamma diversity, resting forms, species richness

1 | INTRODUCTION

Temporary ponds are one of the most common water bodies in the world (Downing et al., 2006; Wetzel, 1990), and a type of ecosystem that harbours high biological diversity (Calhoun et al., 2017). In Mediterranean regions, and especially in the Iberian Peninsula, where natural lakes are very scarce (Miracle et al., 2010), temporary ponds constitute an important part of their lentic ecosystems and are major contributors to the biodiversity of freshwaters (Blondel & Aronson, 2005; Brendonck & Williams, 2000). During the dry season, which is unfavourable for many aquatic organisms, population survival is ensured by resting life stages that accumulate in the sediment, forming the so-called *egg bank*, a reservoir of life forms that ensures the reestablishment of the community during the next wet phase (Brendonck et al., 2017; Brendonck & de Meester, 2003; Wisnoski et al., 2019). The biological communities of a group of ponds can be viewed as a metacommunity. Local and regional factors may both play an important role in structuring metacommunities, besides latency, which can also be essential to understand regional diversity and metacommunity structure (Wisnoski et al., 2019). Resting forms enable both temporal and spatial dispersal when propagules are transported by vectors such as wind, water, and other animals (Brendonck et al., 2017; Brendonck & Riddoch, 1999; Frisch et al., 2007), including human activities (Valls et al., 2016; Waterkeyn et al., 2010).

Alpha, β, and γ diversity measures are relevant to understand metacommunity structure and the underlying processes modulating it. Many studies have analysed the β diversity of aquatic active communities, concluding that turnover is the main factor driving differences in spatial (between pond) β diversity (Atkinson et al., 2021; Fernández-Aláez et al., 2020; Hill et al., 2021; Korhonen et al., 2010; Martins et al., 2019), but other studies have found nestedness as the main factor driving β diversity (Florencio et al., 2011; Gleason & Rooney, 2018; Pires et al., 2017). Only a few studies have assessed the β diversity of the egg bank, and they found turnover to be the main component driving β diversity (Declerck et al., 2011; Freiry et al., 2016; Freiry, Weber, et al., 2020). However, to our knowledge, no study has compared β diversity and its components between active communities in the early stages of the hydroperiod (i.e. initial) and dormant metacommunities.

The egg bank is usually the largest source of propagules for the recolonisation of temporary ponds during the next hydroperiod (Brendonck et al., 2017), having a strong influence on the dynamics of the pond community (Cáceres, 1998; Hairston, 1996), but also on metacommunity organisation (Fukami & Morin, 2003; Loeuille & Leibold, 2008). In recent years, some studies have evaluated the egg bank of temporary ponds from a metacommunity perspective (e.g. Vandekerkhove, Declerck, Brendonck, Conde-Porcuna, Jeppesen, & de Meester, 2005; Valls et al., 2016). Many studies have also compared the assemblages obtained from hatching experiments with those sampled in the field (Freiry, Gouvea, et al., 2020; García-Roger et al., 2008; Rosa et al., 2021; Vandekerkhove, Declerck, Brendonck, Conde-Porcuna, Jeppesen, Johansson, & de Meester, 2005; Wang et al., 2020). However, most of these studies have dealt with one or two groups of aquatic invertebrates (rotifers, ostracods or cladocerans), and only a few have evaluated more comprehensive communities comprising a variety of groups (Olmo et al., 2020; Santangelo et al., 2015).

Works analysing the wide invertebrate diversity of temporary ponds, focusing on the initial metacommunity, are therefore scarce, although these types of comprehensive studies could be important for understanding pond functioning and dynamics. We tried to fill this gap by analysing five groups of aquatic invertebrates (rotifers, cladocerans, copepods, fairy shrimps, and ostracods) of temporary ponds to have a more complete view of their metacommunity organisation at the beginning of the hydroperiod. To this aim, we studied the aquatic invertebrate metacommunity of 32 Mediterranean temporary ponds from the Iberian Peninsula by direct sampling at the beginning of the hydroperiod (initial active community), and by carrying out a hatching experiment using their egg bank. We compared the experimental metacommunity with the field metacommunity to evaluate the similarities between them. The experiment also allowed us to evaluate changes in the hatching metacommunity through time, enabling us to assess differences in hatching time between groups of organisms. We hypothesised that: (1) the hatching experiment and the field datasets would be similar in species composition, but we also expected to find taxa exclusive to each metacommunity; (2) turnover would be the main factor responsible for differences in similarity between the metacommunities and the main component of β diversity that explained differences between ponds

for the active and hatching experiment metacommunities; and (3) the metacommunities may have similar species richness, although the relative abundance of species in each metacommunity might be disparate.

2 | METHODS

2.1 | Study area and sampling methods

We selected 32 temporary ponds of different characteristics (size, altitude, depth, etc.) avoiding brackish waters (Table S1, more details in Olmo et al., 2022) located in the Eastern Iberian Peninsula (Figure 1, Table S1). The area is characterised by a Mediterranean climate with warm temperatures (15–17°C mean annual temperature) and low rainfall (500–600 mm mean annual precipitation; Chazarra et al., 2018) concentrated mainly in autumn (September to November) and spring (March to May). Temporary ponds in the area usually fill after autumn rains, remaining flooded until the end of spring or early summer. Most ponds have and annual hydroperiod, but others are semi-permanent, not drying up regularly every year.

In 2017, the autumn season was very dry and most of the ponds flooded in winter 2018. We took sediment samples from each pond at the end of the dry season in 2017, between September and November. We selected six sampling points in each pond, three in the littoral zone and three in the deepest areas of the basin, in order to take into account the patchiness of egg banks (Brendonck & de Meester, 2003) and to encompass microhabitat heterogeneity. Each sediment sample was collected with a spatula in a square area of 9×9 cm and 3 cm depth. The sediment of each pond was homogenised in a tray and dried at 35°C until sediment weight loss ceased. We stored the sediment at room temperature and darkness until the start of the experiment.

The active community of the ponds was sampled in February 2018, a few weeks after flooding of the seasonal ponds and depth increase in semipermanent ones. We sampled the water column using a 63-μm mesh hand net. We carried out a horizontal trawl of variable length (a total of 10–20 m) depending on pond size, and integrating, in a proportional manner, the different microhabitats observed. Samples were immediately fixed with formaldehyde 4%. Benthic samples were collected with a 250-μm mesh hand net. The sampled 10–20 m was distributed proportionally to the extension of

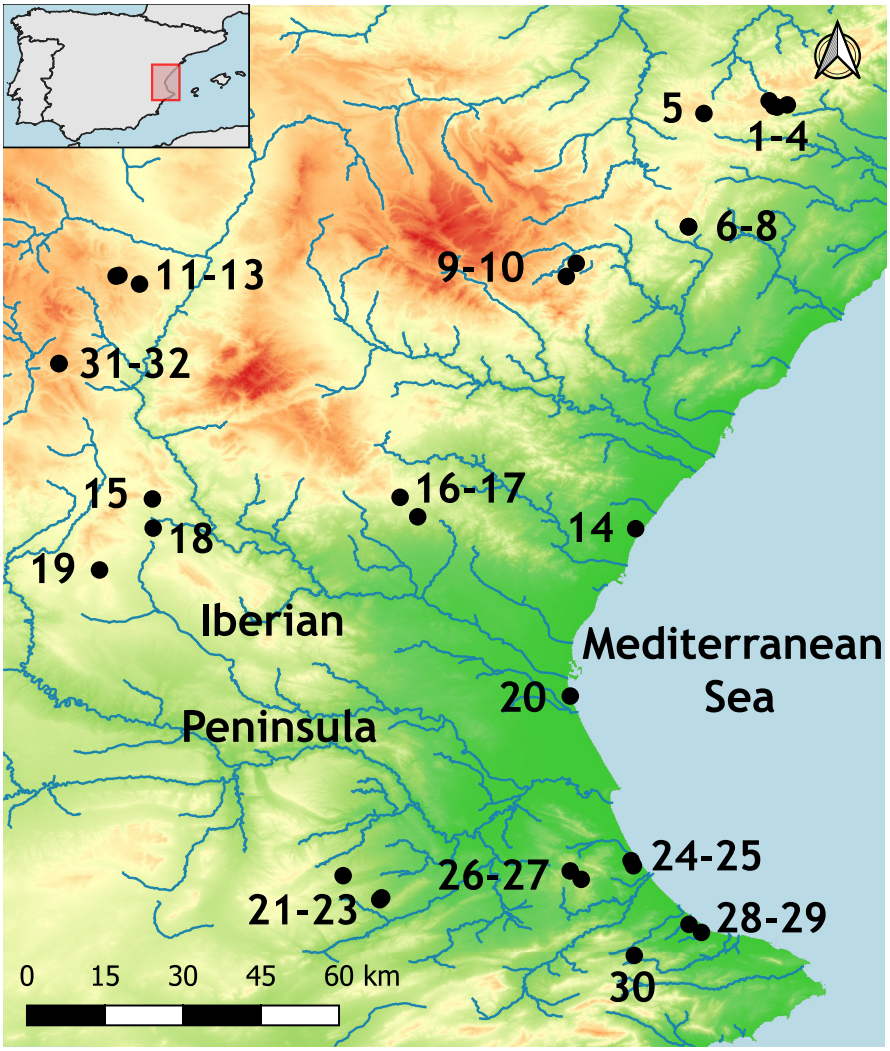

FIGURE 1 Map of the studied region and geographical locations of the 32 ponds sampled (dots). More information about the ponds is available in Table S1 of the supporting information

the different benthic microhabitats observed and fixed with ethanol 70%. We measured in situ water temperature, conductivity, pH and oxygen concentration and saturation percentage with a WTW meter Multi 3,430 (Weilheim, Germany), water depth with a graduated stick, and transparency with a Snell tube (van de Meutter et al., 2006).

2.2 | Hatching experiment design

The hatching experiment was conducted between 11 April and 9 May 2018, in plastic containers measuring 10×10×5 cm (0.5 L). Three replicates were used for each pond. Each container (96 in total) included a glass Petri dish with 30 g of homogenised sediment and was filled with 300 mL of sterilised deionised water. The containers were closed with a transparent plastic cover to avoid contamination with air droplets between them. Four small holes (1 cm diameter) were drilled in each cover to allow for air renewal. All containers were placed in a BINDER™ KBW 240 (E 5.1) culture chamber (Tuttlingen, Germany), randomly distributed over the chamber shelves. Three blank control containers, without sediment, were added to monitor the possible circulation of propagules in the chamber. The experiment was conducted under controlled light and temperature conditions: 12 hr light at 24°C and 12 hr darkness at 18°C. These conditions were selected to simulate the natural light and temperature conditions during the flooding period. The emergence of invertebrates in the containers, including controls, was checked at days 1, 3, 5, 8, 11, 14, 21, and 28 after filling. The procedure consisted of filtering the water through a 20-μm mesh, pouring it carefully to avoid disturbance of the sediment. The filtered water was not discarded but was stored temporarily and then returned to the corresponding plastic container. The 20-μm filter was washed with water on a Petri dish and checked with a stereomicroscope to sort and pick up all observed invertebrates. Hatched rotifers were collected with Pasteur pipettes, isolated in plastic tubes, and immediately fixed with 70% alcohol (these organisms have direct development and can be identified to species level few hours after hatching). To identify crustaceans to species level (and particularly those with indirect development, such as copepods and ostracods, that need periods of weeks to become adults), emerged juveniles were isolated individually in multi-well plates, and placed in a BINDER™ KBW 720 (E 5.1) culture chamber (Tuttlingen, Germany) at a constant temperature of 21°C until reaching adulthood, when they were also fixed. During this growth period, copepods and branchiopods were fed every 2 days with the green algae *Raphidocelis subcapitata* (Korshikov) Nygaard, Komárek, Kristiansen & Skulberg 1987 from a pure laboratory culture; juvenile ostracods were fed with frozen spinach following Schmit et al. (2007). To ensure the removal of all hatched invertebrates, each Petri dish with sediment was also checked under a stereomicroscope to recover hatched individuals that could have remained in the sediment when pouring the water. To do so, the sediment was carefully inspected with a plastic stick drawing a zigzag along the entire plate while being examined. Observed organisms of other taxonomic groups including ciliates, nematodes, tardigrades, turbellaria, and gastrotrichs, were also detected, removed (except for ciliates), and their presence noted during the experiment, although they were not counted or identified to lower taxonomic levels. Finally, the Petri dish with sediment, the filtered water and the remains of resting forms captured during the filtrating process were returned to their corresponding container to avoid the loss of viable resting forms. Water loss and evaporation were compensated by adding sterilised deionised water up to the level of 300 mL. Water conductivity, oxygen concentration and pH were measured three times (days 2, 7, and 23) in each container during the incubation period with a WTW meter Multi 3430.

All individuals from the active metacommunity samples and those emerged during the experiment were counted and identified following Koste (1978) for rotifers, Alonso (1996) for branchiopods, Dussart (1967, 1969) for copepods, and Meisch (2000) for ostracods. Identifications were done at the species level when possible (except for bdelloid rotifers and harpacticoid copepods).

2.3 | Data analysis

Given that a different assemblage of hatched organisms was obtained on each day of the experiment for each pond, we wanted to compare these metacommunities with each other across time, that is, we wanted to analyse whether the metacommunity hatched in the experiment changed over time. To do this, we carried out a Partial Triadic Analysis (PTA; Thioulouse & Chessel, 1987; Thioulouse, 2011), which analyses a three-dimensional matrix (ponds × species × time). In the matrix, *time* is represented by the different days when the hatching experiment was checked (8 days in total). Therefore, PTA shows whether the hatching metacommunities changed through time. We added to the analysis the initial active metacommunity matrix (sampled directly in the field) to check if it was similar to any of the hatching experiment metacommunities. Before PTA, we summed the three replicates for each pond and applied the Hellinger transformation (Legendre & Gallagher, 2001) to the abundance species matrices. PTA provides three related values: vectorial correlation coefficients (RV coefficients), table weights, and $\cos^2$ values. RV coefficients show the similarity between pairs of species matrices, that is, between checking days of the hatching experiment (and between these and the active metacommunity): the higher the values, the greater the similarity and therefore the less temporal variation. Table weights indicate how much each matrix contributes to the compromise table, which is considered an average matrix (Thioulouse, 2011). The information of each matrix that is represented by the compromise table, is indicated by the $\cos^2$ values. Therefore, higher values of the three indicators mean low temporal variation through time, because higher similarity among samples (RV coefficients) leads to higher table weights and $\cos^2$ values.

We performed a Procrustes analysis and PROTEST (Jackson, 1995; Peres-Neto & Jackson, 2001) to test whether the hatching experiment and the initial active metacommunities were correlated.

To represent the hatching experiment metacommunity, we used the compromise table of another PTA (estimated excluding the active metacommunity set) because this matrix can be interpreted as an average of all the experimental matrices. The Procrustes m_{12}^2 statistic in PROTEST represents the optimal fit between the two matrices, so that when the m_{12}^2 value is high (close to 1), the relationship between matrices is high. Following Peres-Neto and Jackson (2001), the significance of m_{12}^2 value was tested by permutation (999 permutations). If the PROTEST is significant, the matrices are related. Prior to the PROTEST analysis, the Hellinger distance was applied to the active metacommunity abundance matrix.

To determine which taxa contributed most to the differences between the hatching experiment and the initial active metacommunities, we carried out a similarity percentage analysis (SIMPER; Clarke, 1993), applied to the untransformed species abundance matrices.

To assess which component of β diversity (turnover or nestedness) accounted for most of the differences between ponds in the hatching experiment and in the active metacommunities, we obtained the Sorensen index and its components for both datasets by means of the function beta.multi of the R package betapart (Baselga & Orme, 2012). We also compared each pond's active community with its corresponding accumulated experimental sample, using the function beta.temp, taking into account that it is aimed at comparing samples through time for the same site.

We analysed the overall (γ) diversity of the two sets of samples (active and hatching experiment metacommunities) in order to assess whether one was more diverse than the other. Considering that it is not possible to detect all the species in a set of samples due to practical limitations (Colwell & Coddington, 1994), to evaluate the diversity detected with our sampling effort and to estimate the proportion of the total diversity that we could assess with our samples, we calculated the size-based rarefaction and extrapolation curve for the two sets of samples and for orders of diversity $q = 0$ (species richness), $q = 1$ (exponential of Shannon entropy), and $q = 2$ (inverse of Simpson dominance), following Chao et al. (2014). The size-based rarefaction and extrapolation curve visually indicates whether our estimates of true diversity are well fitted. Typically, when the sample is extrapolated to double the size of the observed sample, the size-based rarefaction and extrapolation curve for species richness (order 0), does not stabilise and represents a lower bound, so there can be some uncommon species that have not been detected (Chao et al., 2020). In these cases, Chao et al. (2014) and Chao and Jost (2012) proposed to infer diversity for a standardised fraction of the metacommunities, the C_{max}, that is, the minimum value among maximum coverage values for samples when the samples have been extrapolated to twice the sample size. Then, for any value up to C_{max}, we can estimate the diversity and the evenness of our assemblages, and they can be compared. Finally, we assessed the evenness profile following Chao et al. (2020), which can indicate if our samples are evenly distributed for species abundances, for orders $q = 1$ and $q = 2$. When this happens, the profile is a horizontal line at the level of $q = 0$, otherwise it is a decreasing function of order q.

TABLE 1 Number of taxa for each taxonomic group, either exclusive of the hatching experiment setting (HE), exclusive of the initial active community (IA), or shared between settings (HE and IA)

	HE	HE and IA	IA
Rotifera	30	16	33
Copepoda	4	1	12
Cladocera	15	9	8
Anostraca	2	2	1
Ostracoda	16	13	11
Total	67	41	65

All statistical tests and ordination analyses were performed in R ver. 3.6.1 (R Development Core Team, 2019) using libraries vegan (Oksanen et al., 2020), ade4 (Dray & Dufour, 2007), BiodiversityR (Kindt & Coe, 2005), betapart (Baselga & Orme, 2012) and iNEXT (Chao et al., 2014).

3 | RESULTS

3.1 | Metacommunity composition and environmental setting

A total of 106 taxa (including juveniles) were found in the initial active metacommunity and 108 in the hatching experiment metacommunity (Table 1, Table S2). No individuals were found in the control samples without sediment. Among the different taxa that emerged during the experiment, rotifers stood out, as 43% of the taxa found, with a similar frequency in the active samples (46%). The next group, in terms of taxonomic richness, was the ostracods, with 27% of taxa in the experiment and 23% in the active metacommunity. Ostracods were closely followed by cladocerans, with 22% and 16% of taxa, respectively, in both sets of samples. Copepods (5%) and fairy shrimps (4%) had similar representation in the hatching experiment, but in the active community copepods (12%) were more represented than fairy shrimps (3%). Altogether, in the two assemblages, we found a total of 173 different taxa, out of which 41 taxa were shared by both sets of samples, while 67 were exclusive to the hatching experiment and 65 were exclusive to the initial active metacommunity (Table 1).

Regarding environmental variables, oxygen saturation in the experiments was 69 ± 16%, a little bit lower than in field (87 ± 25%, Table S1, S3). Water conductivity was 629 ± 750 μS/cm, in the rank of, but slightly lower, than the field measures (970 ± 1,450 μS/cm). Finally, pH was similar in both datasets; 7.8 ± 0.3 for the experiment, and 8.0 ± 0.4 for the active community samples (Tables S1, S3).

3.2 | Temporal changes in the hatching experiment

The interstructure of the PTA shows the progressive differentiation of the species assemblages throughout the experiment from day

1 to 28 (Figure 2, Table 2). The experimental metacommunity was changing at a higher rate until approximately day 5. Table weights for experimental assemblages varied between 0.22 and 0.44 (Table 2) during the experiment, but the values were slightly higher and similar between times from day 5 onwards. Moreover, the $\cos^2$ values indicate that the compromise table is mostly represented by the period between days 5 and 28 (Table 2). Therefore, the hatching metacommunity changed more rapidly during the first days of the experiment, but afterwards the change rate slowed down and was more stable, and between days 11 and 21 the metacommunity was most similar to the compromise table. Differences through time could be related to variations in the hatching phenology of each species during the experiment. At the beginning, copepods and fairy shrimps hatched more frequently than later on (Figure 3). Until day 8 there was a burst of rotifers and ostracods, and the cladocerans also increased. From day 11 there was a second increase in cladocerans, rotifers, and ostracods, although the latter two groups, unlike the others, do not seem to show saturation at the end of the experiment (28 days), in terms of the appearance of new species (Figure 3). The low RV coefficients and table weight values of the initial active metacommunity (Table 2, Figure 2) indicate that this dataset is quite different from that of the experiment, although it is closer to the experimental assemblages during the first week of the experiment (days 1–5) than to those observed later on (days 11–28).

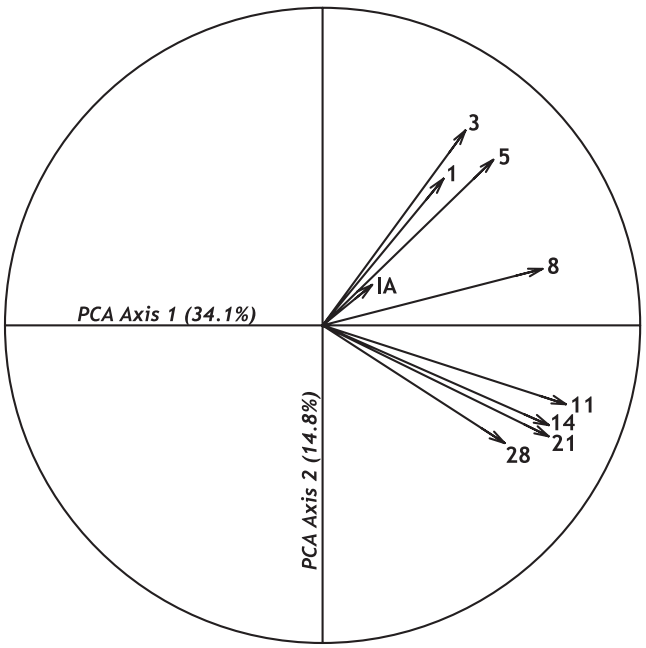

FIGURE 2 Interstructure ordination by means of a partial triadic analysis of the hatching experiment datasets, including a matrix for each day of revision after the starting of the experiment (days 1–28, indicated by the numbers) and the initial active metacommunity (IA). Each arrow represents the correlation of each table included in the analysis (the eight matrices of each revision day plus the matrix of the active metacommunity), with the two axes of a principal component analysis summarising the global structure and the relationships between each moment of the experiment. The circle corresponds to maximum correlation values of −1 and 1 for each axis

3.3 | Differences between the active and experimental metacommunities

Results of the PROTEST analysis suggest a significant concordance ($m_{12}^2 = 0.85$, $p = 0.01$) between the compromise table of the hatching experiment and the active metacommunity. Notwithstanding this correlation between both datasets, SIMPER analysis indicated that 28 taxa are responsible for 75% of the differences between them. Taxa that showed significant differences between the active and experiment datasets were the copepod *Metacyclops minutus*, the cladocerans *Chydorus sphaericus*, and *Ceriodaphnia reticulata*, Cyprididae ostracods, and Bdelloidea rotifers (these last two groups were not identified to species level). The three taxa first mentioned were more abundant, and even exclusive (in some cases) to the active metacommunity but not to the hatching experiment (Table S2), and the last two taxa were found exclusively in the hatching experiment.

3.4 | Diversity analyses

The global Sorensen index was 0.95 for the initial active metacommunity and 0.94 for the hatching experiment. The analysis of β diversity indicated that the differences in species composition between ponds in each of the two datasets were mostly due to turnover (0.89 for the active metacommunity and 0.91 for the hatching experiment). That is, the species of one pond are mostly replaced by other species in other ponds in both the active and the experimental datasets. When we compared pond samples of the active metacommunity with their corresponding ponds in the experiment, the median β diversity was 0.88. Differences in species composition were also mostly due to turnover (median value 0.81). Only in the case of one pond were the differences mostly due to nestedness, and in the case of another pond differences were due to both processes equally (Table S4).

The size-based rarefaction and extrapolation curves (Figure 4) for the active and experimental metacommunities showed that the calculated asymptotic values were good estimators of true diversity for orders 1 and 2. However, for order 0, the asymptotic values corresponded to minimum species richness (Figure 4). Our samples were sufficient to estimate the true diversity in a proportion of 99.9% (C_{max} value). In the remaining 0.1% of both datasets, the individuals may contain infinitely uncommon species (Table 3). The difference in species richness (order 0) between the datasets was only 1.71 species. For orders 1 and 2 the asymptotic values were higher in the active metacommunity than in the experiment (Table 3). The evenness profiles (Figure 5) indicated that individuals were slightly more evenly distributed in the experiment than in the active metacommunity. Most of the differences between the datasets were due to the presence of uncommon species with low abundances (Table S2).

TABLE 2 Partial Triadic Analysis values for each day of revision of the hatching experiment (day 1–day 28) and for the initial active metacommunity (IA): RV coefficients between pairs of matrices (revision days or IA) indicate the similarity between them (the higher the value, the lower the temporal metacommunity variation); table weights indicate the contribution of each moment of the experiment (each day) or the IA to the average matrix; cos^2 values indicate the amount of information represented in the average matrix

RV coefficients											
	Day 1	Day 3	Day 5	Day 8	Day 11	Day 14	Day 21	Day 28	IA	Table weights	cos^2
Day 1	1									0.22	0.34
Day 3	0.28	1								0.26	0.44
Day 5	0.16	0.44	1							0.30	0.51
Day 8	0.29	0.23	0.42	1						0.39	0.68
Day 11	0.18	0.14	0.29	0.46	1					0.44	0.76
Day 14	0.14	0.16	0.24	0.29	0.61	1				0.41	0.72
Day 21	0.11	0.21	0.16	0.36	0.47	0.51	1			0.40	0.74
Day 28	0.10	0.12	0.10	0.29	0.36	0.32	0.46	1		0.33	0.60
IA	0.11	0.10	0.01	0.07	0.06	0.06	0.07	0.08	1	0.09	0.17

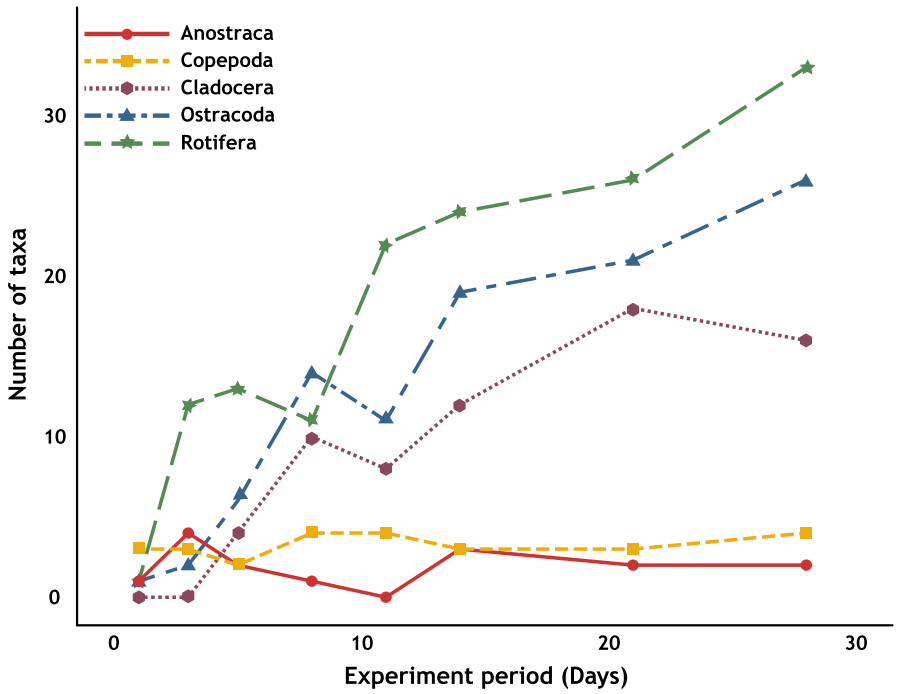

FIGURE 3 Taxonomic richness of the major groups of invertebrates (Anostraca, Copepoda, Cladocera, Ostracoda, and Rotifera) found along the hatching experiment for the whole set of ponds

4 | DISCUSSION

Our results are similar to those found by García-Roger et al. (2008), who compared the rotifer communities of brackish temporary ponds resulting from a hatching experiment with those directly sampled in the field. They found no statistical differences between the metacommunities but reported some unique species in each dataset. Our results show high levels of diversity in the initial metacommunity of Mediterranean temporary ponds, and the need to use both methodologies to fully describe it. This is because, despite both metacommunities being very similar, we have also found many species exclusive to each dataset. The significant similarity found between the assemblages, makes sense since the largest source of recolonisation for non-flying invertebrate species in temporary ponds is the egg bank that accumulates in the sediment (Brendonck et al., 2017). Nevertheless, β diversity is notably high between both datasets, and species turnover is responsible for the differences.

The egg bank has a temporal component (Brendonck & de Meester, 2003) since it can accumulate resting forms for months to years (Brendonck et al., 2017), which makes it possible to have a high diversity of resting forms. However, there are a number of important conditions triggering hatching. For example, oxygen level is crucial for breaking the latency of resting forms in many aquatic invertebrates (Alekseev et al., 2007). During our experiment, oxygen saturation was above 50% in all containers, which might have allowed the hatching of many resting forms, even some that would not hatch under normal (anoxic or hypoxic) conditions in pond sediment.

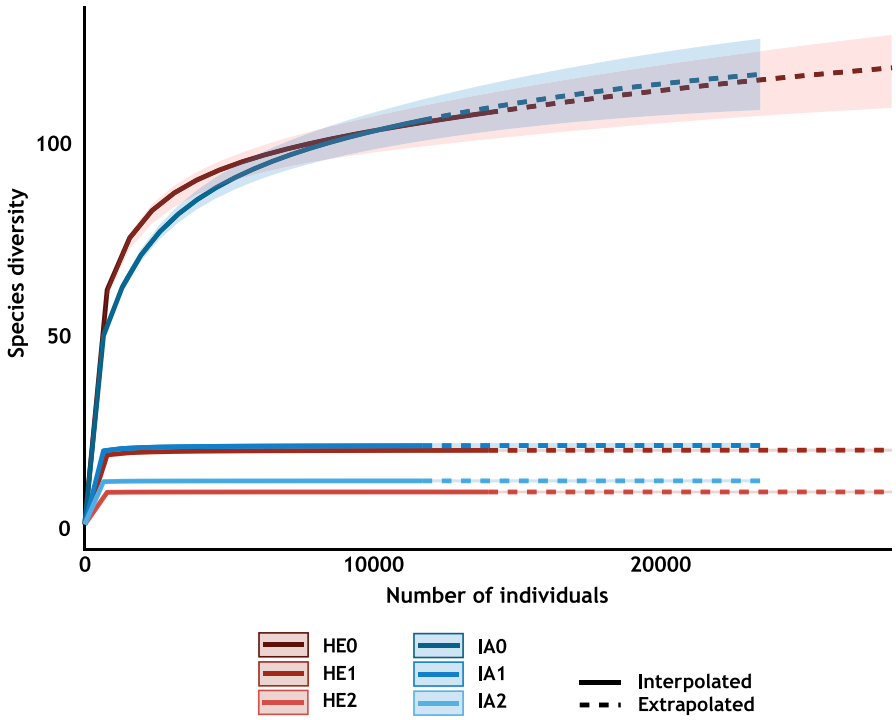

FIGURE 4 Size-based rarefaction (solid lines) and extrapolation (doted lines) curves for the initial active (bluish) and the hatching experiment (brownish) metacommunities. HE: hatching experiment metacommunity; IA: initial active metacommunity. Values 0–2 in the legend indicate the order of diversity (q), where $q = 0$ (species richness), $q = 1$ (exponential of Shannon entropy), and $q = 2$ (inverse of Simpson dominance)

TABLE 3 Diversity values of orders q = 0 (species richness), q = 1 (exponential of Shannon entropy) and q = 2 (inverse of Simpson dominance) for both the initial active and the hatching experiment metacommunities. Three diversity values are presented for each order of diversity: the asymptotic (estimated) value for C_{max} (the minimum among maximum coverage values for samples extrapolated to twice their sample size; see Chao et al., 2020); the empirical value (directly obtained from field and experimental datasets); and the undetected diversity value (difference between the asymptotic and the empirical values)

	Initial active			Hatching experiment		
Orders of diversity	Asymptotic for C_{max}	Empirical	Undetected	Asymptotic for C_{max}	Empirical	Undetected
0	117.92	106	13.92	119.63	108	11.63
1	21.52	21.45	0.07	20.30	20.24	0.06
2	12.32	12.31	0.01	9.44	9.43	0.01

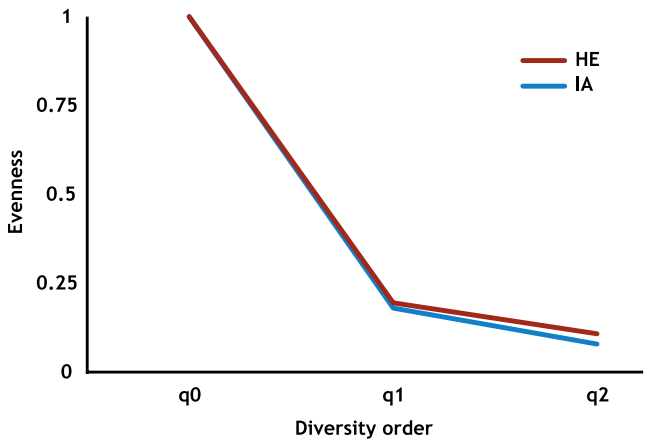

FIGURE 5 Evenness (E) profile for orders of diversity $q = 0$ (species richness), $q = 1$ (exponential of Shannon entropy), and $q = 2$ (inverse of Simpson dominance) for the initial active (IA, blue) and the hatching experiment (HE, brown) metacommunities

In the field, during the first days of inundation, there is usually very little water accumulated in the pond, and oxygen levels may be too low to stimulate hatching in some resting forms. Furthermore, the temperature conditions selected for the hatching experiment were similar to those occurring in Mediterranean ponds in autumn or spring (the expected time for infilling of temporary ponds). However, despite the inundation period being where the greatest emergence occurs (Olmo et al., 2012), the year we sampled was unusual, as the ponds were filled in early winter, when temperatures are lower. This may have caused discrepancies between the species hatched in the laboratory and those found in the field. It is also possible that, because some species require special conditions, or special incubation periods to hatch (Vandekerkhove, Declerck, Brendonck, Conde-Porcuna, Jeppesen, & de Meester, 2005), their resting forms could not hatch in the particular experimental setting and therefore those species were not detected in the experiment. Differences in micro-habitat heterogeneity, either when collecting the sediment or when

sampling the active metacommunity may also be partially responsible for the observed differences in species composition (Strachan et al., 2016a). Nevertheless, overall the two metacommunities were significantly correlated (according to our Procrustes analysis), supporting the use of hatching experiments to show general patterns of species composition in temporary habitats.

The hatching experiment is also a good method to identify the initial species occupying pond metacommunities from the egg bank since, as hatching of individuals proceeds, they can be immediately extracted and identified. In this sense, our results show how the experimental metacommunity develops over time, although we must take into account that interactions among species were artificially reduced (as specimens were removed each time the experiment was checked). At the beginning of the experiment, metacommunity structure changes more rapidly than towards the end of the experiment. This is influenced by the group of organisms that hatch. Depending on the target group, the duration of the hatching experiment can be modified. For example, copepods and especially fairy shrimps usually appear shortly after flooding (Williams, 2006), so that when working with these organisms, the duration of the experiment may be shortened. Other groups of microinvertebrates, including rotifers, cladocerans, and ostracods, also have species that appeared early in the experiment. Nevertheless, they occur at high species richness in these ponds; thus, many species could differ in their hatching time and therefore some species may appear later on (Bandeira et al., 2020; Rosa et al., 2021). We have shown that the best option to gather accurate information from the egg bank about invertebrate diversity in temporary ponds is by establishing a relatively long-term hatching experiment (i.e. 1 month long or longer).

In terms of sampling effort, it is important to note that it can be difficult to integrate all the spatial heterogeneity of the active metacommunity when combining water column (i.e. plankton) and benthic samples. Some species of cladocerans, rotifers, and copepods live associated with the benthos (Wetzel & Likens, 2000), so they can be underestimated in water column samples, and in the benthic ones, since the hand nets we used had larger pore size than the necessary to capture some of these organisms. For example, bdelloid rotifers are associated with benthic environments and they did not appear in plankton field samples, but we found them in 20 (out of 32) different ponds in the hatching experiment. There are also species that live associated with macrophytes (Wetzel & Likens, 2000), and they may be difficult to detect. In the field, we tried to sample different microhabitats including macrophytes, but at the beginning of the hydroperiod, and particularly in winter, macrophyte cover is usually very low. It is therefore possible that we underestimated phytophilous species in the initial active metacommunity. By contrast, some species and their egg banks have patchy distributions (Brendonck & de Meester, 2003; Pinel-Alloul & Ghadouani, 2007); and this heterogeneity may not have been fully covered by our sediment sampling, resulting in some species being underrepresented in the experimental dataset.

Besides hatching from the egg bank, there are other ways by which rotifers and crustaceans can colonise and establish in a temporary pond, such as arriving from other ponds through dispersal or surviving the dry period in a resting form other than resting eggs. Pinceel et al. (2016) showed that not all resting forms are transported uniformly by wind. Some are more easily transportable than others, so that they can be readily dispersed during the dry season and reach new ponds. As the community is re-established from the egg bank (Brendonck et al., 2017), these transported resting forms can also hatch and affect the community in that pond and, consequently, the entire metacommunity. Some species of microcrustaceans, including many Candonidae ostracods, do not produce resting eggs (Mesquita-Joanes et al., 2012). Consequently, they may arrive from nearby water bodies by means of dispersal through water overflows or sometimes by wind or by zoochory (Brendonck & de Meester, 2003). Also, juvenile or adults of some ostracod species can withstand desiccation for long periods buried in the sediment with the valves tightly closed (Horne, 1993). Similarly, some cyclopoid copepods have larval dormancy stages, that is, their resting forms are not eggs but juvenile or subadult copepods entering latency just before reaching adulthood or maturation (Alekseev et al., 2007). The resting forms of species with such strategies, may have remained somewhere in the ponds during the dry phase, and they might not have been sampled during sediment collection (Frisch, 2002; Olmo et al., 2020), but later appeared in the active pond metacommunity.

When studying the zooplankton of temporary ponds, it is common that only a few species are dominant and most species occur in relatively low abundances (Antón-Pardo & Armengol, 2010). Resting eggs produced by uncommon species are scarce and they may have a low probability of being found in egg bank samples. Nevertheless, our results showed similar species richness between both metacommunities, although the evenness values of orders q = 1 and 2 indicate that in the experimental metacommunity the individuals were slightly more homogeneously distributed among species than in the active metacommunity. This may be due in part to these uncommon species, which appear in the active metacommunity with very small abundance, causing the active metacommunity to be slightly more unbalanced than in the experiment. However, it is also possible that the continuous extirpation of individuals in the experiment precluded rapid population growth of some species with high growth rates, which may otherwise become more abundant when growing in the field. The fast growth of fairy shrimps, ostracods, or large cladocerans might allow them to outcompete smaller invertebrates under natural conditions (Aguilar-Alberola & Mesquita-Joanes, 2011; Williams, 2006). Nevertheless, some biological interactions, such as predation, or resource depletion can act as limiting factors in natural conditions. For example, Yousif et al. (2013), showed how ostracods can prey over resting forms of another species acting as a biocontrol.

Freiry, Weber, et al. (2020) studied the diversity of zooplankton resting forms from temporary ponds in a subtropical region. They found that β diversity between ponds was rather high and concluded that this was one of the major contributors to the total diversity of ponds in the study area. We analysed the β diversity between ponds of the active and experimental metacommunities and in both cases it was high. Furthermore, the largest contributor

to β diversity was turnover for both metacommunities. This indicates that each pond is unique; although most of the ponds included in our study are temporary, they usually harbour species that do not appear in other ponds with similar characteristics. Furthermore, the β diversity between ponds in the experimental metacommunity was slightly higher than that of the active one. In the hatching experiment, all invertebrates were extracted shortly after hatching, thus factors such as predation, competition, or rapid population growth did not strongly affect the biological control of this metapopulation. However, in the active metacommunity of ponds, despite being also a pioneer metacommunity, these biotic interactions cannot be avoided. This may be the reason why some species that were detected in the experiment were not found in the active metacommunity. It is also possible that some species were missed during sampling but detected in the experiment.

Another important factor that can influence pond metacommunity structure and development is the length of the hydroperiod. For instance, Stenert et al. (2017) observed that cladoceran communities change according to pond hydroperiod length. This may be extended to the entire microinvertebrate community of these ecosystems, and consequently the variation of hydroperiod duration among ponds, may also partially explain the high β diversity in both metacommunities. In addition, the timing of pond inundation is also important. In the Mediterranean region, rains usually occur during autumn, thus driving a peak of hatching at this time. However, as we have already mentioned, this is variable. In fact, during the sampling year of this study, autumn was very dry and pond inundation occurred in early winter, at a time when environmental conditions are not optimal for the hatching of most species, probably affecting the initial stages of metacommunity development and its biodiversity. This problem may become an established trend over the next years due to climate change. Most probably, the rainy season in Mediterranean environments will be reduced (IPCC, 2014; Sala et al., 2000), affecting the infilling of the ponds and producing long-term changes in their hydroregime (Bagella et al., 2016). This may strongly influence the egg bank and metacommunity dynamics (Pinceel et al., 2018; Pyke, 2005). If the hydroperiod is shortened, the egg bank can be eroded, because hatching organisms may not have enough time to complete their life cycles and produce resting forms (Pinceel et al., 2018). Global warming may also affect the hatching response of resting forms, producing alterations in the life cycles of zooplankton species (Dupuis & Hann, 2009; Jones & Gilbert, 2016), significantly reducing the biodiversity of the egg bank and, eventually, of temporary pond metacommunities.

5 | CONCLUDING REMARKS

Our study focused on the initial metacommunity of temporary ponds, an early phase of their ecological succession with large effects on its subsequent development (Loeuille & Leibold, 2008). In the present study, we showed how the initial metacommunity composition already accounts for high biological diversity, although many species may remain undetected, so consequently even higher diversity values should be expected. In addition, we also showed how valuable hatching experiments are to uncover temporary pond biodiversity, as they can generate diversity estimates close to those obtained from field sampling campaigns and they can be used as a complementary tool to find species not detected in the active metacommunity, possibly achieving in combination, a species richness estimation up to 60% higher than using only one method. This study also highlights the high biodiversity of temporary ponds, and the importance of protecting these ecosystems that are highly sensitive to environmental alterations (Blondel & Aronson, 2005). Furthermore, pond metacommunities can be used as models for climate change studies, focusing on predicting the effects of a global change scenario on freshwater fauna (Blaustein & Schwartz, 2001; Parra et al., 2021); Strachan et al. (2016b) showed that the assemblages in open waters and fringing trees of a coastal plain present resilience and resistance, respectively, to false starts of the hydroperiod. When analysing the threats and conservation measures for temporary ponds, Zacharias et al. (2007), stated that conservation efforts must be focused on several small ponds, such as those included in the present study, in order to maintain high levels of biodiversity. Considering the high spatial and temporal β diversity that we observed, our results support the idea that the maintenance of these networks of temporary ponds must be done on a spatial basis, but also on a temporal scale for the sake of efficient management strategies (Cayrou & Céréghino, 2005; de Bie et al., 2008; Jeffries, 2005).

AUTHOR CONTRIBUTIONS

Conceptualisation: F.M.-J., X.A. Developing methods: M.B.-R., A.M., A.C.-E., Á.G., S.I., B.M, M.M., F.M., C.O. Data analysis: M.B.-R., F.M.-J. Data interpretation: M.B.-R., F.M.-J. Preparation of figures and tables: M.B.-R. Conducting the research and writing: M.B.-R., A.M., A.C.-E., Á.G., S.I., B.M., M.M., F.M., C.O., F.M.-J., X.A.

ACKNOWLEDGMENTS

We would like to thank the editors and two anonymous reviewers for their suggestions to an earlier version of the manuscript.

FUNDING INFORMATION

This research was supported by the Ministerio de Economía, Industria y Competitividad (Spanish Government), through project METACOM-SET (code CGL2016-7826-P). M. Bisquert-Ribes has a Predoctoral grant (FPU19/02264) founded by the Ministerio de Educación y Formación Profesional (Spanish Government). C. Olmo has a FONDECYT Postdoctorado 2020 funding (Project number: 3200340). Á. Gálvez was supported by an FPI fellowship BES-2017-080022 from the Spanish Ministry of Economy, Industry and Competitiveness.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available from the authors upon reasonable request.

ORCID

Maria Bisquert-Ribes https://orcid.org/0000-0003-4279-8295
Andreu Castillo-Escrivà https://orcid.org/0000-0002-4416-4803
Ángel Gálvez https://orcid.org/0000-0002-5562-7316
Sanda Iepure https://orcid.org/0000-0002-3748-3478
Carla Olmo https://orcid.org/0000-0003-4658-5078
Francesc Mesquita-Joanes https://orcid.org/0000-0001-7168-1980
Xavier Armengol https://orcid.org/0000-0002-0312-0396

REFERENCES

Aguilar-Alberola, J. A., & Mesquita-Joanes, F. (2011). Population dynamics and tolerance to desiccation in a crustacean ostracod adapted to life in small ephemeral water bodies. *Limnologica*, *41*, 348–355. https://doi.org/10.1016/j.limno.2011.03.003

Alekseev, V. R., de Stasio, B. T., & Gilbert, J. J. (2007). *Diapause in aquatic invertebrates. Theory and human use*. Springer.

Alonso, M. (1996). *Crustacea: Branchiopoda*, *Fauna Ibérica*. Consejo Superior de Investigaciones Científicas (CSIC).

Antón-Pardo, M., & Armengol, X. (2010). Zooplankton community from restored peridunal ponds in the Mediterranean region (L'Albufera Natural Park, Valencia, Spain). *Limnetica*, *29*, 133–144. https://doi.org/10.23818/limn.29.10

Atkinson, S. T., Cale, D., Pinder, A., Chambers, J. M., Halse, S. A., & Robson, B. J. (2021). Substantial long-term loss of alpha and gamma diversity of lake invertebrates in a landscape exposed to a drying climate. *Global Change Biology*, *27*, 6263–6279. https://doi.org/10.1111/gcb.15890

Bagella, S., Gascón, S., Filigheddu, R., Cogoni, A., & Boix, D. (2016). Mediterranean temporary ponds: New challenges from a neglected habitat. *Hydrobiologia*, *782*, 1–10. https://doi.org/10.1007/S10750-016-2962-9

Bandeira, M. G. S., Martins, K. P., Palma-Silva, C., Hepp, L. U., & Albertoni, E. F. (2020). Hydration time influences microcrustacean hatching in intermittent wetlands: in situ and ex situ approaches. *Hydrobiologia*, *847*, 3227–3245. https://doi.org/10.1007/s10750-020-04315-w

Baselga, A., & Orme, C. D. L. (2012). Betapart: An R package for the study of beta diversity. *Methods in Ecology and Evolution*, *3*, 808–812. https://doi.org/10.1111/j.2041-210X.2012.00224.x

Blaustein, L., & Schwartz, S. S. (2001). Why study ecology in temporary pools? *Israel Journal of Zoology*, *47*, 303–312. https://doi.org/10.1092/CKMU-Q2PM-HTGC-P9C8

Blondel, J., & Aronson, J. (2005). *Biology and wildlife of the Mediterranean region*. Oxford University Press.

Brendonck, L., & de Meester, L. (2003). Egg banks in freshwater zooplankton: Evolutionary and ecological archives in the sediment. *Hydrobiologia*, *491*, 65–84. https://doi.org/10.1023/A:1024454905119

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*, 201–222. https://doi.org/10.1007/s10750-016-3006-1

Brendonck, L., & Riddoch, B. J. (1999). Wind-borne short-range egg dispersal in anostracans (Crustacea: Branchiopoda). *Biological Journal of the Linnean Society*, *67*, 87–95. https://doi.org/10.1111/J.1095-8312.1999.TB01931.X

Brendonck, L., & Williams, W. D. (2000). Biodiversity in wetlands of dry regions (drylands). In B. Gopal, W. J. Junk, & J. A. Davis (Eds.), *Biodiversity in wetlands: Assessment, function and conservation*. Backhuys.

Cáceres, C. E. (1998). Interspecific variation in the abundance, production, and emergence of *daphnia* diapausing eggs. *Ecology*, *79*, 1699–1710. https://doi.org/10.2307/176926

Calhoun, A. J. K., 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. *Biological Conservation*, *211*, 3–11. https://doi.org/10.1016/j.biocon.2016.11.024

Cayrou, J., & Céréghino, R. (2005). Life-cycle phenology of some aquatic insects: Implications for pond conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *15*, 559–571. https://doi.org/10.1002/aqc.739

Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., & Ellison, A. M. (2014). Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs*, *84*, 45–67. https://doi.org/10.1890/13-0133.1

Chao, A., & Jost, L. (2012). Coverage-based rarefaction and extrapolation: Standardizing samples by completeness rather than size. *Ecology*, *93*, 2533–2547. https://doi.org/10.1890/11-1952.1

Chao, A., Kubota, Y., Zelený, D., Chiu, C. H., Li, C. F., Kusumoto, B., Yasuhara, M., Thorn, S., Wei, C. -L., Costello, M. J., & Colwell, R. K. (2020). Quantifying sample completeness and comparing diversities among assemblages. *Ecological Research*, *35*, 292–314. https://doi.org/10.1111/1440-1703.12102

Chazarra, A., Flórez, E., Peraza, B., Tohá, T., Lorenzo, B., Criado, E., … Botey, R. (2018). *Mapas climáticos de España (1981–2010) y Eto (1996–2016)*. Agencia Estatal de Meteorología.

Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, *18*, 117–143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x

Colwell, R. K., & Coddington, J. A. (1994). Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, *345*, 101–118. https://doi.org/10.1098/rstb.1994.0091

de Bie, T., Declerck, S., Martens, K., de Meester, L., & Brendonck, L. (2008). A comparative analysis of cladoceran communities from different water body types: Patterns in community composition and diversity. In B. Oertli, R. Céréghino, J. Biggs, S. Declerck, A. Hull, & M. R. Miracle (Eds.), *Pond conservation in Europe*. Springer. https://doi.org/10.1007/978-90-481-9088-1_3

Declerck, S. A. J., Coronel, J. S., Legendre, P., & Brendonck, L. (2011). Scale dependency of processes structuring metacommunities of cladocerans in temporary pools of high-Andes wetlands. *Ecography*, *34*, 296–305. https://doi.org/10.1111/j.1600-0587.2010.06462.x

Downing, J. A., Prairie, Y. T., Cole, J. J., Duarte, C. M., Tranvik, L. J., Striegl, R. G., McDowell, W. H., Kortelainen, P., Caraco, N. F., Melack, J. M., & Middelburg, J. J. (2006). The global abundance and size distribution of lakes, ponds, and impoundments. *Limnology and Oceanography*, *51*, 2388–2397. https://doi.org/10.4319/lo.2006.51.5.2388

Dray, S., & Dufour, A. (2007). The ade4 package: Implementing the duality diagram for ecologists. *Journal of Statistical Software*, *22*, 1–20. https://doi.org/10.18637/jss.v022.i04

Dupuis, A. P., & Hann, B. J. (2009). Climate change, diapause termination and zooplankton population dynamics: An experimental and modelling approach. *Freshwater Biology*, *54*, 221–235. https://doi.org/10.1111/j.1365-2427.2008.02103.x

Dussart, B. (1967). *Les copépodes des eaux continentales d'Europe occidentale. Tome I: Calanoïdes et Harpacticoïdes*. N. Boubee & Cie.

Dussart, B. (1969). *Les copépodes des eaux continentales d'Europe occidentale. Tome II: Cyclopoïdes et Biologie*. N. Boubée & Cie.

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. *Aquatic Sciences*, *82*, 1–12. https://doi.org/10.1007/S00027-020-0694-4

Florencio, M., Diaz-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*, 469–483. https://doi.org/10.1007/s00442-010-1847-2

Freiry, R. F., Esquinatti, F. M., Stenert, C., Arenzon, A., Nielsen, D. L., & Maltchik, L. (2016). Effects of spatial scale and habitat on the diversity of diapausing wetland invertebrates. *Aquatic Biology*, *25*, 173–181. https://doi.org/10.3354/AB00666

Freiry, R. F., Gouvea, A., Becker, J., Lansac-Tôha, F. A., Lansac-Tôha, F. M., Pires, M. M., Stenert, C., & Maltchik, L. (2020). Community structure and concordance patterns among zooplankton life stages in subtropical temporary ponds. *Aquatic Ecology*, *54*, 257–270. https://doi.org/10.1007/s10452-019-09740-1

Freiry, R. F., Weber, V., Bonecker, C. C., Lansac-Tôha, F. A., Pires, M. M., Stenert, C., & Maltchik, L. (2020). Additive partitioning of the diversity of the dormant zooplankton communities in intermittent ponds along a forest–grassland transition. *Hydrobiologia*, *847*, 1327–1342. https://doi.org/10.1007/S10750-020-04187-0

Frisch, D. (2002). Dormancy, dispersal and the survival of cyclopoid copepods (Cyclopoida, Copepoda) in a lowland floodplain. *Freshwater Biology*, *47*, 1269–1281. https://doi.org/10.1046/j.1365-2427.2002.00865.x

Frisch, D., Green, A. J., & Figuerola, J. (2007). High dispersal capacity of a broad spectrum of aquatic invertebrates via waterfowl. *Aquatic Sciences*, *69*, 568–574. https://doi.org/10.1007/s00027-007-0915-0

Fukami, T., & Morin, P. J. (2003). Productivity-biodiversity relationships depend on the history of community assembly. *Nature*, *424*, 423–426. https://doi.org/10.1038/NATURE01785

García-Roger, E. M., Armengol-Díaz, X., Carmona, M. J., & Serra, M. (2008). Assessing rotifer diapausing egg bank diversity and abundance in brackish temporary environments: An ex situ sediment incubation approach. *Fundamental and Applied Limnology*, *173*, 79–88. https://doi.org/10.1127/1863-9135/2008/0173-0079

Gleason, J. E., & Rooney, R. C. (2018). Pond permanence is a key determinant of aquatic macroinvertebrate community structure in wetlands. *Freshwater Biology*, *63*, 264–277. https://doi.org/10.1111/fwb.13057

Hairston, N. G. (1996). Zooplankton egg banks as biotic reservoirs in changing environments. *Limnology and Oceanography*, *41*, 1087–1092. https://doi.org/10.4319/lo.1996.41.5.1087

Hill, M. J., Wood, P. J., & Mathers, K. L. (2021). Taxonomic and functional macroinvertebrate diversity of high-altitude ponds in the Macun cirque, Switzerland. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *31*, 3201–3214. https://doi.org/10.1002/aqc.3691

Horne, F. R. (1993). Survival strategy to escape desiccation in a freshwater ostracod. *Crustaceana*, *65*(1), 53–61. https://doi.org/10.1163/156854093X00379

IPCC (2014). Climate change 2014: Synthesis report. Contribution of working groups I, II and III to the fifth assessment report of the intergovernmental panel on climate change. In R. K. Pachauri & L. A. Meyer (Eds.). IPCC.

Jackson, D. A. (1995). PROTEST: A PROcrustacean randomization TEST of community environment concordance. *Ecoscience*, *2*, 297–303. https://doi.org/10.1080/11956860.1995.11682297

Jeffries, M. (2005). Local-scale turnover of pond insects: Intra-pond habitat quality and inter-pond geometry are both important. *Hydrobiologia*, *543*, 207–220. https://doi.org/10.1007/s10750-004-7452-9

Jones, N. T., & Gilbert, B. (2016). Changing climate cues differentially alter zooplankton dormancy dynamics across latitudes. *Journal of Animal Ecology*, *85*, 559–569. https://doi.org/10.1111/1365-2656.12474

Kindt, R., & Coe, R. (2005). *Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies*. World Agroforestry Centre (ICRAF).

Korhonen, J. J., Soininen, J., & Hillebrand, H. (2010). A quantitative analysis of temporal turnover in aquatic species assemblages across ecosystems. *Ecology*, *91*, 508–517. https://doi.org/10.1890/09-0392.1

Koste, W. (1978). *Rotatoria die rädertiere mitteleuropas. Monogononta*. Gebrüder Brontraeger.

Legendre, P., & Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia*, *129*, 271–280. https://doi.org/10.1007/s004420100716

Loeuille, N., & Leibold, M. A. (2008). Evolution in metacommunities: On the relative importance of species sorting and monopolization in structuring communities. *The American Naturalist*, *171*, 788–799. https://doi.org/10.1086/587745

Martins, K. P., Bandeira, M. G. S., Palma-Silva, C., & Albertoni, E. F. (2019). Microcrustacean metacommunities in urban temporary ponds. *Aquatic Sciences*, *81*, 1–12. https://doi.org/10.1007/s00027-019-0655-y

Meisch, C. (2000). *Freshwater Ostracoda of western and Central Europe*. Spektrum Akademischer Verlag GmbH.

Mesquita-Joanes, F., Smith, A. J., & Viehberg, F. (2012). The ecology of Ostracoda across levels of biological organiSation from individual to ecosystem: A review of recent developments and future potential. In D. J. Horne, J. A. Holmes, J. Rodríguez-Lázaro, & F. Viehberg (Eds.), *Ostracoda as proxies for quaternary climate change*. Elsevier.

Miracle, M. R., Oertli, B., Céréghino, R., & Hull, A. (2010). Preface: Conservation of European ponds-current knowledge and future needs. *Limnetica*, *29*, 1–8. https://doi.org/10.23818/limn.29.01

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., … Wagner, H. (2020). Vegan: Community Ecology Package. R Package Version 2.5–7. Available at: https://Cran.R-project.org/package=vegan (Accessed November 3, 2021).

Olmo, C., Antón-Pardo, M., Ortells, R., & Armengol, X. (2020). Influence of restoration age on egg bank richness and composition: An ex situ experiment. *Journal of Plankton Research*, *42*, 553–563. https://doi.org/10.1093/plankt/fbaa034

Olmo, C., Armengol, X., & Ortells, R. (2012). Re-establishment of zooplankton communities in temporary ponds after autumn flooding: Does restoration age matter? *Limnologica*, *42*, 310–319. https://doi.org/10.1016/J.LIMNO.2012.08.005

Olmo, C., Gálvez, Á., Bisquert-Ribes, M., Bonilla, F., Vega, C., Castillo-Escrivà, A., de Manuel, B., Rueda, J., Sasa, M., Ramos-Jiliberto, R., Monrós, J. S., Armengol, X., & Mesquita-Joanes, F. (2022). The environmental framework of temporary ponds: A tropical-mediterranean comparison. *Catena*, *210*, 105845. https://doi.org/10.1016/j.catena.2021.105845

Parra, G., Guerrero, F., Armengol, J., Brendonck, L., Brucet, S., Finlayson, C. M., Gomes-Barbosa, L., Grillas, P., Jeppesen, E., Ortega, F., Vega, R., & Zohary, T. (2021). The future of temporary wetlands in drylands under global change. *Inland Waters*, *11*, 445–456. https://doi.org/10.1080/20442041.2021.1936865

Peres-Neto, P. R., & Jackson, D. A. (2001). How well do multivariate data sets match? The advantages of a procrustean superimposition approach over the mantel test. *Oecologia*, *129*, 169–178. https://doi.org/10.1007/s004420100720

Pinceel, T., Brendonck, L., & Vanschoenwinkel, B. (2016). Propagule size and shape may promote local wind dispersal in freshwater zooplankton—A wind tunnel experiment. *Limnology and Oceanography*, *61*, 122–131. https://doi.org/10.1002/LNO.10201

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*, 1–9. https://doi.org/10.1186/S12898-018-0158-Z

Pinel-Alloul, B., & Ghadouani, A. (2007). Spatial heterogeneity of planktonic microorganisms in aquatic systems. In R. B. Franklin & A. L. Mills (Eds.), *The spatial distribution of microbes in the environment*. Springer.

Pires, M. M., Stenert, C., & Maltchik, L. (2017). Partitioning beta-diversity through different pond hydroperiod lengths reveals predominance of nestedness in assemblages of immature odonates. *Entomological Science*, *20*, 318–326. https://doi.org/10.1111/ens.12263

Pyke, C. R. (2005). Interactions between habitat loss and climate change: Implications for fairy shrimp in the central valley ecoregion of California, USA. *Climatic Change*, *68*, 199–218. https://doi.org/10.1007/S10584-005-6011-3

R Development Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rosa, J., Golec, C., Bonecker, C. C., Martens, K., & Higuti, J. (2021). A comparison between active and passive communities of Ostracoda (Crustacea) in a tropical temporary lake. *Studies on Neotropical Fauna and Environment*, *56*, 112–123. https://doi.org/10.1080/01650521.2020.1758600

Sala, O., Chapin, F., Armesto, J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L., Jackson, R., Kinzig, A., Leemans, R., Lodge, D., Mooney, H., Oesterheld, M., Poff, N., Sykes, M., Walker, B., Walker, M., & Wall, D. (2000). Global biodiversity scenarios for the year 2100. *Science*, *287*, 1770–1774. https://doi.org/10.1126/SCIENCE.287.5459.1770

Santangelo, J. M., Lopes, P. M., Nascimento, M. O., Fernandes, A. P. C., Bartole, S., Figueiredo-Barros, M. P., Leal, J. J. F., Esteves, F. A., Farjalla, V. F., Bonecker, C. C., & Bozelli, R. L. (2015). Community structure of resting egg banks and concordance patterns between dormant and active zooplankters in tropical lakes. *Hydrobiologia*, *758*, 183–195. https://doi.org/10.1007/s10750-015-2289-y

Schmit, O., Rossetti, G., Vandekerkhove, J., & Mezquita, F. (2007). Food selection in Eucypris virens (Crustacea: Ostracoda) under experimental conditions. In R. Matzke-Karasz, K. Martens, & M. Schudack (Eds.), *Ostracodology — Linking bio- and geosciences*. Springer.

Stenert, C., Wüsth, R., Pires, M. M., Freiry, R. F., Nielsen, D., & Maltchik, L. (2017). Composition of cladoceran dormant stages in intermittent ponds with different hydroperiod lengths. *Ecological Research*, *32*, 921–930. https://doi.org/10.1007/S11284-017-1498-4

Strachan, S. R., Chester, E. T., & Robson, B. J. (2016a). Fringing trees may provide a refuge from prolonged drying for urban wetland invertebrates. *Urban Ecosystem*, *19*, 1213–1230. https://doi.org/10.1007/s11252-016-0548-y

Strachan, S. R., Chester, E. T., & Robson, B. J. (2016b). Habitat alters the effect of false starts on seasonal-wetland invertebrates. *Freshwater Biology*, *61*, 680–692. https://doi.org/10.1111/fwb.12738

Thioulouse, J. (2011). Simultaneous analysis of a sequence of paired ecological tables: A comparison of several methods. *Annals of Applied Statistics*, *5*, 2300–2325. https://doi.org/10.1214/10-AOAS372

Thioulouse, J., & Chessel, D. (1987). Les analyses multitableaux en ecologie factorielle. I: de la typologie d'etat a la typologie de fonctionnement par l'analyse triadique. *Acta Oecologica Oecologia Generalis*, *8*, 463–480.

Valls, L., Castillo-Escrivà, A., Mesquita-Joanes, F., & Armengol, X. (2016). Human-mediated dispersal of aquatic invertebrates with waterproof footwear. *Ambio*, *45*, 99–109. https://doi.org/10.1007/s13280-015-0689-x

van de Meutter, F., Stoks, R., & de Meester, L. (2006). Rapid response of macroinvertebrates to drainage management of shallow connected lakes. *Journal of Applied Ecology*, *43*, 51–60. https://doi.org/10.1111/j.1365-2664.2005.01115.x

Vandekerkhove, J., Declerck, S., Brendonck, L., Conde-Porcuna, J. M., Jeppesen, E., & de Meester, L. (2005). Hatching of cladoceran resting eggs: Temperature and photoperiod. *Freshwater Biology*, *50*, 96–104. https://doi.org/10.1111/j.1365-2427.2004.01312.x

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. *Limnology and Oceanography: Methods*, *3*, 399–407. https://doi.org/10.4319/lom.2005.3.399

Wang, X., Wang, Q., Yang, Y., & Yu, W. (2020). Comparison of invertebrate diversity in lake waters and their resting eggs in sediments, as revealed by high-throughput sequencing (HTS). *Knowledge and Management of Aquatic Ecosystems*, *421*, 1–19. https://doi.org/10.1051/kmae/2020011

Waterkeyn, A., Vanschoenwinkel, B., Elsen, S., Anton-Pardo, M., Grillas, P., & Brendonck, L. (2010). Unintentional dispersal of aquatic invertebrates via footwear and motor vehicles in a Mediterranean wetland area. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *20*, 580–587. https://doi.org/10.1002/aqc.1122

Wetzel, R., & Likens, G. (2000). *Limnological analysis*. Springer-Verlag.

Wetzel, R. G. (1990). Land-water interfaces: Metabolic and limnological regulators. *Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen*, *24*, 6–24. https://doi.org/10.1080/03680770.1989.11898687

Williams, D. D. (2006). *The biology of temporary waters*. Oxford University Press.

Wisnoski, N. I., Leibold, M. A., & Lennon, J. T. (2019). Dormancy in metacommunities. *American Naturalist*, *194*, 135–151. https://doi.org/10.1086/704168

Yousif, F., Hafez, S., El Bardicy, S., Tadros, M., Taleb, H. A., & Huat, L. B. (2013). Experimental evaluation of *Candonocypris novaezelandiae* (Crustacea: Ostracoda) in the biocontrol of *schistosomiasis mansoni* transmission. *Asian Pacific Journal of Tropical Biomedicine*, *3*(4), 267–272. https://doi.org/10.1016/S2221-1691(13)60061-1

Zacharias, I., Dimitriou, E., Dekker, A., & Dorsman, E. (2007). Overview of temporary ponds in the Mediterranean region: Threats, management and conservation issues. *Journal of Environmental Biology*, *28*, 1–9.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Bisquert-Ribes, M., Martínez, A., Castillo-Escrivà, A., Gálvez, Á., Iepure, S., de Manuel, B., Marinho, M., Martins, F., Olmo, C., Mesquita-Joanes, F., & Armengol, X. (2023). An evaluation of crustacean and rotifer diversity and composition in a temporary pond metacommunity: Comparing results from field samples and a hatching experiment. *Freshwater Biology*, *68*, 378–390. https://doi.org/10.1111/fwb.14032