

RESEARCH ARTICLE

# Ecological restoration promotes zooplankton network complexity in Mediterranean coastal lagoons

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Ecological recovery following restoration is typically evaluated using metrics based on species diversity and composition. However, increasing evidence suggests the success of long-term ecological recovery increases when more complex attributes such as biotic interaction networks are targeted. In created lagoons, the influence of nearby habitats can generate early similarities in the community structure, but communities often diverge from surrounding water bodies at later successional stages. These changes have been attributed to the effect of biotic interactions, but few studies have tested this assumption. Here, we analyze the zooplankton community recovery after the creation of new lagoons in a Mediterranean coastal wetland using beta diversity approaches and mixed graphical models to infer interaction networks from abundance data. Increasing differences in the community structure between new and old lagoons were detected the second year after their creation. The overall interaction network was more complex in new than in old lagoons. Interestingly, the network structure in old lagoons increased its complexity during the third and fourth years after restoration. The creation of new lagoons with overall milder environmental conditions contributed to a greater differentiation of the zooplankton community structure between new and old lagoons. Moreover, our results suggest that the creation of a heterogeneous and more connected landscape can increase the interaction network in newly created and pre-existing habitats, even if environmental conditions remain unchanged. We show how the inclusion of interaction networks for the monitoring of ecosystem recovery reflects unique facets of community complexity, otherwise overlooked when targeting diversity metrics alone.

**Key words:** biotic interactions, created lagoons, ecological restoration, ecological succession, mixed graphical models

## Implications of Practice

- The early resemblance but later differentiation between zooplankton community structures in newly created and pre-existing habitats highlights the importance of long-term monitoring programs after restoration actions in Mediterranean coastal lagoons.
- Changes observed in the interaction network in pre-existing lagoons after the creation of new water bodies suggest that restoration can affect natural communities when spatial connectivity is enhanced.
- Although practitioners typically focus on species diversity and community structure, the use of interaction networks could help assess restoration success by providing additional information about community complexity.

## Introduction

Traditional metrics used to monitor ecosystem recovery after restoration focus on attributes such as species diversity, species composition, or specific ecosystem functions. When those metrics are targeted alone, restored ecosystems often recover only part of their lost biodiversity and functionality (Moreno-Mateos et al. 2020). To address this issue, some authors have called for

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including Biotic Interaction Networks (BIN) in ecosystem management plans (Kaiser-Bunbury & Blüthgen 2015; Harvey et al. 2017) or even going one step further and considering interaction networks as conservation targets themselves (McCann 2007; Moreno-Mateos et al. 2020) since their structure can be an indicator of ecosystem functionality, stability, and resilience (Tylianakis et al. 2010). Importantly, the probability of long-term recovery after ecological restoration increases when considering biotic interactions (Halpern et al. 2007; Heleno et al. 2012; White et al. 2021) and the effect that restoration actions may have on the interaction network (Tylianakis et al. 2010; Rodewald et al. 2015; O'Connell et al. 2021).

BINs are representations of the community where organismal groups (nodes) are linked by pairwise interactions (edges) and therefore capture an additional facet of the system's complexity. Among other things, they have proven useful for assessing the impacts of alien species on the food web (Carvalho et al. 2008), identifying keystone species (Ortiz et al. 2017), and predicting the community response to climate change (Staniczenko et al. 2017). BINs have also been implemented in the monitoring of restoration actions to compare restored networks with reference ecosystems (Kaiser-Bunbury et al. 2017; Morriën et al. 2017; Gao et al. 2021). Interaction networks are usually built from the direct or indirect observation of interactions (Delmas et al. 2019), species co-occurrences (Stephens et al. 2009), or correlations between species abundances (Morriën et al. 2017). The direct detection of interaction events is useful when they are easily observed or deduced, but that is seldom the case. On the other hand, co-occurrence networks and correlation networks are more general methods based on species composition or abundance. However, the former fails to account for environmental constraints, the latter is prone to producing spurious results, and none of them accounts for covariates (Carr et al. 2019). To overcome these limitations, some authors have implemented sparse partial correlation networks of biotic and abiotic interactions (BAINs) using the Graphical Lasso approach (Ohlmann et al. 2018; García-Girón et al. 2020; Momal et al. 2020). In addition, the recent development of mixed graphical models (MGM) and their extensions (moderated MGM and time-varying MGM; Haslbeck & Waldorp 2020) allows for the comparison of BAIN structures and the study of their temporal changes. In the conservation field, this represents an opportunity to assess the effect of restoration on the BAIN and to compare BAIN structures with reference habitats.

Following classical succession models, newly restored ecosystems should converge toward a climax community (Clements 1936). Environmental policies often accept this deterministic view, offsetting the destruction of natural ecosystems with the construction of new ones (Clifford & Hefferman 2018; Directive 2004/35/EC). Still, ecological succession (and thus the restoration outcome) is subject to a high level of contingency linked to the spatial variability of abiotic conditions, differences in the food-web assembly processes, and the type of ecosystem (Stuble et al. 2017). In newly created water bodies, observed patterns during initial successional stages can be greatly explained by the colonization of pioneering taxa from nearby aquatic environments (Ruhí et al. 2009; Miguel-

Chinchilla et al. 2014; Cabrera et al. 2019). This is particularly true for fast-colonizing groups such as zooplankton or macroinvertebrates, which are a common target for monitoring programs. New communities can thus resemble that of natural habitats in terms of composition even if local dynamics differ because they are offset by dispersal. In contrast, BINs could take longer to recover since the evolution of the network structure can be partially decoupled from changes in species composition due to the availability of determined resources or priority effects that might affect how species interact with each other (Moreno-Mateos et al. 2020). The BIN assembly process in response to abiotic conditions can create differences between new and pre-existing habitats (Ruhí et al. 2013). Although the evolution of BINs throughout succession after restoration has not been studied in aquatic environments, other systems have shown a gradual increase in the number of interactions along succession (Neutel et al. 2007) that can surpass that of reference ecosystems (Morriën et al. 2017).

Among aquatic organisms, zooplankton assemblages have one of the fastest responses to abiotic changes (Quintana et al. 1998a; Bruce et al. 2005; Badosa et al. 2006) and new communities may resemble natural ones as soon as 1 year after the creation of a water body (Cabrera et al. 2019). This makes them a good candidate to assess short to mid-term restoration success. Organisms in this group are passive dispersers able to reach new water bodies rapidly as they are easily transported by wind, animals, tides, and floods (Cohen & Shurin 2003; Louette & de Meester 2005; Frisch et al. 2012). Therefore, reference communities can be easily reached after restoration, although changes may occur later if the abiotic conditions do not match the ones in the surrounding environments.

Here, we combined graphical models with more common methods based on spatiotemporal community dissimilarity to analyze the zooplankton community response to restoration in a Mediterranean coastal wetland where new lagoons were created. The aim was to compare the community structure and the biotic interaction network of natural and newly created lagoons for 4 years after restoration. Given the fast colonization rates of zooplankton species (Cohen & Shurin 2003; Louette & de Meester 2005; Frisch et al. 2012), we hypothesized that the community composition would be similar in old and new lagoons. However, a slower recovery of the BAIN structure was expected since species interactions tend to take longer to recover (Moreno-Mateos et al. 2020).

## Methods

### Study Site

Data were collected from La Pletera (Baix Ter Wetlands), a salt marsh free from tidal influence located in the northeastern Iberian Peninsula. Strong fluctuations in abiotic conditions induced by a flooding-confinement seasonal pattern seem to rule the zooplankton community dynamics in this system (Quintana et al. 1998a, 2021; Badosa et al. 2006). In 1987, an urbanistic project placed artificial physical barriers that modified the landscape and ecological functionality (Quintana et al. 2009).

However, changes in urban classification and later protection under the Natura 2000 network avoided further damage to the ecosystem (Quintana et al. 2018). By 1999, only two permanent lagoons, Bassa Pi (BPI; Fig. 1) and Fra Ramon (FRA), persisted. Three new lagoons (including G02) were built in 2002 in the frame of a LIFE restoration project (LIFE99NAT/E/006386). A second LIFE project (LIFE13NAT/ES/001001) took place between 2014 and 2016 to recover the ecological functionality by removing all the remaining structures of the abandoned urbanization and replacing them with new water bodies (including L01, L04, and M03). In addition, the topography of pre-existing lagoons was altered to enhance the connectivity between water bodies during flooding events.

**Field Sampling and Laboratory Analyses.** Samples were obtained from six lagoons. Three of them were designated as *old* lagoons, including BPI, FRA, and the naturalized G02. The remaining three lagoons (L04, L01, and M03), designated as *new*, were excavated in 2016 and filled with infiltration from

the subsurface water of the wetland. Monthly sampling was conducted from April 2014 to August 2019. A total volume of 10 L was taken from 20 random points using a 500-mL plastic pot, integrating the water column from the surface to up to a 50 cm depth. Five liters of water were filtered using a 50  $\mu$ m net and fixed in 4% formalin to obtain zooplankton samples. This volume was sufficient given the high density of individuals (an average of 3,275 individuals per sample). We used a Box-Type Plankton Sample Splitter to obtain two subsamples when the high density of individuals diffculted the analyses. Counting, measurement, and taxonomic identification of individuals at the lowest taxonomic level possible were performed by means of an inverted microscope and using a sedimentary chamber. We counted the organisms by scanning the entire chamber. If the number of individuals of a single species was greater than 400, we counted them in a fraction of the sample (1/2 or 1/4). Organisms were identified under the inverted microscope at the lowest taxonomical level possible without specimen manipulation using Koste (1978) and different volumes of the collection *Guides to the identification of macroinvertebrates of the continental waters of the world* (Rayner 1999; Dussart & Defaye 2001; Segers 2006). Measurements of 25 randomly selected individuals of each taxon were used to estimate the biomass in dry weight. Crustacean biomass was estimated using pre-established equations that describe allometric relationships between body length and biomass, whereas rotifer and ciliate biomass were estimated using their volume (Ruttner-Kolisko 1977; Malley et al. 1989; Putt & Stoecker 1989).

Electrical conductivity, temperature, pH, and dissolved oxygen were measured in situ using a Hach HQ30d multiparameter probe. One hundred twenty-five milliliters of unfiltered water were collected to analyze total nutrients. Total nitrogen and total organic carbon (TOC) were measured using a TOC analyzer (TOC-V CSH SHIMADZU). Water samples were filtered using Whatman® GF/F filters to analyze dissolved nutrients. Ammonium ( $\text{NH}_4^+$ ), nitrate ( $\text{NO}_3^-$ ), and nitrite ( $\text{NO}_2^-$ ) were measured following standardized procedures (APHA, AWWA, WEF 1992), and soluble phosphate ( $\text{PO}_4^{3-}$ ) was measured according to UNE-EN-ISO6878. Dissolved organic carbon (DOC) and dissolved inorganic carbon (DIC) were obtained by analyzing filtered samples with the TOC analyzer. All samples were frozen a few hours after their collection. Chlorophyll-*a* (Chl-*a*) concentrations were estimated using high-performance liquid chromatography following existing protocols (Zapata et al. 2000; López-Flores et al. 2006).

**Analyzing Environmental Abiotic Variability.** Abiotic variables were analyzed using principal component analysis (PCA) with two purposes: (1) visually explore temporal dynamics and possible differences between *old* (BPI, FRA, and G02) and *new* lagoons (L01, L04, and M03) and (2) reduce abiotic data dimensionality to a few meaningful axes that could be used in further analyses. All variables except pH, temperature, dissolved oxygen, and DIC, which already presented a symmetrical distribution, were logarithmically transformed to reduce skewness. To avoid multicollinearity issues, highly correlated pairs of variables (Pearson correlation coefficient >0.7) that reflected

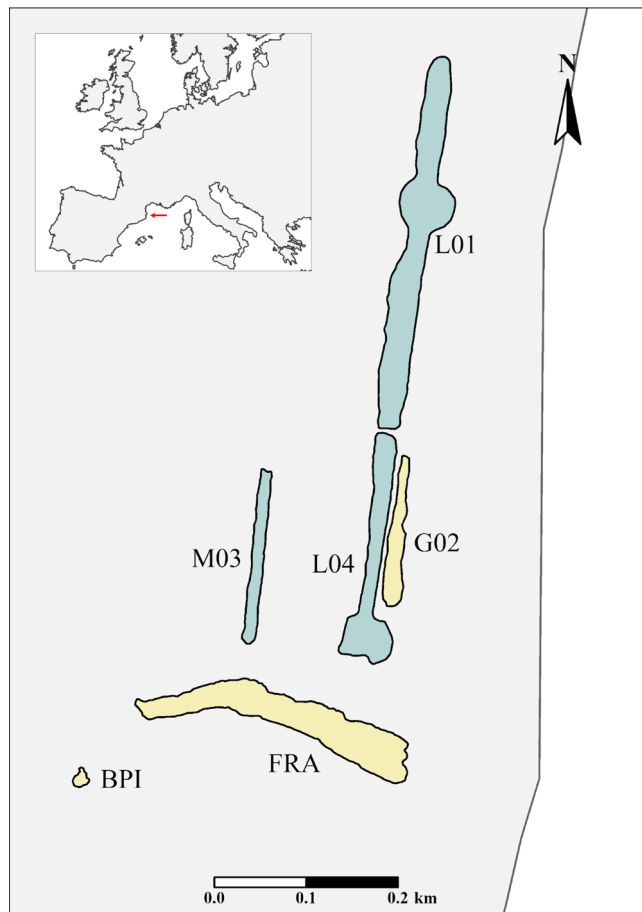


Figure 1. Study site: La Pletera (NE Iberian Peninsula). New lagoons (blue) were created between 2014 and 2016 as part of a restoration project (see the main text). Gray and white areas represent land and sea, respectively. Codes have been chosen for consistency with previous publications, including the old lagoons BPI, FRA, and Pletera Nova (G02) (yellow), and the newly created M03, L01, and L04 (blue).

similar ecological information were reduced to only one, keeping temperature, conductivity, DOC,  $\text{PO}_4^{3-}$ , DIC,  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ , and oxygen (%). Overall environmental seasonality was assessed using the temporal autocorrelation functions (ACF) of the sample coordinates on the first two PCA axes. Potential differences among sampled years and new and old lagoons were assessed with a non-parametric permutation-based multivariate analysis of variance (PERMANOVA) with a two-way factorial design (restoration  $\times$  year) using the *adonis2* function of *vegan* (Oksanen et al. 2020). Permutation blocks were designed to account for differences among months.

**Analyzing the Zooplankton Community.** We calculated pairwise  $\beta$ -diversities among samples using the Bray–Curtis dissimilarity index, which considers differences in species composition and biomass. Differences in zooplankton community structures between old and new lagoons and between years were tested using PERMANOVA with a two-way factorial design. Permutation blocks were designed to account for differences among months. Biomass data were log-transformed before the analyses.

BAINs were built using the biomass of each zooplankton group, the environmental abiotic variables as summarized in the first two axes of the PCA, and the Chl-*a* concentration as a proxy of phytoplankton biomass, the main food source for zooplankton organisms (Fig. 2). Networks were inferred using

MGM, a type of graphical model that allows combining different types of variables within the exponential family. In brief, MGM (as implemented in the *mgm* R package; Haslbeck & Waldorp 2020) uses  $\ell_1$ -penalized (LASSO) GLM to generate sparse undirected graphs from joint distributions between variables without previous assumptions about their dependencies. Within the graph, nodes that are not directly connected represent conditionally independent variables. The *lasso* tuning parameter ( $\lambda$ ) that minimized the extended Bayesian information criteria of the model was selected. Groups present in less than 10% of the samples of both new and old lagoons (*Hydrachnidia*, *Nematoda*, and *Polychaeta*) were not considered. Following Epskamp and Fried (2018), a non-paranormal transformation was applied to fit the assumption of multivariate normal distribution of the numerical variables (Liu et al. 2009) using the *huge* R package (Zhao et al. 2020).

A moderated MGM (M-MGM) was fitted to evaluate the overall differences between the BAINs of new and old lagoons. With this technique, certain specified nodes (i.e. moderators) are allowed to participate in two-way ( $k = 2$ ) and three-way ( $k = 3$ ) interactions, whereas the rest are limited to two-way interactions. The *restoration* factor (i.e. new or old lagoon) was set as the network moderator, implying that three-way interactions indicate pairwise interactions with a distinct weight between new and old lagoons. Networks were analyzed based on their interaction weights, node weighted degree centralities (i.e. adding the

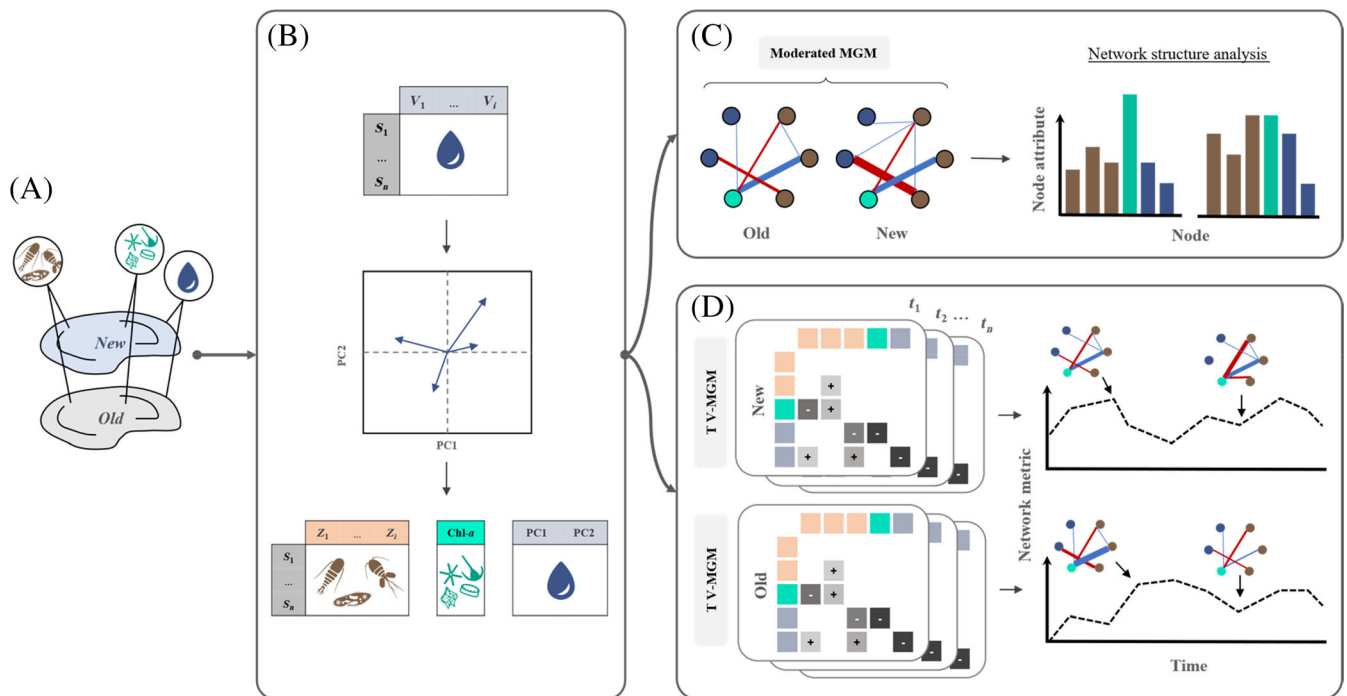


Figure 2. Schematic flowchart of the analyses performed to obtain and compare BAINs. (A) Three ecosystem components were measured for both pre-existing (old) and newly created (new) lagoons: zooplankton biomass ( $Z$ ), environmental variables ( $V$ ), and chlorophyll-*a* concentration as a proxy of phytoplankton biomass (Chl-*a*). (B) Environmental variables were summarized into the first two axes of a PCA (PC1 and PC2). (C) An M-MGM was fitted to the data. The model explicitly accounted for differences between *old* and *new* lagoons by setting the *restoration* factor (i.e. new or old lagoon) as a moderator. The M-MGM was then solved for both types of lagoons to obtain the respective networks. To build the network, each variable was represented as a single node and the edge weight between nodes was the partial correlation between variables. (D) In addition, TV-MGMs were built for both types of lagoons to analyze temporal changes in the BAIN. The model was solved for each specified time ( $t$ ).

absolute weight of every edge), and network connectance. The network connectance is a measure of network complexity and informs about the number of detected interactions as a proportion of all possible interactions. To assess the model stability, we reconstructed the model using 1,000 bootstrap samples of the original data. For each possible interaction (both  $k = 2$  and  $k = 3$ ), we analyzed the mean weight value, the 0.95 and 0.05 percentiles, and the proportion of models with an absolute interaction weight greater than zero.

Finally, we compared the temporal trends in the BAIN structure of old and new lagoons. To do so, we adjusted a time-varying MGM (TV-MGM) for each lagoon type. TV-MGM allows reconstructing the BAIN at any given time ( $t$ ) by assigning a heterogeneous weight to each sample that depends on their distance from  $t$ . Note that time is treated as a continuous variable, so  $t$  can take any value within the sampled period. The weight of each sample is given by a kernel function with an adjustable bandwidth that was optimized using the *bwSelect* function of the R package *mgm* (Haslbeck & Waldorp 2020) to 0.40. We reconstructed the BAIN at 40 arbitrary time points at fixed intervals. For each  $t$ , the model with the minimum BIC was selected. We used the *mgm* R package to compute the M-MGM and TV-MGM and the *igraph* R package (Csardi & Nepusz 2006) to calculate all network metrics, except the edge weight.

## Results

### Comparing Abiotic Conditions

The PCA summarized 55.15% of abiotic environmental variability into two ecologically meaningful axes (Fig. 3). The first axis (PC1, 41.31%) was closely related to seasonal changes in water physicochemistry linked to the degree of confinement (i.e. high  $\text{PO}_4^{3-}$ , DOC, and conductivity; see Fig. S1), whereas the second

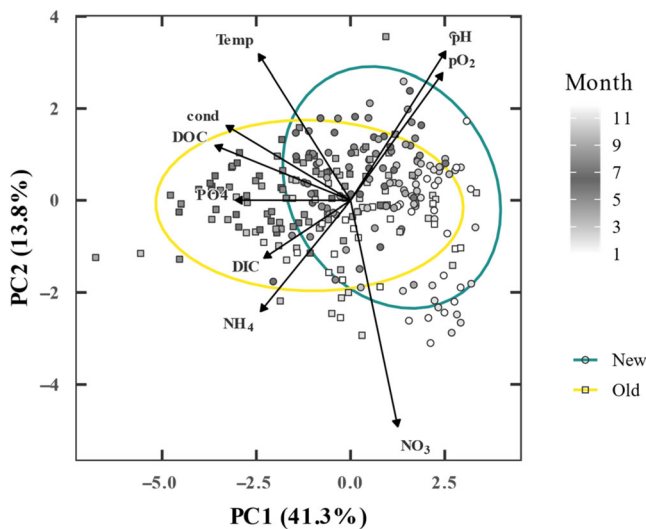


Figure 3. PCA of abiotic variables: temperature (Temp), conductivity (cond), DIC, DOC, ammonium ( $\text{NH}_4$ ), nitrate ( $\text{NO}_3$ ), dissolved oxygen ( $\text{pO}_2$ ), and phosphate ( $\text{PO}_4$ ). A 95% confidence ellipse has been displayed for each lagoon type.

axis (PC2, 13.84%) was more related to sudden water inputs (i.e. high  $\text{NO}_3^-$ , lower temperature, pH, and dissolved oxygen).

The ACF of the first principal component showed a significant seasonal pattern with negative autocorrelations at a 6-month lag and positive autocorrelation at a 12-month lag in all lagoons (see Table S1; Fig. S2a). Some lagoons presented similar correlation coefficients at lags 1 and 12, possibly indicating low autocorrelation compared to the fast seasonal changes in environmental conditions. On the other hand, ACF for PC2 did not show such a clear seasonal pattern (see Fig. S2b).

PERMANOVA analysis accounting for monthly variability revealed significant differences in the environmental conditions between old and new lagoons when using restoration as a single predictor ( $R^2 = 0.223$ , pseudo- $F_{[1,250]} = 71.55$ ,  $p$ -value  $< 0.001$ ). The model including sampling year together with restoration in a two-way factorial design (i.e. restoration  $\times$  year) showed a similar effect of restoration ( $R^2 = 0.223$ , pseudo- $F_{[1,248]} = 71.43$ ,  $p$ -value  $< 0.001$ ) but no significant effect of year ( $R^2 = 0.001$ , pseudo- $F_{[3,248]} = 0.18$ ,  $p$ -value = 0.781) and no interaction between factors ( $R^2 = 0.004$ , pseudo- $F_{[3,248]} = 1.38$ ,  $p$ -value = 0.221). The PCA representation for each lagoon (see Fig. S3) and the pairwise PERMANOVA models (see Table S2) revealed similarities among new lagoons but greater differences among the old ones (see Fig. S4).

### Differences in Community Composition

Overall, calanoid copepods were the most abundant taxa (Fig. 4) with maximum local biomass ranging from  $4,047.5 \text{ mg/m}^3$  in BPI in January 2018 to  $278.1 \text{ mg/m}^3$  in L04 in February 2017. It was the most abundant group in all lagoons except for L04, where filter-feeding rotifers reached a slightly higher abundance ( $280.54 \text{ mg/m}^3$ ). Filter-feeding rotifers were the subdominant groups in old lagoons (BPI:  $862.1 \text{ mg/m}^3$ , FRA:  $289.2 \text{ mg/m}^3$ , G02:  $1020.2 \text{ mg/m}^3$ ) as well as in the new lagoon M03, while ostracods were the second most abundant group in the newly created L01 ( $90.8 \text{ mg/m}^3$ ). The community structure presented three main states: (1) dominance of calanoid copepods occurring mostly in winter, (2) dominance of filter-feeding rotifers occurring mostly in summer, and (3) more diverse communities with higher abundances of less dominant groups such as ostracods or water mites. Communities in both old and new lagoons alternated between states 1 and 2, but structure 3 became dominant in new lagoons during the last 2 years of the study (Fig. 4, see also Fig. S5).

PERMANOVA analysis accounting for monthly variability revealed significant differences in the community structure between old and new lagoons when using restoration as a single predictor ( $R^2 = 0.031$ , pseudo- $F_{[1,250]} = 8.07$ ,  $p$ -value  $< 0.001$ ). Likewise, we found significant differences between both types of lagoons ( $R^2 = 0.031$ , pseudo- $F_{[1,245]} = 8.98$ ,  $p$ -value  $< 0.001$ ), among years ( $R^2 = 0.085$ , pseudo- $F_{[3,245]} = 8.10$ ,  $p$ -value  $< 0.001$ ), and a significant interaction between restoration and year ( $R^2 = 0.030$ , pseudo- $F_{[3,245]} = 2.85$ ,  $p$ -value  $< 0.001$ ) when including year as a predictor in a two-way factorial design (i.e. restoration  $\times$  year). This result aligns with the increasing divergence over time observed between old and new lagoons (see Fig. S6), which was confirmed by the PERMANOVA

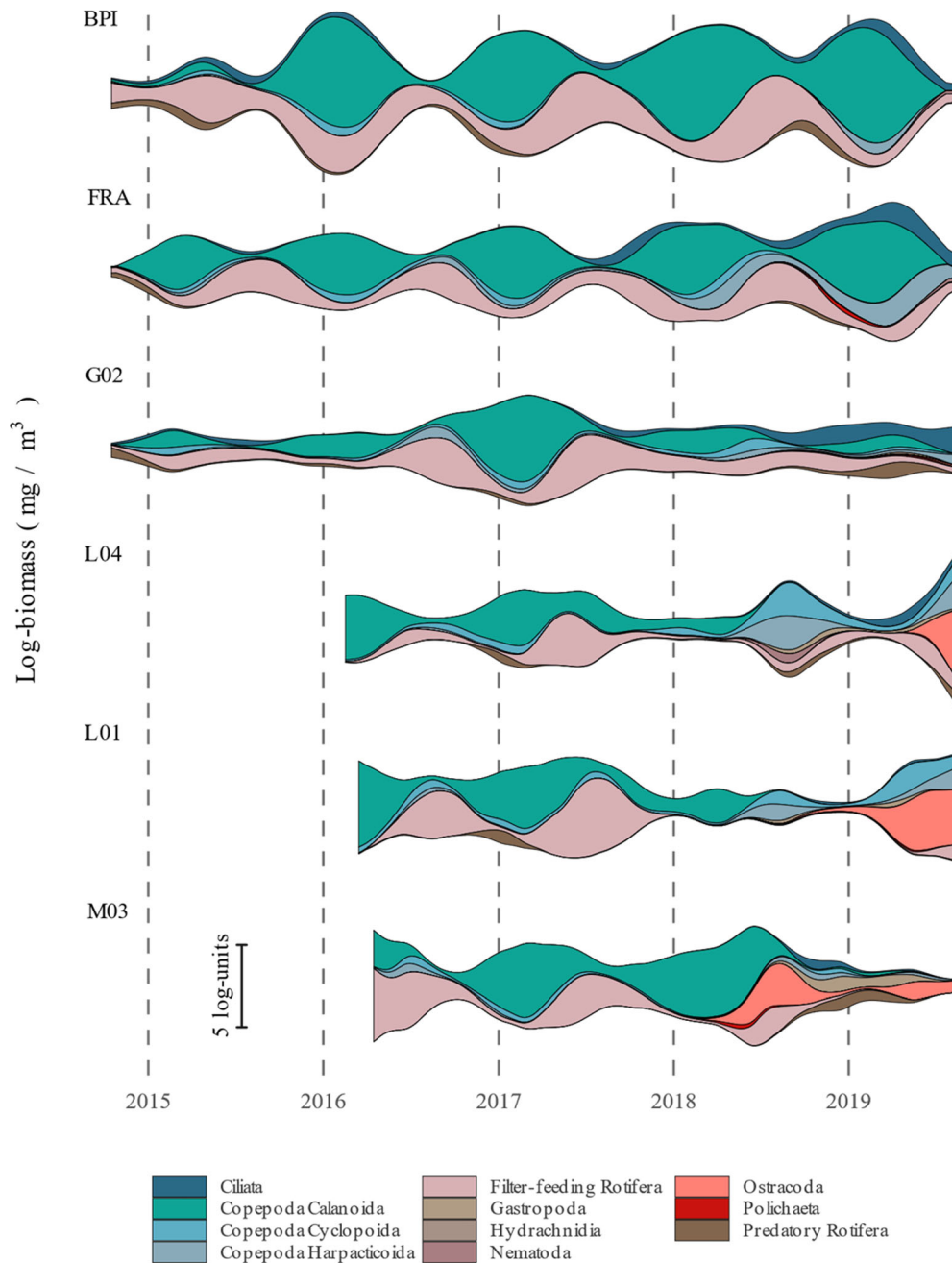


Figure 4. Evolution of the zooplankton biomass in old (BPI, FRA, and G02) and new lagoons (L01, L04, and M03). The scale is homogeneous among lagoons.

analyses for each year (see Table S3). Pairwise PERMANOVA comparison of individual lagoons showed significant differences between every new and old lagoon (see Table S4). It also revealed high heterogeneity among old lagoons, while some new lagoons presented similar communities ( $p$ -value > 0.05).

#### BAIN Comparison

A total of 23 interactions were detected between the 12 nodes included in the MMGM, which represent groups of zooplankton, environmental gradients, Chl-*a* concentration, and the

restoration factor (i.e. new or old lagoon). The restoration factor had a direct effect ( $k = 2$ ) on seven nodes and a moderating effect ( $k = 3$ ) on seven edges (Fig. 5A). The strongest detected edge linked the restoration factor and PC1 (weight = 0.491), corroborating that new and old lagoons present distinct environmental characteristics. Moreover, this edge was detected in all bootstrap samples (see Fig. S7). The interaction between ciliates and gastropods was the most varying between lagoon types (0.484 in new lagoons, 0.134 in old lagoons), and the moderated effect over this edge was detected in 98% of bootstrap samples.

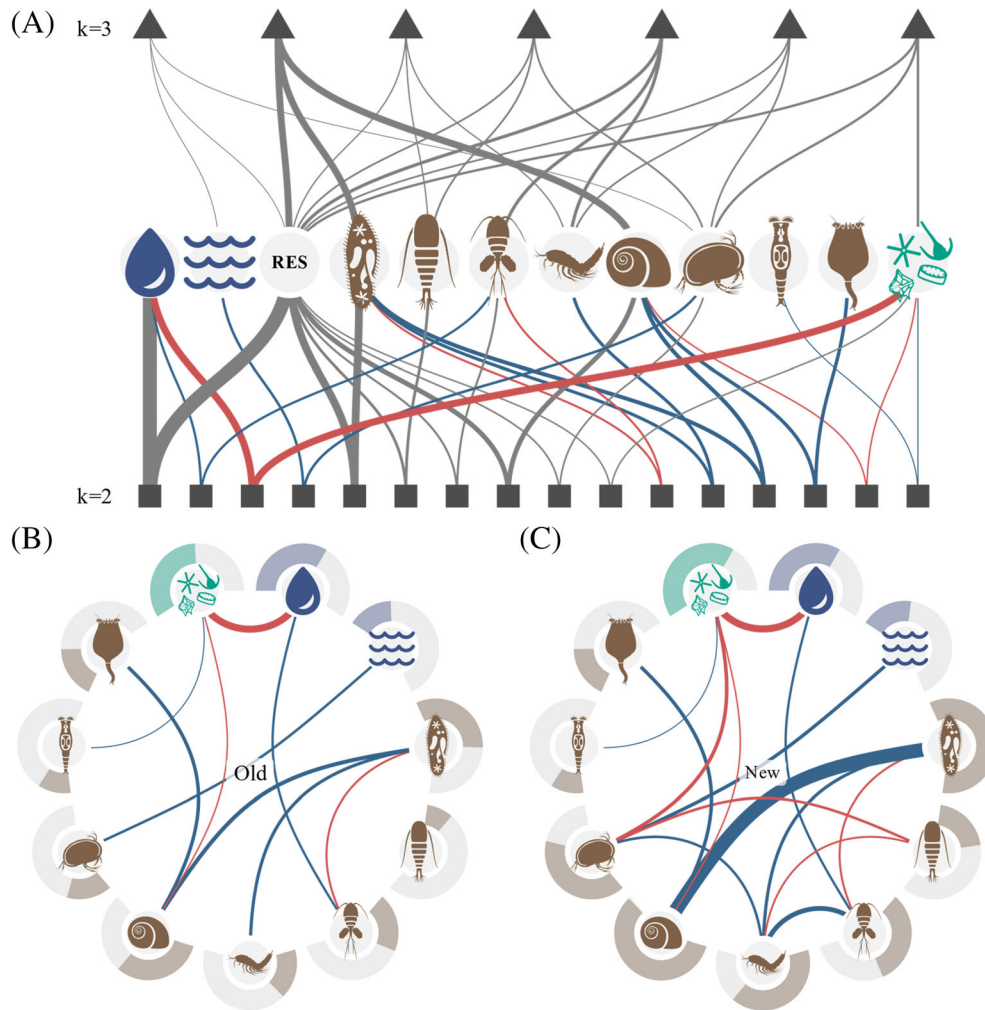


Figure 5. M-MGM of the zooplankton community (brown), the environmental conditions as summarized by the two first axes of a PCA (blue) and the Chl-*a* concentrations (turquoise). (A) Network representation of the M-MGM showing two-way ( $k = 2$ ) and three-way interactions ( $k = 3$ ). (B,C) The BAINs of pre-existing (old) and newly created (new) lagoons, respectively. Red edges indicate negative interactions, blue edges indicate positive interactions and gray edges represent interactions involving the restoration factor (RES). The edge width is proportional to the absolute interaction weight. Arches around nodes show their weighted degree proportional to the maximum observed value (ciliates in new lagoons: 0.655). Symbols represent ciliates (♁), calanoid copepods (♁), cyclopoid copepods (♁), harpacticoid copepods (♁), gastropods (♁), filter-feeding rotifers (♁), predatory rotifers (♁), Chl-*a* concentration (♁), PC1 (♁), and PC2 (♁).

The BAIN of new lagoons was more densely connected than the BAIN of old lagoons (Fig. 5B & 5C) with a network connectance of 0.118 and 0.082, respectively. New lagoons had a greater connectance in all bootstrap samples, with a mean difference of  $0.061 \pm 0.020$ . Interestingly, there was no unique interaction in the old lagoon' BAIN; all interactions detected in old lagoons were present in the new lagoon' network. In the old lagoon' BAIN, PC1 (degree = 3, weighted degree = 0.319) and Chl-*a* concentration (degree = 3, weighted degree = 0.318) were the most influential nodes and had the strongest interaction detected in this network (weight =  $-0.243$ ), which was detected in all 1,000 bootstrap samples (see Fig. S7). The second strongest interaction was the positive relationship between ciliates and gastropods (weight = 0.134). In the new lagoon' BAIN, Chl-*a* had a strong influence on the network structure (degree = 4, weighted degree = 0.436) but ciliates

(degree = 3, weighted degree = 0.655) and gastropods (degree = 3, weighted degree = 0.645) were the overall most influential nodes. The strongest detected interaction in the new lagoons was a positive relationship between ciliates and gastropods (weight = 0.484) followed by the negative interaction between PC1 and Chl-*a* (weight =  $-0.243$ ) also detected in the BAIN of old lagoons.

#### Temporal Changes in the BAIN

BAIN structures of old and new lagoons experienced significant changes during the study period (Fig. 6). The BAIN in new lagoons consistently increased its complexity throughout the first 2 years after restoration from 4 interactions at the beginning of 2016 to a peak of 11 interactions by summer 2017. After this, the trend stabilized and no major changes in the network

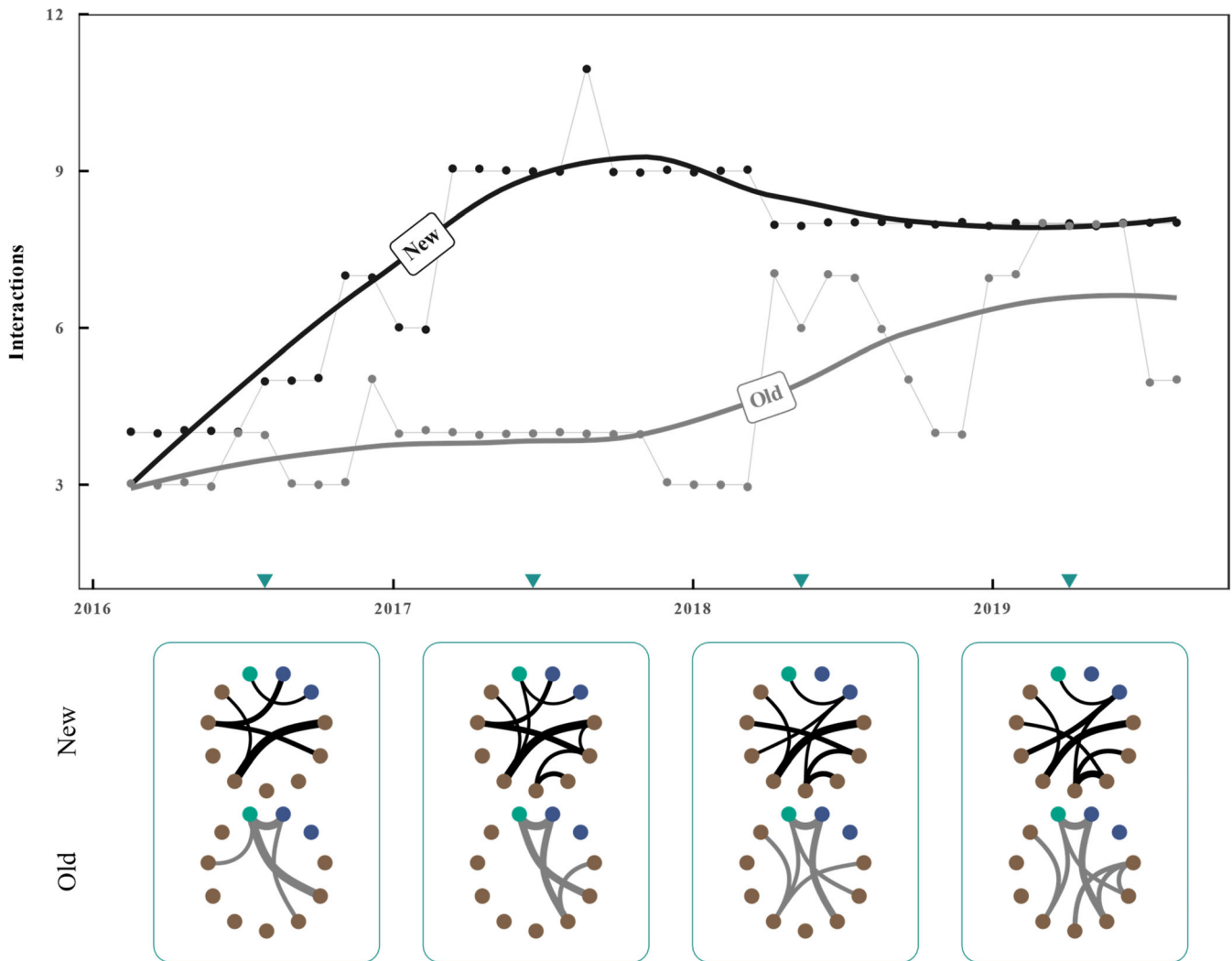


Figure 6. Evolution of the BAIN after restoration. The BAIN structure has been inferred with a TV-MGM for each lagoon type (new or old) at 40 arbitrary time points at fixed intervals and a kernel bandwidth of 0.40. Four network structures have been represented at isochronic times indicated with triangles. Nodes represent groups within the zooplankton community (brown), environmental conditions as summarized by the two first axes of a PCA (blue), and the Chl-*a* concentration (turquoise). LOESS regression lines have been drawn to illustrate the temporal trend.

structure were detected during the third and fourth years. Interestingly, the network in old lagoons increased from three to eight interactions in spring 2019. This increase in the number of interactions started during the third year after restoration and did not stabilize during the study period. Importantly, no shared interaction between the BAINs of new and old lagoons appeared until the third year after restoration, when the edges gastropods-ciliates and gastropods-predatory rotifers, two of the most stable interactions in new lagoons, were detected in old lagoons as well.

**Discussion**

The observed patterns of abiotic variability match the commonly described summer–winter confinement gradient and stochastic flooding events (first and second PCA axes,

respectively) that characterize the hydrology of many Mediterranean coastal lagoons (Quintana et al. 1998b; Badosa et al. 2006). Conditions of strong confinement imply high salinity and temperature as well as the accumulation of phosphate and carbon compounds. These confinement events generally happen in summer during the dry season. On the other hand, stochastic flooding events supply nitrogen and decrease temperature, pH, and oxygen levels. Flooding events occur during episodes of strong rains or seastorms that flood these coastal lagoons and that are less predictable during the year in Mediterranean climates, although they normally happen in autumn or spring (see Quintana et al. 1998b for more details on the confinement–flooding dynamics). Even if old and new lagoons followed this trend, confinement was consistently stronger in the old ones. This difference is key for biodiversity since the high salinity, hypoxia, hypercapnia, and acidosis episodes



associated with strong confinement conditions in estuarine systems can generate naturally stressed communities comparable to initial successional stages (Elliott & Quintino 2007). Although new and old lagoons have distinct environmental conditions, these differences will probably fade in the coming years as new lagoons accumulate nutrient loads due to the flooding-confinement dynamics (Levin et al. 2001).

Zooplankton communities in new lagoons resembled those of old lagoons even if the environmental conditions differed between both (see also Cabrera et al. 2019). However, in alignment with previous studies (Ruhí et al. 2009, 2013), the community composition diverged during the subsequent years. Matthews and Spyreas (2010) theorized that an early resemblance and later differentiation of the species composition are expected in plant communities when ubiquitous and fast-colonizing species are replaced by more adapted ones during ecological succession. Likewise, given the fast dispersal capabilities of zooplankton organisms (Cohen & Shurin 2003; Louette & de Meester 2005; Frisch et al. 2012), the initial uniformity of the community structure between newly created and pre-existing water bodies could be explained by the influence of surrounding communities rather than specific environmental conditions. In the case of Mediterranean coastal lagoons, natural communities tend to be poor in species (Bruce et al. 2005; Gascón et al. 2005) and resemble initial successional stages due to the harsh environmental conditions that act as strong environmental filters (Elliott & Quintino 2007). The gradual colonization of better-adapted organisms due to the less stressful abiotic environment in new lagoons could consequently explain the divergence toward communities with different compositions and more structurally complex (Ruhí et al. 2013).

The complexity of the BAIN in newly created lagoons was higher than in pre-existing ones as shown by the M-MGM. Similar to high species diversity, densely interconnected network structures are usually linked to increased functionality (Tylianakis et al. 2010) and have been associated with pristine ecosystems that harbor diverse communities (Gilbert 2009). Although our results align with this idea, this *rule of thumb* could misleadingly imply that new lagoons present a more desirable state of the zooplankton community than pre-existing lagoons from a biodiversity conservation perspective. In confined coastal lagoons, ecological complexity is constrained by the environmental harshness and strong temporal variability of abiotic conditions (Elliott & Quintino 2007). Consequently, finding a greater network complexity in Mediterranean coastal lagoons after restoration suggests a less natural state of the community.

Previous studies show contradictory results regarding the connectance of interaction networks in different types of restored ecosystems, making some authors question the theorized relation between connectance and conservation value (Heleno et al. 2012). For instance, Forup et al. (2008) found that plant–pollinator networks were less densely connected in restored heathlands, whereas Morriën et al. (2017) reported the opposite for correlation networks in soil communities. Hence, network connectance must be interpreted independently in

different ecosystems as it is subjected to a high level of contingency (Heleno et al. 2012).

Some studies on the temporal variability of interaction networks during community succession have reported a build-up of network complexity (Neutel et al. 2007), while others have found no substantial change in this metric (Sun et al. 2017; Gao et al. 2021). Using TV-MGM, we found that the BAIN complexity (i.e. connectance) increased in new lagoons throughout the first 2 years after their creation. This result suggests that the observed structural divergence of the zooplankton community between old and new lagoons could respond to the food-web assembly process in the latter, as theorized by Ruhí et al. (2013). Moreover, the evolution of both BAIN structures reveals that even if they had a similar composition the first year after restoration, the links between groups of organisms were already different. Distinct environmental water conditions could have caused such early differences in the network as they can trigger behavioral changes that modify the way species interact, even when the community composition is similar (Staudacher et al. 2018). Hence, although the rapid colonization from surrounding habitats favors the community recovery in terms of species composition, interaction networks, and ecosystem functions may take longer to resemble that of reference (i.e. natural) systems.

Surprisingly, the BAIN of old lagoons also changed over time, increasing the number of detected interactions during the third and fourth years after the creation of new lagoons. As no significant variation in the abiotic conditions was observed, we suspect that the increased complexity can be a consequence of biotic processes enhanced by restoration. Two actions carried out as part of the restoration project could have caused this effect on the BAIN: (1) the construction of new lagoons with distinct environmental conditions and (2) the modification of the topography to enhance the overall connectivity during floods. The consequently improved connectivity may have swamped local population dynamics, especially during floods, and influenced secondary succession after extreme confinement episodes. In other words, the creation of a more heterogeneous and connected landscape may have affected the interaction network of pre-existing lagoons. This is consistent with previous studies linking more interconnected networks to higher environmental heterogeneity (Moreira et al. 2015) and improved biodiversity in wetland complexes or pond networks after the creation of new water bodies (Petranka et al. 2007; Sebastián-González & Green 2014; Minot et al. 2021). It also aligns with metacommunity studies showing that landscape connectivity can play a major role in shaping local communities by modifying dispersal dynamics (Thompson et al. 2017; Chase et al. 2020).

Our results demonstrate that the inclusion of interaction networks for the monitoring of ecosystem recovery after restoration may reflect unique facets of the community complexity, otherwise overlooked when targeting diversity metrics alone. For instance, we show how the recovery of the community composition shortly after restoration does not necessarily imply the recovery of the network structure. More complex metrics such as those associated with BAINs could involve long recovery

periods (Moreno-Mateos et al. 2020), which highlights the need for long-term monitoring programs. In addition, the possible link between restoration actions and the observed changes in the interaction network of pre-existing habitats should be studied in more detail. Practitioners must consider the implications of creating new pieces of habitat for the overall system when designing restoration projects, especially if natural environmental conditions cannot be met. In this sense, actions aimed at increasing the chances of recovery by enhancing the connectivity between natural and restored habitats could impact the remaining natural communities.

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## Supporting Information

The following information may be found in the online version of this article:

**Figure S1.** Pearson's correlation between the first two components of the PCA and the abiotic variables.

**Figure S2.** Autocorrelation functions of environmental variables.

**Figure S3.** Principal component analysis of environmental water variables.

**Figure S4.** Comparison of the first axis of a principal component analysis.

**Figure S5.** NMDS based on Bray–Curtis dissimilarities of the zooplankton community composition.

**Figure S6.** NMDS representation of the zooplankton community calculated using Bray–Curtis dissimilarities.

**Figure S7.** Bootstrapping of the edges obtained from a MMGM with the RES set as the network moderator.

**Table S1.** Autocorrelation coefficient of environmental variables.

**Table S2.** Pairwise PERMANOVA based on Euclidean dissimilarities of the environmental conditions.

**Table S3.** Yearly PERMANOVA based on Bray–Curtis dissimilarities in the zooplankton community structures.

**Table S4.** Pairwise PERMANOVA based on Bray–Curtis dissimilarities of the zooplankton community structure.

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