

Environmental filtering determines metacommunity structure in wetland microcrustaceans

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Abstract Metacommunity approaches are becoming popular when analyzing factors driving species distribution at the regional scale. However, until the popularization of the variation partitioning technique it was difficult to assess the main drivers of the observed patterns (spatial or environmental). Here we propose a new framework linking the emergence of different metacommunity structures (e.g., nested, Gleasonian, Clementsian) to spatial and environmental filters. This is a novel approach that provides a more profound analysis of how both drivers could lead to similar metacommunity structures. We tested this framework on 110 sites covering a strong environmental gradient (i.e., microcrustacean assemblages organized along a salinity gradient, from freshwater to brackish

water wetlands). First we identified the metacommunity structure that better fitted these microcrustacean assemblages. Then, we used hierarchical variation partitioning to quantify the relative influences of environmental filters and the distance among wetlands on the identified structure. Our results showed that under strong environmental filtering metacommunity structures were non-random. We also noted that even passive dispersers, that are supposed to be poorly spatially filtered, showed spatial signals at a large geographical scale. However, some difficulties arose when inferring biotic interactions at finer-scale spatial signals. Overall, our study shows the potential of elements of metacommunity structure combined with variation partitioning techniques to detect environmental drivers and broad-scale patterns of metacommunity structure, and that some caution is needed when interpreting finer-scale spatial signals.

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Introduction

Understanding the mechanisms that determine the assembly of species into local communities is a key question in community ecology. Empirical evidence suggests that these mechanisms can be driven by environmental factors (Heino 2011; Fernandes et al. 2014), although most available studies have analyzed the influence of the environment on organisms from a local perspective (e.g., Bagella et al. 2010). As a consequence, community dynamics at regional scales had been largely overlooked until the popularization of the concept of metacommunity (Leibold et al. 2004). Metacommunities have been defined as “sets of local

communities, potentially linked by dispersal” (Holyoak et al. 2005), thus introducing the importance of regional processes in structuring local communities. The inclusion of a metacommunity perspective serves to help understand how the links between dispersal ability, environmental factors and biotic interactions affect the assembling of species within landscapes (e.g., Leibold et al. 2004; Cottenie 2005).

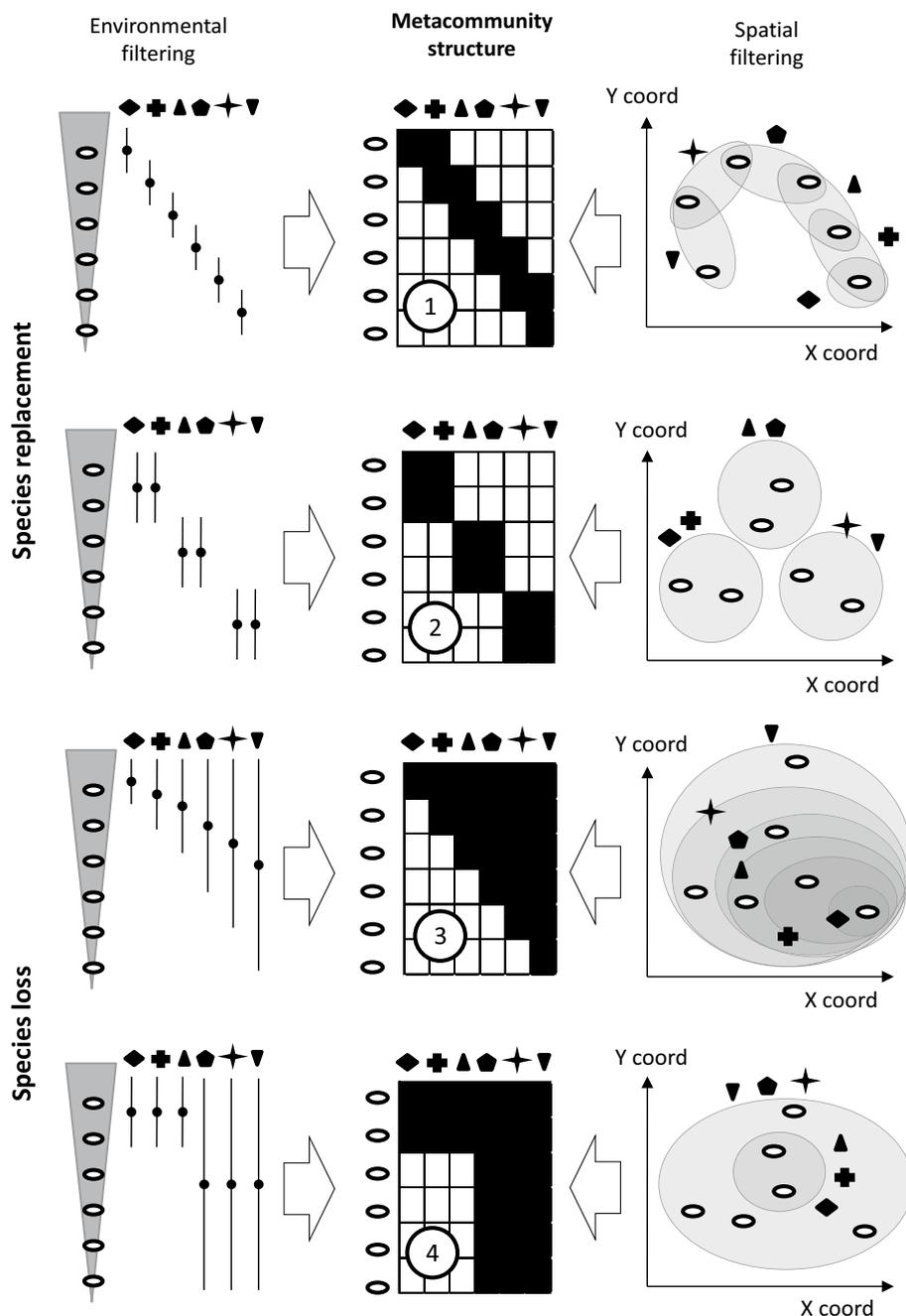
Within the metacommunity framework, multiple idealized non-random patterns of species distribution have been described: checkerboard, nested, evenly spaced, Clementsian and Gleasonian distributions (Leibold and Mikkelson 2002). These idealized structures are the result of ecologists’ efforts to typify the observed patterns of species distribution among sites. A checkerboard structure would correspond to a metacommunity composed of pairs of mutually exclusive species (Diamond 1975). Traditionally, the origin of checkerboard structures has been related to biotic interactions, such as competitive exclusion (Stone and Roberts 1992). Abiotic processes determining species distributions could also contribute to create a variety of metacommunity structures. In this sense, environmental gradients can be understood as filters that include or exclude species in local communities because the organisms’ traits may match or mismatch the selective characteristics of the environment (Poff 1997; McAbendroth et al. 2005). For example, nestedness occurs when species-poor assemblages are subsets of successively larger assemblages (Atmar and Patterson 1993). The loss of species across sites has been frequently related to dispersal abilities (e.g., De Bie et al. 2012; Cañedo-Argüelles et al. 2015) but environmental gradients could also explain the appearance of nested structures (e.g., Wright et al. 1997; Tornés and Ruhí 2013). Environmental gradients can also lead to other metacommunity structures. For instance, if several species compete along an environmental gradient, then their ability to exploit alternative resources would determine their distribution, creating an evenly spaced structure at the regional scale (Tilman 1982; Henriques-Silva et al. 2013). In contrast, Clementsian structures (Clements 1916) could emerge when groups of species with similar environmental requirements replace each other across an environmental gradient (Presley et al. 2010). Under this type of metacommunity structure, species and sites are organized in different compartments, each one grouping sites that share species with similar environmental boundaries (Lewinsohn et al. 2006). The identification of such compartments is of ecological relevance, and may be analyzed independently of each other since different metacommunity dynamics may operate in different compartments, affecting the final species distribution (Presley et al. 2010). Finally, communities can change in composition gradually along the environmental gradient, since individual species may present

somewhat idiosyncratic responses to abiotic factors, with coexistence resulting from chance similarities in requirements or tolerances (Presley et al. 2010). In such cases, a Gleasonian structure would arise (Gleason 1926). Overall, environmental gradients may be important drivers of metacommunity structure, creating non-random and ecologically meaningful patterns such as nested, Clementsian, Gleasonian and evenly spaced distributions.

Furthermore, many studies have already evidenced the influence of geographical distances between sites on biological similarities [e.g., distance decay of similarity concept (Nekola and White 1999; Soininen et al. 2007)]. However, there is a surprising lack of empirical studies that explicitly include some kind of spatial information when analyzing metacommunity structure patterns (i.e., checkerboard, nested, evenly spaced, Clementsian and Gleasonian distributions). Available studies suggest that both environmental and spatial filters may contribute to the “final” species distribution that configures the metacommunity structure (Henriques-Silva et al. 2013; Meynard et al. 2013; Heino et al. 2015), suggesting that the spatial configuration of local communities needs to be taken into account when studying metacommunities (e.g., Cottenie 2005; Brown et al. 2011). Many environmental gradients occur at hierarchical spatial scales, ranging from microhabitats to watersheds (Poff 1997; Díaz et al. 1998; Bonada et al. 2008). Thus, when including spatial information it is important to discriminate between broad- and fine-scale patterns, since they could be related to different ecological processes. While broadscale patterns are usually related to biogeographical constraints (e.g., climate expressed as weather) or dispersal/colonization limitations, fine-scale patterns are more usually related to biotic interactions (Borcard et al. 2011). Recently developed techniques allow quantification of the importance of drivers operating at different scales in shaping communities (Dray et al. 2012). Here we expand their use to quantify their effect on the metacommunity structure, through elements of metacommunity structure (EMS) analysis.

Although EMS allows one to distinguish the observed structures, it does not inform about the drivers shaping such structures. In fact, both environmental and spatial drivers could lead to similar metacommunity structures (Fig. 1). In this sense, different metacommunity structures could be identified regarding their turnover type (negative indicating species loss structures, or positive indicating species replacement structures) and the gradualism of the species loss or replacements (from one by one species, corresponding to evenly spaced or hyperdispersed structures to groups of species corresponding to Clementsian or clumped species loss; see Fig. 1). Species loss structures would appear when species show different environmental tolerances or dispersal abilities, whereas species replacement structures

Fig. 1 Conceptual framework diagram indicating the metacommunity structure expected under different types of filters: spatial or environmental. *White ellipses* indicate the sites, and *black symbols* the species. Species tolerance (*black vertical lines*) and optima (*black points*) along the environmental gradient, indicated by the *gray triangle* (wide part of the triangle corresponds to less environmental constraint, and the *narrow part* of the triangle to higher environmental constraint), are shown. The *gray ellipses* in the spatial filtering part indicate species dispersal range along the space (*X–Y coordinates*). Only the result of opposite situations in the type of turnover (“*Species replacement*” corresponding to examples 1 and 2; or “*Species loss*” corresponding to examples 3 and 4), and the degree of species boundary clumping (“*hyperdispersed*” corresponding to examples 1 and 3; or “*clumped*” corresponding to examples 2 and 4) are shown. Therefore the resulting combinations of characteristics give the following different metacommunity structures: (1) an evenly spaced distribution, (2) a Clementsian distribution, (3) hyperdispersed species loss, (4) clumped species loss



would emerge when species show similar tolerances but with different optima, or similar dispersal abilities but different dispersal sources resulting in population or assemblages overlaps (Fig. 1). However, the detection of such non-random structures in the species distribution could be difficult if, for example, species do not respond similarly to the same driver (Leibold and Mikkelsen 2002). In these cases it is probable to find no significant coherence, which would indicate a random structure. Nevertheless, this does not necessary mean that species occur randomly, since they could be responding to different gradients (Presley et al.

2010). Therefore, the existence of strong environmental gradients can be relevant from a metacommunity structure perspective.

Here we propose a novel framework linking environmental and spatial filtering to the emergence of different metacommunity structures. We also provide empirical evidence of its usefulness by applying it to two different data sets: one exemplifying a metacommunity under a strong environmental filter and another one excluding that filter. To do so, we used wetland microcrustacean assemblages distributed along a strong salinity gradient. We have chosen a salinity gradient

as the filter to be tested because salinity is known to strongly affect the distribution of aquatic biota (e.g., Boix et al. 2008; Bradley 2009; Gutiérrez-Cánovas et al. 2013). Our data set included freshwater (FW) and brackish water (BW) wetlands. We first predicted that the whole metacommunity would follow a clumped association because species would generally segregate between FW and BW sites (i.e., the overall microcrustacean metacommunity structure would fit a Clementsian pattern). A priori, we expected that a strong environmental gradient would lead to a positive coherent structure (i.e., species replacement or species loss structure in BW). But, without a strong environmental gradient (i.e., FW) a random distribution could emerge, assuming that no other key environmental or spatial filter was acting. Therefore, we expected to find a relatively more environmentally controlled metacommunity in BW than in FW. Secondly, as we studied highly efficient dispersal organisms (Sohn 1996; Lopez et al. 2002; Havel and Shurin 2004; Louette and De Meester 2005), we hypothesized that distance among wetlands should not constrain dispersal at the spatial scale used here. We therefore predicted that environmental conditions would be more important than spatial wetland distribution in shaping metacommunities.

Materials and methods

Study site, field sampling and environmental variables

This study was conducted in 110 wetlands in Catalonia (north-eastern Iberian Peninsula; Fig. 2). Since we were primarily interested in analyzing the salinity effect, the studied wetlands encompassed a wide conductivity gradient ranging

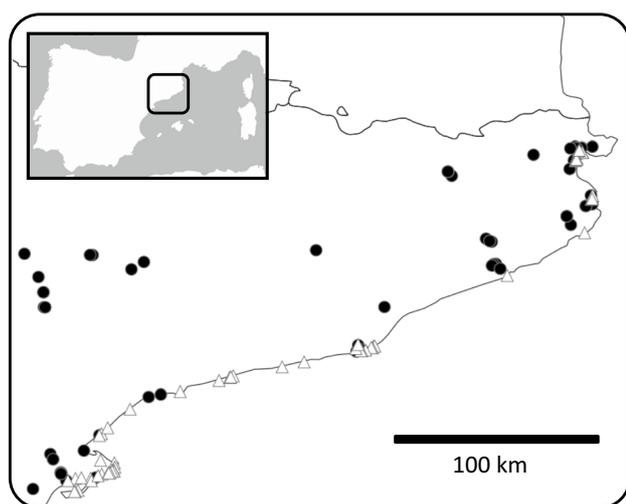


Fig. 2 Geographical location of the studied brackish water (BW; open triangles, $n = 55$) and freshwater (FW) wetlands (filled circles, $n = 55$)

from 0.2 to 119 mS cm^{-1} . According to its mean conductivity value, two wetland types were distinguished (Boix et al. 2008): FW wetlands (FW; conductivity $<5 \text{ mS cm}^{-1}$), and BW wetlands (BW; conductivity $>5 \text{ mS cm}^{-1}$). Previous studies did not find significant differences in species composition when comparing permanent and temporary BW wetlands (Boix et al. 2008), so we have considered temporary and permanent wetlands of the BW type, and only permanent wetlands of the FW type. A total of 55 sites per typology were sampled. All studied wetlands were located below 800 m a.s.l. in order to ensure that they were under the influence of a Mediterranean climate. The survey took place in 2003 and 2007, with one visit per wetland (between June and July). Potential bias due to variation in sample timing (months and years) was checked with an analysis of similarity (factor month nested within factor year). No significant differences were observed for year (FW, global $R = 0.045$, $P = 0.421$; BW, global $R = 0.591$, $P = 0.167$) or month (FW, global $R = -0.234$, $P = 0.722$; BW, global $R = 0.263$, $P = 0.276$), indicating that bias in the data set due to this variation in sampling timing was unlikely.

Microcrustaceans were sampled with a 22-cm-diameter dip-net (250- μm mesh size). At each wetland, 20 sweeps were carried out, covering all microhabitats. Samples were preserved in situ with 4 % formaldehyde. The samples were taken to the laboratory for further processing and identification. Three groups of microcrustaceans, namely Copepoda, Cladocera and Ostracoda, were identified to species level.

The considered environmental variables included physical, chemical and biological variables. Water temperature, dissolved oxygen (Hach, Loveland, CO), conductivity (Crisson 524 conductivity meter), pH (model HACH HQ30d) and water column depth were measured in situ. We calculated the deviation of oxygen saturation in absolute numbers. Dissolved inorganic nitrogen (DIN = ammonium + nitrite + nitrate), as well as phosphate (PO_4^{3-}), were obtained from filtered samples (250 ml) through GF/C Whatman filters. Total phosphorus and nitrogen were obtained from unfiltered samples. Dissolved and total nutrient concentrations were measured following the methodology used by Grasshoff et al. (1983). After filtering the water samples, chlorophyll-*a* was extracted with 90 % acetone and measured following Talling and Driver (1963). Information on fish presence and macroinvertebrate predator richness was also registered. Wetland size was obtained using geographic information systems (Institut Cartogràfic i Geològic de Catalunya, <http://www.icc.cat>). For more information on the environmental characteristics see Table 1.

Identification of potential environmental gradients

In order to know if BW showed a stronger salinity gradient than FW, as we expected, an *F*-test was performed (i.e.,

Table 1 Environmental characteristics for each wetland type

Wetland type	BW ($n = 55$)	FW ($n = 55$)	Ratio of variances
Water characteristics			
Temperature (°C)	26.5 ± 3.6 (17.7–34.7)	23.6 ± 3.7 (13.3–31.7)	0.93
Conductivity (mS cm ⁻¹)	25.0 ± 22.4 (2.40–119.7)	1.2 ± 0.9 (0.2–3.8)	559.72***
pH	8.3 ± 0.5 (7.4–9.7)	7.9 ± 0.5 (7.1–8.8)	1.20
aDO (%)	33.8 ± 26.5 (1.0–95.0)	39.1 ± 29.7 (2.9–99.6)	0.79
TP (mg P L ⁻¹)	0.9 ± 1.5 (<0.1–7.8)	1.1 ± 2.5 (<0.1–13.7)	0.29***
PO ₄ ³⁻ (mg P L ⁻¹)	0.3 ± 1.1 (<0.1–7.4)	0.2 ± 0.6 (<0.1–4.1)	2.86***
TN (mg N L ⁻¹)	2.9 ± 3.0 (0.4–14.2)	5.0 ± 9.5 (0.2–68.4)	0.10***
DIN (mg N L ⁻¹)	0.3 ± 0.7 (<0.1–3.7)	2.6 ± 5.3 (<0.1–30.6)	0.01***
Biotic characteristics			
Chl- <i>a</i> (µg L ⁻¹)	22.0 ± 36.2 (0.6–169.9)	24.9 ± 31.9 (<0.1–150.5)	1.29
Fish presence (no. of wetlands)	50	43	
Macroinvertebrate predators (species richness per site)	2.8 ± 1.9 (0–7)	2.4 ± 1.8 (0–7)	1.09
Pond characteristics			
Wetland size (m ²)	2.8 × 10 ⁵ ± 8.2 × 10 ⁵ (3.3 × 10 ² –4.6 × 10 ⁶)	1.4 10 ⁴ ± 2.4 × 10 ⁴ (8.2 × 10 ¹ –1.2 × 10 ⁵)	1099.53***

Mean values ± SD, and minimum and maximum values (*in parentheses*). Results of an *F*-test performed to compare variances [ratio of variances—brackish water (BW)/ freshwater (FW)] are also shown; significant values >1 indicate that BW had a higher variance than FW; significant values <1 indicate that FW had a higher variance than BW

aDO Deviation of oxygen saturation, *TP* total phosphorus (P), *TN* total nitrogen (N), *DIN* dissolved inorganic N, *Chl-a* chlorophyll-*a*

*** $P < 0.001$

ratio variances test = BW variance/FW variance). This test showed if there was higher salinity variability (i.e., conductivity) in BW wetlands (i.e., >1 and a significant result). We performed the same test for the rest of environmental variables to explore the existence of other potential gradients (Table 1).

Spatial descriptors

We generated spatial predictors using Moran's eigenvector maps (MEMs) as detailed in Dray et al. (2006). First, Universal Transverse Mercator coordinates were used to build a topology-based map of water body positions (using Euclidean distance and Gabriel graph criteria to construct the connection network among sites), which was binary transformed and weighted. Only positive and significant eigenvectors were retained (significantly positive Moran's *I*), because they represent positive spatial associations of water bodies (Griffith and Peres-Neto 2006). Smaller eigenvectors describe broader-scale patterns (i.e., sites with opposite scores for these spatial eigenvectors are geographically distant), whereas higher eigenvectors describe finer scale variations (i.e., sites very close to each other within a region have opposite scores for these spatial eigenvectors). This process was repeated three times: one using the overall data set (i.e., BW + FW), one using only FW, and

one using only BW wetlands. All spatial analyses were performed using the spacemakeR package (Dray et al. 2006) with R version 3.0.1 (R Development Core Team 2015).

Data analyses

All analyses were done for the overall data set (BW + FW = 110 sites) and repeated for BW (55 sites) and FW (55 sites) separately. Because the procedure used to identify the metacommunity structures relies on a correspondence analysis (CA) (see below), and our metacommunity was quite sparse (many absences), the explained variation of the first CA axis (the one used to test the observed metacommunity structure) was low (all cases below 10 %; Table 2). Thus, we also performed the analysis excluding the species present in less than 5 % of the samples, which in general increases the explanatory power (to above 10 %; see Online Resource 1). We performed correlation analyses between the CA axis extracted with the complete (all species) and the reduced matrix (excluding the species present in less than 5 % of the samples) to explore if the reduction in the species number significantly altered the solution. Although the reduction in the number of species could be important (e.g., more than half of the species reduction in the overall data set; Table 2 and Online Resource 1), correlation analyses showed that the ordering of sites along

Table 2 Results of the hierarchical approach used to examine the elements of metacommunity structure

	BW + FW	FW	BW
No. of species	74	56	49
No. of sites	110	55	55
First CA axis	7 %	7 %	9 %
Coherence			
Observed value	2731	1319	585
Expected values \pm SD	4290 \pm 256	1477 \pm 92	1124 \pm 97
<i>P</i>	<0.001	0.060	<0.001
Turnover			
Observed value	1,090,422	144,830	77,487
Expected values \pm SD	722,105 \pm 158,684	112,243 \pm 30,611	66,036 \pm 20,363
<i>P</i>	0.020	0.268	0.589
Clumping			
Morisita's index	3.83	2.84	3.05
<i>P</i>	<0.001	<0.001	<0.001

CA Correspondence analysis; for other abbreviations, see Table 1

the first axis remained almost invariable (correlation values always significant and higher than 0.9). We also performed the rest of the analyses twice (EMS and variable selection, see below), one with the complete and one with the reduced matrix, obtaining similar results. Since the reduction of less represented species could blur species boundaries and thus potentially affect the resulting metacommunity structure (Presley and Willig 2010), we report the results obtained with all species (see results obtained with the reduced matrix in Online Resource 1).

Elements of metacommunity structure

To analyze which metacommunity structure best fitted the microcrustacean species distribution, we used the EMS methodology described by Leibold and Mikkelsen (2002), which was posteriorly expanded by Presley et al. (2010). The metacommunity structure was assessed by evaluating the coherence, turnover and boundary clumping of a site-by-species incidence matrix, which was ordinated through CA (Fig. 3). This allowed us to obtain a gradient in which sites were ordered according to species resemblances, and species were ordered according to site occurrences. The arrangement of sites along the first axis of ordination represents a latent environmental gradient that shapes species distributions (Gauch 1982). Consequently, no a priori assumptions are needed concerning the environmental factors to which species respond. The resulting species \times sites ordination along the primary axis provided the basis on which to test the different metacommunity characteristics in a hierarchical way (Fig. 3): coherence (step 1), turnover (step 2), boundary clumping (step 3).

Coherence was the first pattern tested (step 1 in Fig. 3). This was done by comparing the number of embedded

absences in the ordinated empirical incidence matrix to a distribution of embedded absences derived from 1000 ordinated null matrices. The applied null model permuted species across sites but fixed site richness (i.e., equal to the observed values). This type of permutation was chosen in previous studies, not only because it better represents site properties such as site species richness (e.g., Presley et al. 2009; Henriques-Silva et al. 2013), but also because of its appropriate type I error rates and appropriate power to detect distribution patterns (Gotelli and Graves 1996). For each analysis (overall, FW, and BW) we generated 1000 random matrices which were also ordered via CA. Negative significant coherence (more absences than expected by chance) is the defining characteristic of checkerboard distributions, with strong interspecific competition that results in mutual exclusion as the implied structuring mechanism. A significant positively coherent metacommunity implies that species distributions arise in response to a common gradient. The lack of significant coherence characterizes random distributions, indicating that species ordering is not responding to a common gradient. When coherence was found to be positive and significant, the turnover was tested (step 2 in Fig. 3). To do this, the number of empirical replacements was compared to the distribution of randomly generated values based on a null model that randomly shifts entire ranges of species (Leibold and Mikkelsen 2002). The null model used to test turnover had the same characteristics as the one used for the coherence analysis, and allowed discriminating between a species loss structure (i.e., negative turnover because there were less replacements than the ones expected by chance) and a species replacement structure (i.e., positive turnover because there were more replacements than the ones expected by chance). In both cases, the underlying

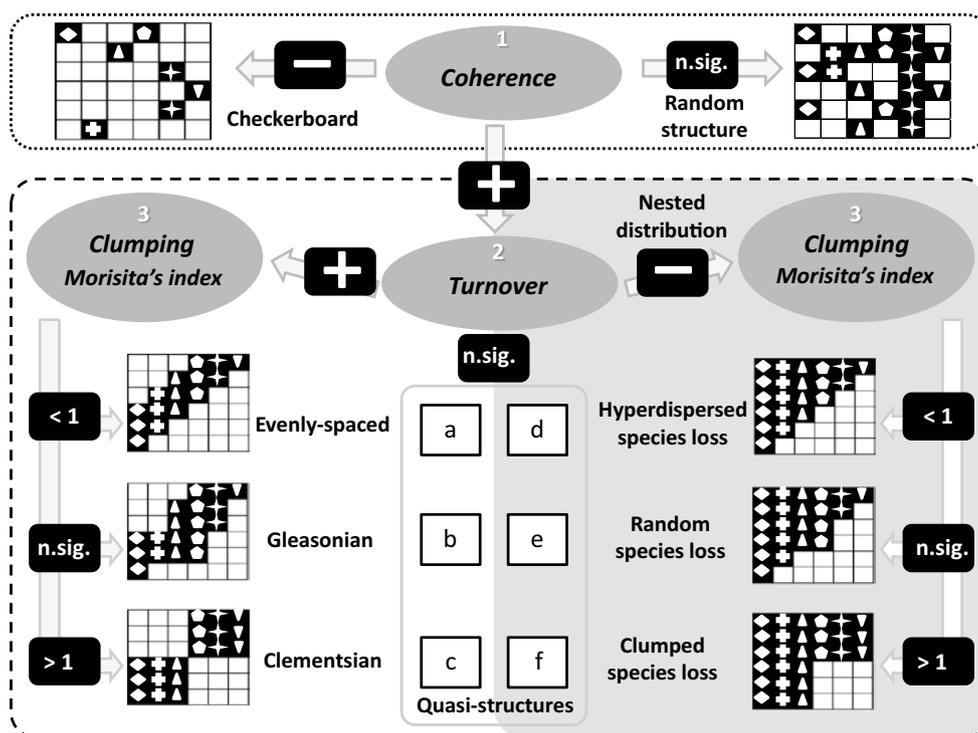


Fig. 3 Schematic representation of the approach used to examine the elements of metacommunity structure (*numbers* indicate the different steps followed). Species \times sites distributions corresponding to the principal metacommunity structures are represented as follows: *columns* represent species (*different shapes* are different species), and *rows* represent sites. Combining turnover and boundary clumping results, six principal metacommunity structures can be identified: evenly spaced, Gleasonian, Clementsian, hyperdispersed species loss, random species loss, and clumped species loss. Quasi-structures are indicated by *letters*: *a–c* indicate quasi-structures obtained for non-

significant but positive turnover, and *d–f* the ones obtained for non-significant but negative turnover. According to Morisita’s index we can distinguish: a quasi-evenly spaced structure (*a*), a quasi-Gleasonian structure (*b*), a quasi-Clementsian structure (*c*), quasi-hyperdispersed species loss (*d*), quasi-random species loss (*e*), and quasi-clumped species loss (*f*). Metacommunity structures within the *dotted frame* do not show any coherence (random distribution), or show negative coherence (checkerboard distribution). Modified from Presley et al. (2010) and Henriques-Silva et al. (2013)

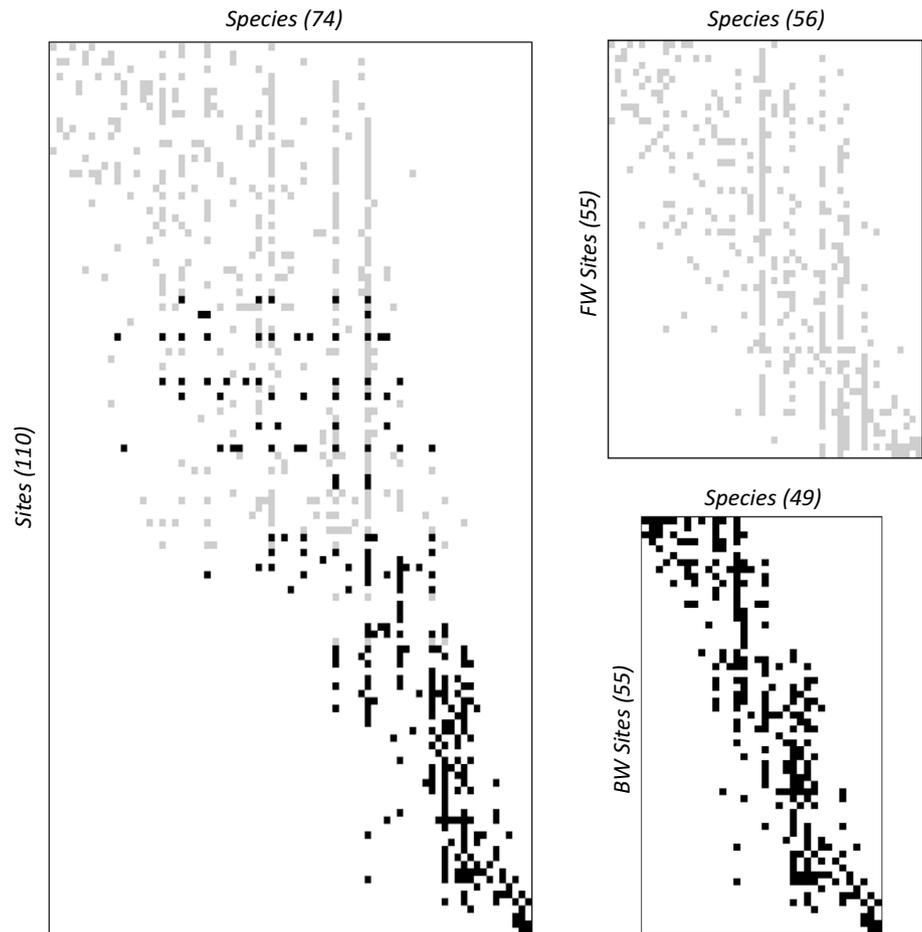
structure was further analyzed with the Morisita index-based test, which gives information about the boundary clumping of the structures (step 3 in Fig. 3). In this third step, significance was determined by a χ^2 -test that compared the empirical distribution of boundaries to an expected uniform distribution. While significant values >1 indicate clumped boundaries, significant values <1 indicate hyperdispersed boundaries. Species distributions that occur independently and idiosyncratically with respect to each other are indicated by a non-significant χ^2 -test. The combination of turnover results with those obtained from the boundary clumping allowed us to discern between six principal metacommunity structures and six quasi-structures (Fig. 3), that appear when non-significant turnover results occurs (*a–f* in Fig. 3). For all analyses, we used an α -level of 0.05 to determine significance (Fig. 3). Analyses of metacommunity structure were performed using the metacom package version 1.3 (Dallas 2013) in R version 3.0.1 (R Development Core Team 2015). A complete,

comprehensive, and detailed, explanation of the EMS procedure can be found in Presley et al. (2010).

Hierarchical variation partitioning

To know which environmental variable and spatial eigenvectors were related to the observed metacommunity structure, we performed a forward selection procedure using the double stopping criterion (Blanchet et al. 2008). As environmental variables we included water, pond, and biotic characteristics (see Table 1). All water characteristics (except pH), and wetland size were previously \log_{10} (var + 1) transformed to better achieve normality and homoscedasticity assumptions. The significant variables (Online Resource 2) were posteriorly used to quantify the variation explained by the overall selected spatial and environmental filters (variation partitioning). Forward selection was done using the functions forward.sel available in the packfor package (Dray et al. 2007).

Fig. 4 Species \times sites incidence matrices after reciprocal averaging ordering (1st axis) resulting from the overall, FW, and BW analyses. FW wetlands are represented in gray, and BW wetlands in black. Numbers in parentheses indicate number of species, and sites, used in each analysis. For abbreviations, see Fig. 2



We used a variation partitioning specially developed to better account for the orthogonality of MEM variables (Legendre et al. 2012). We separated the selected variables into three subsets of predictors: environmental filters, broadscale spatial descriptors (Moran eigenvectors 1–4), and finer-scale spatial descriptors (the rest of the Moran eigenvectors). We used a hierarchical approach because environmental conditions vary at a broader scale than biotic interactions, and a hierarchical influence of their effects on species distribution is expected (Legendre et al. 2012). For example, differences in salinity may be very important when comparing wetlands located far away, but within the same cluster of similarly saline wetlands finer-scale patterns may emerge due to biotic interactions. Therefore, the total explained variation was partitioned among: (1) the effects of environmental filters, (2) those related to broad and finer-scale spatial patterns, and (3) the shared influence of environmental filters and spatial descriptors. The hierarchical variation partitioning was carried out with the function `varpart3.MEM` (Legendre et al. 2012) in R version 3.0.1 (R Development Core Team 2015). We tested the significance of the different fractions using the function `anova.cca` available in the `vegan` package (Oksanen et al. 2013).

Results

Wetland size and conductivity were the variables that showed the highest differences in variation when comparing BW and FW, both showing higher variances in BW than in FW. In contrast, nutrients, with the exception of PO_4^{3-} , showed higher variances in FW than in BW (Table 1).

The first step of the EMS analysis (Fig. 3) for the whole data set (BW + FW) indicated that the metacommunity had a positive and coherent structure (Table 2). Following the second step (Fig. 3), a significant and positive turnover was observed (i.e., the observed value was higher than expected by chance), indicating that microcrustaceans followed a species replacement structure (Table 2). Finally, when analyzing the boundary clumping (step 3 in Fig. 3), Morisita's index was significantly higher than one (Table 2). Therefore, the whole data set presented a Clementsian structure, as expected. Moreover, reciprocal averaging analyses ordered sites according to conductivity differences, with FW sites showing opposite scores to BW (Welch two-sample *t*-test; $t = 8.4782$; $df = 60.55$; $P < 0.001$; Fig. 4).

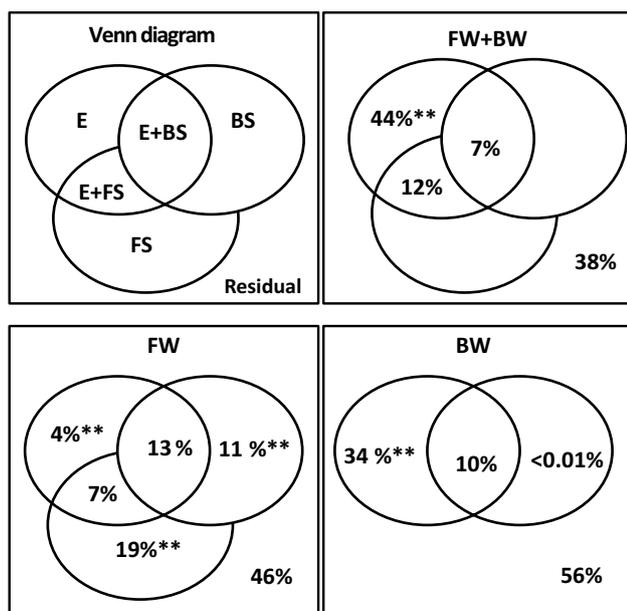


Fig. 5 Venn diagrams of the hierarchical variation partitioning for the whole data set (BW + FW), FW, and BW sites: the effects linked to environmental filters (*E*), those related to broadscale spatial patterns (*BS*), those resulting from finer-scale spatial patterns (*FS*), shared influence of environmental filters with broadscale (*E* + *BS*) and finer-scale spatial descriptors (*E* + *FS*). Numbers indicate percentage of variation explained; negative fractions are not shown. ** $P < 0.01$

When splitting the data set into FW and BW data, different metacommunity structures emerged. For FW, non-coherent structures arose, indicating a possible lack of a key variable structuring the metacommunity or species being affected by different non-collinear key variables (Table 2). In contrast, BW microcrustaceans showed a coherent structure, indicating that a key variable was structuring the metacommunity (Table 2). However, although positive, the turnover was not significant (Table 2). Finally, the Morisita index indicated that the metacommunity was clumped. As a result, BW microcrustacean metacommunity structure fitted a quasi-Clementsian pattern (Fig. 3).

The variation partitioning carried out for the whole data set (BW + FW) showed a high proportion of total variation (close to 60 %) being mainly explained by the environmental filters (Fig. 5). It should be noted that the environmental filter matrix only included conductivity information, since it was the only variable selected in the forward procedure (Online Resource 2). Moreover, no significant spatial patterns were detected. BW showed a similar pattern to that observed for the overall data set (Fig. 5). Again, conductivity was the only variable selected as an environmental filter, but in this case the shared variation was restricted to broadscale patterns (Fig. 5). In contrast, when analyzing FW (Fig. 5) environmental filters only explained 4 % of

the variation (in this case only temperature was selected; Online Resource 2), whereas broad- and finer-scale spatial descriptors explained 11 and 19 % of the variation, respectively.

Discussion

EMS and variation partitioning techniques are becoming increasingly popular in empirical metacommunity studies (e.g., Hájek et al. 2011; Dallas and Presley 2014). The combination of both methodologies is recommended, since it allows disentangling the main drivers of the metacommunity structures more precisely (e.g., Henriques-Silva et al. 2013; Fernandes et al. 2014; Heino and Alahuhta 2015). Moreover, we have replaced the conventional variation partitioning approach by a hierarchical one. The hierarchical approach is more appropriate for the analysis of environmental variability from broad to finer spatial scales (Legendre et al. 2012), and we strongly recommend its use in combination with EMS. Such combination has allowed us to better understand and identify the relationships between environmental and spatial filters.

In our case study, the overall metacommunity fitted a Clementsian pattern, following our expectations (Fig. 6). Clementsian structures are not rare, and they have already been reported for a number of plant (e.g., Keith et al. 2011; Meynard et al. 2013) and animal metacommunities (e.g., Henriques-Silva et al. 2013; Dallas and Presley 2014). This structure arises when distinct communities are composed of groups of species (species association) that respond in a similar way to one (or more) structuring factors, and has generally been related to the effects of strong environmental filters (e.g., Keith et al. 2011; Meynard et al. 2013; Dallas and Presley 2014). The variation partitioning results, which indicated weak spatial structuring compared to the salinity effect, together with the clumped association related to changes in salinity, support this idea. Moreover, the existing salinity gradient constrained communities (Boix et al. 2008; Waterkeyn et al. 2008; Brucet et al. 2009), with species richness being relatively lower in sites with higher salinity (t -test; $t = -3.64$; $df = 108$; $P < 0.001$). In fact, our results suggest that salinity acts as a key variable shaping the metacommunity structure, since no variation was exclusively linked to any spatial pattern.

Each wetland type showed distinct metacommunity structures: quasi-Clementsian in BW, and random in FW (Fig. 6). Random structures may be an artefact associated with the rarity of many species in the ensemble (Cisneros et al. 2015). However, we obtained the same result even when reducing rarity (i.e., suppressing species with occurrences lower than 5 % of the samples; Online Resource 1). Our results agree with idiosyncratic responses of

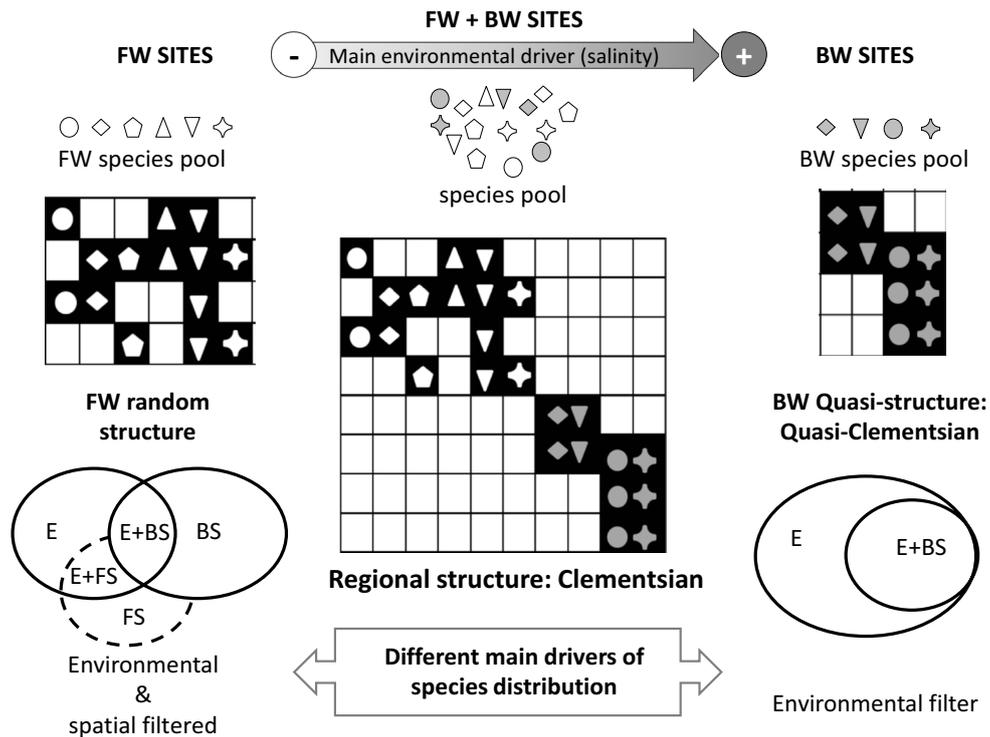


Fig. 6 Schematic representation of the main results obtained in this study. *Discontinuous line* indicates that the finer scale could actually be explained by local environmental conditions. *E* Environmental variables, *BS* broadscale spatial descriptors, *FS* finer-scale spatial

descriptors, *E + BS* shared variation between environmental filters with broadscale descriptors, *E + FS* shared variation between environmental filters with finer-scale spatial descriptors

individual microcrustaceans species to environmental conditions (Jeffries 2003). Indeed, random structures do not indicate that species occur at random in the metacommunity, but that species' distributions are mainly independent of one another (Dallas and Presley 2014). Thus, random structures may not necessary imply lack of environmental control. Supporting this idea, our results showed the existence of environmental control in the metacommunities of both wetland types, but as expected, the BW metacommunity was more environmentally controlled than the FW one.

BW sites were transitional ecotones in which both FW (e.g., *Macrocyclus albidus*, *Cypridopsis vidua*) and brackish species (e.g., *Amonardia cf. normanni*, *Cletocamptus confluens*) could be found (Online Resource 3). Microcrustacean assemblages in BW sites were again organized according to salinity preferences, similarly to the macroinvertebrate species distribution observed in mixed estuaries (Attrill and Rundle 2002). This kind of species distribution creates different species subsets, and thus the emergence of clumped structures. However, euryhaline species (i.e., tolerating wide salinity gradients) might be blurring the boundaries, leading to the existence of a quasi-structure. Nevertheless, it is also possible that the quasi-Clementsian structure

observed was the result of an artefact because species niche breadth extended beyond the range observed in the data set, affecting the identification of boundaries. This could have some importance, especially for the species with more FW affinity, since when splitting the data set the lower part of their niche breadth may be beyond 5 mS cm^{-1} (our cut-off point between typologies). On the other hand, temperature was the only variable related to the species distribution in FW, explaining a low proportion of the observed variation (4 % of the observed species distribution could be associated with differences in water temperature). A high proportion of eurythermal organisms should be expected in warm and hydrological variable habitats (Poff et al. 2010) like Mediterranean wetlands. Other studies on factors determining microcrustacean species distribution in Mediterranean ponds similarly found that temperature may play a secondary role (Sahuquillo and Miracle 2013). Likewise, although temperature was related to species distribution, in our study it was not a key variable shaping metacommunity structure (otherwise metacommunity structure would have shown a positive and significant coherence).

Unexpectedly, we found signals of broadscale spatial patterns determining the metacommunity structure in FW. The studied region has a complicated orography

that creates different climatic conditions. Accordingly, we observed a high amount of variation shared between temperature and broadscale spatial descriptors in FW. Previous studies developed within the same geographical context (lowland wetlands in Catalonia) found that aquatic communities differed between mesothermal and semiarid climates not only in their compositions but also in their dynamics (Ruhí et al. 2014). Nevertheless, we also found a significant proportion of variation uniquely explained by broadscale patterns in FW. The complex orography might also contribute to diminish dispersal efficiency, even when considering high dispersal organisms such as microcrustaceans. Several studies have highlighted that the potential for frequent and widespread dispersal of passively dispersed invertebrates does not directly translate into real dispersal rates (Bohonak and Jenkins 2003; Incagnone et al. 2015). Within this context, specific experiments directly measuring zooplankton dispersal rates have found lower than expected rates (Allen 2007). All these findings support the existence of broadscale spatial signals on the structure of metacommunities of passive dispersers. Similarly to what happens with environmental controls on the expression of priority effects (Mergeay et al. 2011), the lack of pure effects of broadscale spatial patterns in BW suggests that environmental sorting was paramount and weakened eventual mass effects (Fig. 6).

We also found some variation in species distribution related to finer-scale patterns in the less environmentally controlled wetlands (FW). We initially hypothesized that this could be the result of biotic interactions. However, we found no relationships between metacommunity structure and our biotic proxies (fish presence and predator macroinvertebrate richness). Previous studies suggest that spatial signals can result from non-measured finer scale environmental variability (Cottenie 2005). FW sites included artesian spring ponds (six sites). In these systems temperature values are very stable due to a continuous groundwater feed (Sahuquillo and Miracle 2013), which could explain the shared variation observed. Moreover, these artesian spring ponds appear in small clusters in the landscape. This particular spatial arrangement, and not biotic interactions, could explain the high proportion of variation derived for the finer-scale spatial descriptors. To test this idea, we repeated the analysis without including the artesian natural springs in the data set, and none of the spatial descriptors of finer-scale patterns were selected (i.e., variation uniquely linked to temperature was 9 %, broadscale patterns 10 %, and the shared variation 5 %). Therefore, even if at a first sight some biotic control could be inferred, a more careful analysis indicated that the most plausible explanation for this significant finer-scale spatial signal was unmeasured environmental variability.

In summary, from a methodological perspective, our study shows the potential of EMS combined with variation partitioning techniques to detect broadscale patterns (Fig. 6). However, we also report its weakness when aiming to infer biotic interactions from finer-scale signals (Dray et al. 2012), which highlights the conservative approach that should guide the interpretation of these signals (Legendre et al. 2012).

Knowing the type of structure and the drivers that shape metacommunities is also relevant from the applied perspective, and so our approach could be useful to understand and predict the impacts of eventual stressors. For example, increases in salinity values are expected as the result of anthropogenic activities such as agriculture or resource extraction (Williams 2001; Cañedo-Argüelles et al. 2013). Our results indicate that microcrustacean metacommunities follow clumped species replacement structures that are highly influenced by salinity. Consequently, communities found at low salinities share few taxa with those found at high salinities. Thus, an eventual increase in salinity, reaching the limit of the species' tolerance, potentially results in the disappearance of a whole group of species and not to a gradual species loss.

Recent advances have been made to understand how environmental management can affect biodiversity at local and regional scales (e.g., Sokol et al. 2015). The existence of structures due to species replacement or species loss can have strong implications in terms of management and biodiversity conservation (Baselga 2010). While species replacement structures imply that each site hosts some kind of exclusive taxa, and so it is essential to preserve the whole network to maintain biodiversity, species loss structures allow the prioritization of sites in terms of management efforts (e.g., those that are the richest in species). This information is highly relevant to the single large or several small debate applied to the conservation of FW biodiversity, and we advance the notion that it needs to consider the influence of a network's spatial arrangement.

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Author contribution statement S. G., I. A., A. R., J. S., X. Q. and D. B. conceived the ideas; all authors participated in the data collection; S. G., I. A., and A. R. analyzed the results; S. G. wrote the first draft of the manuscript, and coordinated revisions. All authors contributed to the writing.

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