Mecanismes estructuradors de les metacomunitats d'ostracodes d'aigües continentals
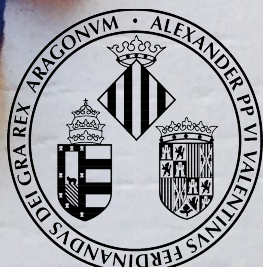
Andreu Castillo Escrivà
Director: Francesc Mesquita Joanes
Tesi Doctoral – Doctorat en Biodiversitat – Setembre 2016

Facultat de Ciències Biològiques
Universitat de València
Programa de Doctorat en Biodiversitat

Mecanismes estructuradors de les metacomunitats d'ostracodes d'aigües continentals

Andreu Castillo Escrivà

Tesi doctoral
Setembre 2016

Director
Francesc Mesquita Joanes

Imatge de portada: La portada és una fotografia presa per Mercè Gomar i Andreu Castillo d'un joc infantil de formes. La imatge intenta fer un símil entre aquest joc i el concepte de metacomunitat, mentre ens desafia a pensar quines formes o espècies podrien encaixar en cada peça gran o nínxol. Per què cada forma ocupa un lloc i no un altre?

Tesi titulada **Mecanismes estructuradors de les metacomunitats d'ostracodes d'aigües continentals**, presentada per **Andreu Castillo Escrivà** per optar al grau de Doctor en Biodiversitat per la Universitat de València.

Firmat: Andreu Castillo Escrivà

Tesi dirigida pel Doctor **Francesc Mesquita Joanes**, Professor Titular d'Ecologia a la Universitat de València

Firmat: Francesc Mesquita Joanes

Agraïments

Resum

Un dels objectius principals de l'estudi de les metacomunitats és entendre els patrons de distribució de grups d'espècies i els mecanismes ecològics que condicionen aquestos patrons. Recentment, els estudis sobre metacomunitats han estat centrats en determinar la importància relativa de l'ordenació d'espècies (*i.e.* l'efecte filtrador de l'ambient) i la dispersió (*i.e.* els efectes espacials) com a mecanismes estructuradors de les metacomunitats. En aquesta tesi hem analitzat el paper d'aquestos mecanismes estructuradors sobre diferents metacomunitats d'ostracodes i altres invertebrats en tres sistemes aquàtics diferents situats a l'est de la Península Ibèrica: llacunes temporals, basses de roca i rius. Els nostres resultats mostren que l'ordenació d'espècies és un mecanisme que afecta generalment a aquestes metacomunitats, però afegint que els processos dispersius també són importants en alguns casos. Per exemple, la limitació dispersiva explicava part de l'estructura de les comunitats de les llacunes i de les basses de roca, i els efectes de massa foren més forts que l'ordenació d'espècies en les comunitats dels rius. Per altra banda, també hem estudiat com aquesta importància relativa dels mecanismes estructuradors varia al llarg del temps en les llacunes temporals. En aquest estudi vam observar com l'ordenació d'espècies mantenia en el temps el seu paper dominant, excepte al principi de l'hidroperíode, quan els ous de moltes espècies oportunistes eclosionen ràpidament després de la inundació, provocant distribucions aleatòries independents de l'ambient i l'espai. Per tant, fenòmens estocàstics i altres mecanismes no relacionats amb l'ambient i l'espai podrien també influenciar les metacomunitats. En aquest sentit, hem utilitzat els assemblatges de restes d'ostracodes (*i.e.* tafocenosi) trobant una gran concordança entre les comunitats vives (*i.e.* biocenosi) i la tafocenosi, i determinant un possible paper dels efectes prioritaris, com un mecanisme estructurador relacionat amb la contingència històrica de les comunitats. Els estudis sobre metacomunitats ens ensenyen la relació entre la distribució de les espècies i les característiques del paisatge i els seus ecosistemes, i per tant oferixen un coneixement bàsic necessari per a una millor gestió i conservació del medi natural.

Resumen

Uno de los objetivos principales en el estudio de las metacomunidades es entender los patrones de distribución de grupos de especies y los mecanismos ecológicos que condicionan estos patrones. Recientemente, el estudio de las metacomunidades se ha centrado en determinar la importancia relativa de la ordenación de especies (*i.e.* el efecto filtrador del ambiente) y la dispersión (*i.e.* los efectos espaciales) como mecanismos estructuradores de las metacomunidades. En esta tesis hemos analizado el papel de estos mecanismos estructuradores sobre diferentes metacomunidades de ostrácodos y otros invertebrados en tres tipos de sistemas acuáticos situados en el este de la Península Ibérica: lagunas temporales, charcas de roca y ríos. Nuestros resultados muestran que la ordenación de especies es un mecanismo que afecta generalmente a estas metacomunidades, aunque los procesos dispersivos también son importantes en algunos casos. Por ejemplo, la limitación dispersiva explicaba parte de la estructura de las comunidades de las lagunas y de las charcas de roca, y los efectos de masa fueron más fuertes que la ordenación de especies en las comunidades de los ríos. Por otro lado, también hemos estudiado como esta importancia relativa de los mecanismos estructuradores varía con el paso del tiempo en las lagunas temporales. En este estudio observamos como la ordenación de especies mantenía en el tiempo su papel dominante, excepto al principio del hidroperiodo, cuando los huevos de muchas especies oportunistas eclosionan rápidamente después de la inundación, provocando distribuciones aleatorias independientes del ambiente y el espacio. Por lo tanto, fenómenos estocásticos y otros mecanismos no relacionados con el ambiente o el espacio también podrían influenciar las metacomunidades. En este sentido, hemos utilizado los restos de ostrácodos (*i.e.* tafocenosis), encontrando una gran concordancia entre las comunidades vivas (*i.e.* biocenosis) y la tafocenosis, y determinando un posible papel de los efectos prioritarios, como mecanismo estructurador relacionado con la contingencia histórica de las comunidades. Los estudios sobre metacomunidades nos enseñan la relación entre la distribución de las especies y las características del paisaje y sus ecosistemas, y de este modo ofrecen un conocimiento básico necesario para una mejor gestión y conservación del medio natural.

Abstract

One of the main aims of the study of metacommunities is to understand species distribution patterns and their ecological drivers. Recently, ecologists have focused metacommunity analysis on determining the relative importance of species sorting (*i.e.* environmental effects) and dispersal (*i.e.* spatial effects), as structuring mechanisms of metacommunities. In the present thesis, we analyzed the role of these structuring mechanisms on metacommunities of ostracods and other invertebrates in three aquatic systems located in the Eastern Iberian Peninsula: shallow lakes, rock pools and streams. We found that in general species sorting drives these metacommunities, but dispersal processes are also important in some cases. For instance, dispersal limitation explained a fraction of the community structures in the studied lakes and rock pools, whereas mass effects were stronger than species sorting in explaining stream communities. On the other hand, we also studied the relative importance of the structuring mechanisms through time in shallow lakes. In this study, we observed that species sorting was dominant through time, except at the onset of the flooding period when no mechanism significantly affected the species composition, likely because of random structures generated by an abundant hatching of opportunistic species from the egg bank. Therefore, stochastic phenomena and other mechanisms unrelated to environment and space could also influence metacommunities. In this line, we analyzed the ostracod remain assemblages (*i.e.* taphocoenoses), finding a significant concordance between living communities (*i.e.* biocoenoses) and taphocoenoses, and determining a possible role of priority effects, as a structuring mechanism related to the historical contingency of these communities. Metacommunity studies highlight the relationship between species distribution and landscape features and their ecosystems, and provide basic knowledge necessary for the management and preservation of the natural environment.

Taula de continguts

Introducció general

Basses de roca (Alfarb)

Introducció general

Per què uns organismes habiten uns llocs i no uns altres? La distribució heterogènia dels organismes és considerada el principi fonamental de l'ecologia teòrica (Scheiner & Willig, 2011), i és una de les principals qüestions que tracta l'ecologia de comunitats, la part de l'ecologia dedicada a entendre la manera en què grups d'espècies es distribuïxen en l'espai i el temps. També és la qüestió fonamental d'aquesta tesi centrada en les comunitats d'uns organismes diminuts que pràcticament habiten qualsevol cos d'aigua, els ostracodes.

Històricament, els ecòlegs han estudiat les comunitats des de dos punts de vista o escales espacials diferents: l'escala local i l'escala regional (Leibold *et al.*, 2004). Els primers van assumir que les comunitats a escala local eren sistemes aïllats, on únicament les condicions locals (biòtiques o abiòtiques) determinen la composició d'espècies de cada localitat. Per exemple, els models de Lotka-Volterra i les seues extensions (*e.g.*, May, 1973; Pimm & Lawton, 1978; McCann *et al.*, 1998) prediuen com diferents poblacions locals interactuen, modificant les taxes de natalitat i mortalitat entre elles dins de cada comunitat aïllada. Els segons van centrar els seus estudis en dinàmiques regionals, indicant la importància dels fenòmens dispersius entre localitats. En aquest context destaquen els estudis sobre colonització en el marc de la Teoria Insular (MacArthur & Wilson, 1967), l'efecte rescat (Brown & Kodric-Brown, 1977), els efectes de massa (Schmida & Wilson, 1985) i les dinàmiques de font-embornal (Pulliam, 1988). Gràcies a aquestos estudis, ara sabem que l'estructura de les comunitats és conseqüència de les condicions locals i de les dinàmiques regionals (Levin, 1992), el que ens porta al concepte de metacomunitat.

El concepte de metacomunitat

El concepte de metacomunitat integra els dos punts de vista anteriors. Una metacomunitat és un conjunt de comunitats connectades mitjançant la dispersió de múltiples espècies (Hanski & Gilpin, 1991; Wilson, 1992). Aquest concepte ha impulsat als ecòlegs a integrar les condicions ambientals (com efectes locals) amb les variables

espacials (com a substitutes dels efectes de la dispersió) per a explicar l'estructura de les comunitats (*e.g.*, Cottenie, 2005; Logue *et al.*, 2011; Dray *et al.*, 2012). Leibold *et al.* (2004) en una revisió, i també Holyoak *et al.* (2005), van proposar que depenent de la importància dels processos ambientals i espacials, les metacomunitats podien pertànyer a quatre paradigmes diferents: dinàmica de pegats, ordenació d'espècies, efectes de massa o al model neutre.

La dinàmica de pegats (a partir de l'anglès «*patch dynamics*») assumix que no existix variació ambiental entre localitats diferents o pegats, però considera que les espècies exhibixen diferents capacitats de dispersió. Les espècies que tenen gran capacitat de dispersió arriben a tots els pegats i, les que no, es queden restringides a les més properes. En aquest cas, l'estructura de les comunitats estarà únicament determinada per les distàncies entre els pegats. De manera contrària, l'ordenació d'espècies («*species sorting*») dóna menys importància als fenòmens de dispersió i es fonamenta en què l'ambient varia entre localitats, existint una relació molt forta entre l'ambient i les espècies que habiten una localitat. En conseqüència, les espècies es troben distribuïdes en aquelles localitats en què les condicions ambientals són favorables. El paradigma dels efectes de massa («*mass effects*»), és una ampliació de l'ordenació d'espècies, considerant l'existència de processos dispersius forts que permeten que algunes poblacions es puguen mantindre en condicions ambientals desfavorables, gràcies a dinàmiques de font-embornal (Pulliam, 1988). Per últim, el model neutre (Hubbell, 2001) seria la hipòtesi nul·la dels altres tres, i considera que totes les espècies són iguals i que la distribució és deguda a processos de dispersió aleatoris.

No obstant, hem d'interpretar aquestos paradigmes com casos teòrics que ens ajuden a entendre de manera simple com s'estructuren les comunitats, perquè realment s'ajusten poc amb la realitat, on la composició d'espècies depèn d'una combinació de processos que pertanyen a paradigmes diferents (Logue *et al.*, 2011). Recentment, s'han deixat de banda aquestos paradigmes en els estudis empírics i els ecòlegs s'han centrat en el paper que juguen els distints mecanismes estructuradors de les metacomunitats (veure Winegardner *et al.*, 2012).

Mecanismes estructuradors

Els mecanismes estructuradors són aquells processos ecològics que determinen la composició de les comunitats. Els mecanismes més estudiats (però no els únics) són l'ordenació d'espècies i els processos dispersius. L'ordenació d'espècies, com abans hem explicat, és el mecanisme pel qual les condicions ambientals filtren la composició de la comunitat, i com a conseqüència, cada espècie la trobem en aquelles localitats on les condicions ambientals són favorables (Chase & Leibold, 2003; Leibold *et al.*, 2004). No obstant, per a que això passe és necessària una taxa de dispersió relativament moderada, per a que els individus de cada espècie puguen aplegar a cada localitat favorable (Fig. 1).

Els processos dispersius poden modificar l'efecte de l'ordenació d'espècies si la taxa de dispersió és relativament baixa o alta (Fig. 1; Heino *et al.*, 2015a). Amb una taxa de dispersió baixa, els organismes no poden arribar a tots els llocs favorables, el que
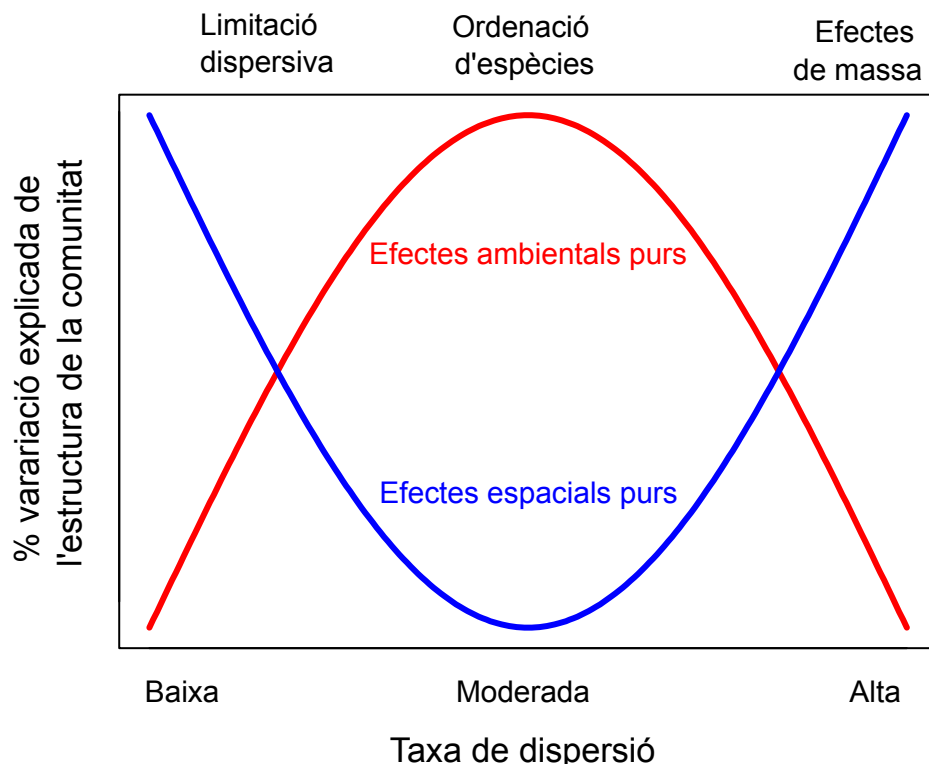
Figura 1. Model hipotètic de la relació entre el percentatge explicat per l'ambient i l'espai i els mecanismes que estructuren les metacomunitats, depenent de la taxa de dispersió en cada metacomunitat (modificat a partir de Heino *et al.*, 2015a).

anomenem limitació dispersiva. En aquest cas no trobaríem algunes espècies en localitats on potencialment es donen les condicions adequades. En l'altre extrem, una taxa de dispersió alta homogeneïtzaria la composició de les comunitats, el procés que ja havíem definit com efectes de massa, emmascarant l'efecte filtrador de les condicions ambientals.

Altres mecanismes, com els efectes prioritaris, podrien ser importants estructuradors de les metacomunitats. Els efectes prioritaris són els efectes relacionats amb els esdeveniments passats en la composició de la comunitat actual (Fukami, 2015). Per exemple, els primers colonitzadors d'un lloc determinat poden limitar o facilitar l'entrada de colonitzadors, modificant l'ambient o monopolitzant tots els recursos disponibles (De Meester *et al.*, 2002). De moment, aquestos efectes s'han tingut poc en compte en ecologia de metacomunitats (però veure Mergeay *et al.*, 2011).

Actualment, els ecòlegs estan interessats en la importància relativa de cada mecanisme. Per exemple, si l'ordenació d'espècies (utilitzant les variables ambientals de cada localitat) explica un major percentatge que els processos dispersius (utilitzant variables espacials) en la variació de la composició d'espècies de cada localitat. Aquesta importància relativa varia depenent del context regional i del grup d'organismes que estudiem.

Els mecanismes depenen del context regional

Segons Heino *et al.*, (2015b), una regió és l'extensió espacial que engloba a totes les localitats visitades en cada estudi. Les característiques principals que definixen cada regió són l'heterogeneïtat ambiental, l'extensió espacial i el tipus de sistema.

L'heterogeneïtat ambiental és la variabilitat ambiental entre un conjunt de localitats dins d'una regió (Anderson, 2006). Una alta heterogeneïtat ambiental proporciona una gran quantitat de nínxols ecològics diferents, provocant un major filtratge ambiental de les espècies (Chase & Leibold, 2003). En les regions amb major heterogeneïtat ambiental pot ser major la influència de l'ordenació d'espècies que en altres amb poca variabilitat ambiental (Heino, 2011). Però aquesta relació no és universal perquè, com ja hem dit, les taxes de dispersió de cada metacomunitat poden modificar l'efecte de l'ordenació d'espècies

(Heino *et al.*, 2015b).

L'extensió espacial és la grandària geogràfica de la regió (Wiens, 1989). Aquest factor pot influenciar als mecanismes estructuradors de dues maneres. En primer lloc, una major extensió espacial pot estar relacionada amb una major heterogeneïtat ambiental (Jackson *et al.*, 2001), perquè augmenten les probabilitats de tindre paisatges diferents dins d'una regió, amb més diversitat geològica i climàtica. Per tant, l'extensió espacial pot tindre un efecte positiu indirecte sobre l'ordenació d'espècies (Heino, 2011). En segon lloc, l'extensió espacial condiciona els processos dispersius (Ng *et al.*, 2009). Grans extensions equivalen a llargues distàncies entre localitats provocant limitació dispersiva (Mykrä *et al.*, 2007; Maloney & Munguia, 2011; Soininen *et al.*, 2011), i xicotetes extensions propicien els efectes de massa, perquè les localitats estan més pròximes (Ng *et al.*, 2009).

Cada tipus de sistema té unes característiques intrínseques que fan que les metacomunitats de cada sistema es comporten de manera diferent. En els sistemes aquàtics el flux d'aigua és el factor principal que condiciona aquestes diferències (Heino *et al.*, 2015a). Nosaltres hem analitzat les metacomunitats de tres sistemes aquàtics diferents, cadascun amb diferents fluxos d'aigua entre localitats: llacunes, basses de roca i rius.

Les llacunes que hem estudiat són cossos d'aigua temporals sense connexió d'aigua entre elles (Alonso, 1998; Williams, 2006). En aquests sistemes aïllats la limitació dispersiva pot dominar sobre l'ordenació d'espècies (De Bie *et al.*, 2012). No obstant, les espècies que habiten sistemes aïllats solen presentar altes capacitats dispersives (Wellborn *et al.*, 1996), cosa què podria reduir la limitació dispersiva i afavorir l'ordenació d'espècies. Per altra banda, els sistemes temporals són molt dinàmics, el que afavoreix que altres mecanismes estructuren les comunitats, com ara els fenòmens estocàstics i els efectes prioritaris (Chase, 2007).

Les basses de roca o cocons són xicotets cossos d'aigua temporals (Brendonck *et al.*, 2010). Nosaltres hem estudiat dos tipus de basses. Unes basses estan connectades per un flux d'aigua efímer entre elles, i les altres no tenen cap connexió aquàtica. Aquestos fluxos faciliten la dispersió dels organismes entre les basses connectades (Hulsmans *et al.*, 2007; Vanschoenwinkel *et al.*, 2008a), afavorint que l'ordenació d'espècies o els efectes de massa estructuren les metacomunitats (Vanschoenwinkel *et al.*, 2007). Sense aquestos

fluxos d'aigua la limitació dispersiva pot dominar sobre l'ordenació d'espècies (De Bie *et al.*, 2012).

El corrent d'aigua dels rius connecta totes les localitats dins d'una mateixa conca (Grant *et al.*, 2007). En els rius, almenys en xicotetes conques, l'ordenació d'espècies sol dominar sobre els efectes espacials (Heino *et al.*, 2012; Landeiro *et al.*, 2012; Grönroos *et al.*, 2013). No obstant, els efectes espacials són importants quan l'estudi es realitza en diferents conques (Astorga *et al.*, 2012), augmentant l'extensió espacial. A més, existixen diferències entre les capçaleres dels rius, aïllades i subjectes a dinàmiques estocàstiques d'extinció i colonització, i les parts baixes dels rius on els efectes de massa poden ser importants (Brown & Swan, 2010). D'altra banda, els rius poden tindre un alt grau de variació temporal i d'impredictibilitat, degut a crescudes i a l'assecament de certs punts, el que provoca fenòmens estocàstics (Miyazono & Taylor, 2013; Datry *et al.*, 2015).

Més enllà d'aquestes diferències regionals, la importància relativa dels diferents mecanismes estructuradors varia en el temps dins d'una mateixa regió (Erős *et al.*, 2012; Göthe *et al.*, 2013; Fernandes *et al.*, 2014). En la pràctica, els estudis s'han dedicat sovint a recollir les espècies i les variables ambientals i espacials d'un conjunt de llocs, però solament en un moment donat (com una instantània fotogràfica), sense tindre en compte la variabilitat temporal de les comunitats. Això podria donar conclusions inconsistents i la pèrdua de certa informació rellevant del funcionament de les metacomunitats. No obstant, els estudis temporals requerixen un major esforç i augmenten els costos d'investigació. En conseqüència, les sèries temporals llargues de dades són molt escasses i valuoses. Tot i això, l'ús de la paleolimnologia podria ser una solució assequible per tractar llargues sèries temporals, i s'ha assenyalat com una eina potent de cara al desenvolupament futur del coneixement de les metacomunitats (Gregory-Eaves & Beisner, 2011).

Els mecanismes depenen del grup d'organismes

Les capacitats dispersives de cada grup d'organismes també determinen la importància relativa de cada mecanisme estructurador. Els ecòlegs han estudiat aquestes diferències agrupant les espècies de tres maneres: per distàncies dispersives esperades (Thompson & Townsend, 2006; Astorga *et al.*, 2012), per grups taxonòmics (Bonada *et al.*,

2012; De Bie *et al.*, 2012; Heino *et al.*, 2012) o per modes de dispersió (Vanschoenwinkel *et al.*, 2007; Schulz *et al.*, 2012; Grönroos *et al.*, 2013).

En general, la importància de cada mecanisme depèn del mode dispersió i de la grandària de l'organisme (De Bie *et al.*, 2012). Els organismes amb dispersió passiva aprofiten vectors que els transporten d'una localitat a una altra, com els corrents d'aigua (Vanschoenwinkel *et al.*, 2008a), el vent (Vanschoenwinkel *et al.*, 2008b) i altres animals (Brochet *et al.*, 2010), mentre què els organismes amb dispersió activa poden moure's entre localitats per ells mateixos. En principi, l'espai hauria d'afectar més als organismes amb dispersió passiva i l'ordenació d'espècies als organismes amb dispersió activa, ja que esperem que aquestos últims tinguen més capacitat de buscar localitats amb condicions ambientals favorables, i evitar les no favorables (Resetarits, 2001). No obstant, l'ordenació d'espècies també pot dominar en organismes de dispersió passiva de grandària molt reduïda, com els bacteris (Van der Gucht *et al.*, 2007). Aquest fet és degut a que els organismes de grandària xicoteta solen presentar-se en altes densitats i tendixen a produir gran quantitat de propàguls afavorint la seua dispersió (Finlay, 2002; Brown *et al.*, 2004; Fenchel & Finlay, 2004).

Les metacomunitats d'ostracodes no-marins

Els ostracodes són uns crustacis xicotets (entre 0.3 i 5 mm; veure Baltanás & Danielopol, 2013) que habiten pràcticament qualsevol sistema aquàtic (Meisch, 2000), encara què a nivell d'espècies la seua distribució i abundància és molt sensible a les condicions ambientals (Mesquita-Joanes *et al.*, 2012). Des d'un punt de vista pràctic, el que fa especials a aquestos crustacis és que són excel·lents organismes model en estudis paleolimnològics, gràcies a les valves de carbonat de calci les quals tenen una gran facilitat de fossilitzar-se (Holmes, 2001).

Molts estudis han tractat la influència de les condicions ambientals sobre les comunitats d'ostracodes no-marins (veure Mezquita *et al.*, 2005). Neale (1964) va suggerir que la salinitat i la temperatura eren els factors més importants que determinen la distribució d'ostracodes. Estudis posteriors han recolzat la importància de la salinitat (De Deckker, 1981; Aladin, 1993; Reed *et al.*, 2012), encara què la composició iònica de cada

localitat -enlloc de la salinitat *per se*- també afecta la composició d'espècies (Carbonel & Peypouquet, 1983; Baltanás *et al.*, 1990; Curry, 1999). Aquestos resultats posen de manifest el paper que juguen els mecanismes de regulació iònica en la distribució dels ostracodes, especialment en el procés de calcificació de les valves. Per altra banda, molts autors han observat que la temperatura determina la distribució biogeogràfica dels ostracodes (Horne & Mezquita, 2008; Poquet & Mesquita-Joanes, 2011; Curry *et al.*, 2012), degut al seu efecte sobre el cicle vital, el creixement i la grandària final dels ostracodes adults (Cohen & Morin, 1990; Aguilar-Alberola & Mesquita-Joanes, 2014). A banda de la salinitat i la temperatura, altres factors ambientals poden afectar la distribució d'ostracodes no marins, com la temporalitat del cos d'aigua, el pH, la concentració d'oxigen, la concentració d'elements tòxics, la velocitat del corrent d'aigua o el tipus de substrat (Delorme, 1969; Mezquita *et al.*, 1999a, 1999b; Griffiths & Holmes, 2000).

Alguns estudis han demostrat que els ostracodes són transportats entre distintes localitats (bé com a individus juvenils i adults, o bé com a ous) per una gran quantitat de vectors com ara el vent (Vanschoenwinkel *et al.*, 2008b), les aus (Brochet *et al.*, 2010), o inclús els ecòlegs amb el fang de les seues botes (Valls *et al.*, 2016). Pocs estudis sobre comunitats d'ostracodes han considerat els efectes espacials sobre les comunitats d'ostracodes. Zhai *et al.* (2015) van determinar que tant els efectes ambientals com els espacials afectaven l'estructura de les comunitats d'ostracodes en fonts dels Carpats (centre d'Europa). Aquestos resultats són semblants als obtinguts en capçaleres de rius de la Península Ibèrica (Escrivà *et al.* 2015) i en diferent cossos d'aigua de la comarca del Baix Maestrat (est de la Península Ibèrica; Escrivà 2015). Aquestos anàlisis s'han realitzat també utilitzant restes de valves d'ostracodes en sediments superficials en l'illa de San Salvador (Bahames), encara què en aquest cas els efectes espacials no foren significatius (Michelson, 2012). Aquestos estudis ens indiquen que els efectes espacials també poden ser importants en l'estructuració de les comunitats d'ostracodes, els quals es dispersen de manera passiva.

Zhai *et al.* (2015) van suggerir que les raons per les quals no s'havien analitzat els efectes espacials sobre les comunitats d'ostracodes eren, per una banda l'ús de variables ambientals geogràfiques correlacionades amb l'espai -per exemple dades climàtiques-, i per

altra l'abundant presència d'espècies cosmopolites sense limitacions dispersives esperades. A més d'això, però, hem de tenir en compte que el desenvolupament de mètodes de càlcul potents i accessibles per treballar amb variables espacials és relativament recent (Dray *et al.*, 2006; Blanchet *et al.*, 2008), i és molt probable que en els propers anys els estudis sobre comunitats d'ostracodes tinguen en compte amb més freqüència els efectes espacials.

Objectius

L'objectiu general d'aquesta tesi és analitzar el paper que juguen els mecanismes estructuradors en diferents metacomunitats d'invertebrats aquàtics, centrant-se en els ostracodes, situades en diferents contextos regionals. Els objectius específics d'aquesta tesi són:

1. Determinar la importància relativa de l'ambient i l'espai en l'estructura de les comunitats d'ostracodes en llacunes temporals.

2. Comparar els efectes dels mecanismes estructuradors de basses de roca temporals en dos contextos de característiques espacials diferents, i entre organismes amb dispersió activa i passiva.

3. Determinar la importància relativa dels efectes espacials i ambientals que determinen l'estructura de les comunitats d'ostracodes en rius mediterranis.

4. Analitzar els patrons temporals de l'estructura de les comunitats d'ostracodes en llacunes temporals al llarg d'un cicle hidrològic, i quins són els trets ambientals i espacials que més hi afecten.

5. Comparar la biocenosi (comunitat viva) i la tafocenosi (subfòssils) dels ostracodes de llacunes somes, fent referència a la relació que té cada assemblatge amb les components ambientals i espacials, per tal de poder avaluar la possible influència dels efectes prioritaris.

Estructura de la tesi

La present tesi està estructurada en una introducció general, seguida de cinc

capítols, que corresponen a cinc articles acadèmics, i una discussió general. Els articles científics han sigut prèviament acceptats o estan pendents d'acceptació (en revisió).

En el **Capítol 1**, vam analitzar els efectes de l'ordenació d'espècies i del processos dispersius sobre la metacomunitat d'ostracodes de les llacunes temporals de la Reserva de la Biosfera de La Mancha Húmeda. En el **Capítol 2**, vam tractar amb un enfocament semblant unes basses de roca temporals situades en el terme municipal de Rafelguaraf (València). Aquestes basses les subdividirem en dos sectors. En el primer sector existix un barranc pel que pot discórrer un corrent d'aigua efímera que connecta les basses de manera temporal. En el segon sector no existix cap connexió d'aquest tipus. En aquest capítol, a banda de determinar els mecanismes estructuradors en aquestos contextos, també analitzarem les diferències entre animals aquàtics amb dispersió activa i passiva. En el **Capítol 3**, vam canviar de nou de sistema aquàtic, i ens vam centrar en els ostracodes d'un conjunt de rius mediterranis: el Millars, el Palància i la Rambla de Veo. En aquest cas, vam comparar el paper de dues vies de dispersió, la dispersió a través del corrent d'aigua, i la dispersió per fora del corrent d'aigua (a través del vent o mitjançant altre animals). En els capítols 4 i 5, tornarem a les llacunes de La Mancha. En el **Capítol 4**, vam estudiar com varia la importància relativa dels mecanismes estructuradors de la comunitat d'ostracodes al llarg del temps, mitjançant mostrejos periòdics al llarga d'un cicle hidrològic. En el **Capítol 5**, vam comparar la composició d'espècies d'ostracodes en la biocenosi (comunitat viva) i en la tafocenosi (subfòssils) de les llacunes, fent referència a la relació que té cada assemblatge amb les components ambientals i espacials, i la possible influència de les contingències històriques de colonització de les llacunes.

A la discussió general tractarem de fer una anàlisi conjunta dels resultats dels cinc capítols anteriors, comparant els diferents estudis, i suggerirem futures investigacions en el camp de les metacomunitats.

Els articles presentats són els que es mostren a continuació:

1. **Castillo-Escrivà, A.,** L. Valls, C. Rochera, A. Camacho, & F. Mesquita-Joanes, 2016. Spatial and environmental analysis of an ostracod metacommunity from endorheic lakes. *Aquatic Sciences* 78: 707–716. DOI: 10.1007/s00027-015-0462-z

2. **Castillo-Escrivà, A.,** J. A. Aguilar-Alberola, & F. Mesquita-Joanes, (en revisió). Spatial and environmental effects on a rock pool metacommunity depend on landscape setting and dispersal mode. *Freshwater Biology*

3. **Castillo-Escrivà, A.,** J. Rueda, L. Zamora, R. Hernández, M. del Moral, & F. Mesquita-Joanes, 2016. The role of watercourse versus overland dispersal and niche effects on ostracod distribution in Mediterranean streams (eastern Iberian Peninsula). *Acta Oecologica* 73:1–9. DOI: 10.1016/j.actao.2016.02.001

4. **Castillo-Escrivà, A.,** L. Valls, C. Rochera, A. Camacho, & F. Mesquita-Joanes, (en revisió). Metacommunity dynamics of Ostracoda in temporary lakes: overall strong niche effects except at the onset of the flooding period. *Limnologica*

5. **Castillo-Escrivà, A.,** L. Valls, C. Rochera, A. Camacho, & F. Mesquita-Joanes, (en premsa). Disentangling environmental, spatial, and historical effects on ostracod communities in shallow lakes. *Hydrobiologia.* DOI:10.1007/s10750-016-2945-x

Referències

Aguilar-Alberola, J. A., & F. Mesquita-Joanes, 2014. Breaking the temperature-size rule: thermal effects on growth, development and fecundity of a crustacean from temporary waters. *Journal of Thermal Biology* 42: 15–24.

Aladin, N. V., 1993. Salinity tolerance, morphology and physiology of the osmoregulatory organ in Ostracoda with special reference to Ostracoda from the Aral Sea. In: Mc Kenzie, K. J., & P. J. Jones (eds), *Ostracoda in the Earth and Life Sciences,* A. A. Balkema, Rotterdam: 387–403.

Alonso, M., 1998. Las lagunas de la España peninsular. *Limnetica* 15: 1–176.

Anderson, M. J., 2006. Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* 62: 245–253.

Astorga, A., J. Oksanen, M. Luoto, J. Soininen, R. Virtanen, & T. Muotka, 2012. Distance decay of similarity in freshwater communities: do macro- and microorganisms follow the same rules? *Global Ecology and Biogeography* 21: 365–375.

Baltanás, A., & D. L. Danielopol, 2013. Body-size distribution and biogeographical patterns in non-marine ostracods (Crustacea: Ostracoda). *Biological Journal of the Linnean Society* 109: 409–423.

Baltanás, A., C. Montes, & P. Martino, 1990. Distribution patterns of ostracods in Iberian saline lakes. Influence of ecological factors. *Hydrobiologia* 197: 207–220.

Blanchet, F. G., P. Legendre, & D. Borcard, 2008. Modelling directional spatial processes in ecological data. *Ecological Modelling* 215: 325–336.

Referències

Bonada, N., S. Dolédec, & B. Statzner, 2012. Spatial autocorrelation patterns of stream invertebrates: exogenous and endogenous factors. *Journal of Biogeography* 39: 56–68.

Brendonck, L., M. Jocque, A. Hulsmans, & B. Vanschoenwinkel, 2010. Pools "on the rocks": freshwater rock pools as model system in ecological and evolutionary research. *Limnetica* 29: 25–40.

Brochet, A. L., M. Gauthier-Clerc, M. Guillemain, H. Fritz, A. Waterkeyn, Á. Baltanás, & A. J. Green, 2010. Field evidence of dispersal of branchiopods, ostracods and bryozoans by teal (*Anas crecca*) in the Camargue (southern France). *Hydrobiologia* 637: 255–261.

Brown, B. L., & C. M. Swan, 2010. Dendritic network structure constrains metacommunity properties in riverine ecosystems. *Journal of Animal Ecology* 79: 571–580.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, & G. B. West, 2004. Toward a metabolic theory of ecology. *Ecology* 85: 1771–1789.

Brown, J. H., & A. Kodric-Brown, 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58: 445–449.

Carbonel, P., & J. P. Peypouquet, 1983. Ostracoda as indicators of ionic concentrations and dynamic variations: methodology (Lake Bogoria, Kenya). In: Maddoks, R. F. (ed), *Applications of Ostracoda,* Proc. 8th Int. Symp. Ostr. University of Houston, Houston: 264–276.

Chase, J. M., 2007. Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences* 104: 17430–17434.

Chase, J. M., & M. A. Leibold, 2003. *Ecological Niches: Linking Classical and Contemporary approaches*. University of Chicago Press, Chicago.

Cohen, A. C., & J. G. Morin, 1990. Patterns of reproduction in ostracodes: a review. *Journal of Crustacean Biology* 10: 184–211.

Cottenie, K., 2005. Integrating environmental and spatial processes in ecological community dynamics. *Ecology Letters* 8: 1175–1182.

Curry, B. B., 1999. An environmental tolerance index for ostracodes as indicators of physical and chemical factors in aquatic habitats. *Palaeogeography, Palaeoclimatology, Palaeoecology* 148: 51–63.

Curry, B. B., L. D. Delorme, A. J. Smith, D. F. Palmer, & B. J. Stiff, 2012. The biogeography and physicochemical characteristics of aquatic habitats of freshwater ostracods in Canada and the United States. In: Horne, D., J. A. Holmes, J. Rodríguez-Lázaro, & F. A. Viehberg (eds), *Ostracoda as Proxies for Quaternary Climate Change.* Elsevier, Amsterdam: 85–115.

Datry, T., N. Bonada, & J. Heino, 2015. Towards understanding the organisation of metacommunities in highly dynamic ecological systems. *Oikos* 125: 149–159.

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

De Deckker, P., 1981. Ostracods of athalassic saline lakes. *Hydrobiologia* 81: 131–144.

Delorme, L. D., 1969. Ostracodes as quaternary paleoecological indicators. *Canadian Journal of Earth Sciences* 6: 1471–1475.

De Meester, L., A. Gómez, B. Okamura, & K. Schwenk, 2002. The Monopolization Hypothesis and the

dispersal–gene flow paradox in aquatic organisms. *Acta Oecologica* 23: 121–135.

Dray, S., P. Legendre, & P. R. Peres-Neto, 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecological Modelling* 196: 483–493.

Dray, S., R. Pélissier, P. Couteron, M.-J. Fortin, P. Legendre, P. R. Peres-Neto, E. Bellier, R. Bivand, F. G. Blanchet, M. De Cáceres, A. B. Dufour, E. Heegaard, T. Jombart, F. Munoz, J. Oksanen, J. Thioulouse, & H. H. Wagner, 2012. Community ecology in the age of multivariate multiscale spatial analysis. *Ecological Monographs* 82: 257–275.

Erős, T., P. Sály, P. Takács, A. Specziár, & P. Bíró, 2012. Temporal variability in the spatial and environmental determinants of functional metacommunity organization – stream fish in a human-modified landscape. *Freshwater Biology* 57: 1914–1928.

Escrivà, A., 2015. *Ecologia de Comunitats d´Invertebrats Aquàtics de la Península Ibèrica, amb Especial Rellevància als Ostracoda*. Tesi Doctoral, Universitat de València, València.

Escrivà, A., J. M. Poquet, & F. Mesquita-Joanes, 2015. Effects of environmental and spatial variables on lotic ostracod metacommunity structure in the Iberian Peninsula. *Inland Waters* 5: 283–294.

Fenchel, T., & B. J. Finlay, 2004. The ubiquity of small species: patterns of local and global diversity. *BioScience* 54: 777–784.

Fernandes, I. M., R. Henriques-Silva, J. Penha, J. Zuanon, & P. R. Peres-Neto, 2014. Spatiotemporal dynamics in a seasonal metacommunity structure is predictable: the case of floodplain-fish communities. *Ecography* 37: 464–475.

Finlay, B. J., 2002. Global dispersal of free-living microbial eukaryote species. *Science* 296: 1061–1063.

Fukami, T., 2015. Historical contingency in community assembly: integrating niches, species pools, and priority effects. *Annual Review of Ecology, Evolution, and Systematics* 46: 1–23.

Göthe, E., D. G. Angeler, & L. Sandin, 2013. Metacommunity structure in a small boreal stream network. *Journal of Animal Ecology* 82: 449–458.

Grant, E. H. C., W. H. Lowe, & W. F. Fagan, 2007. Living in the branches: population dynamics and ecological processes in dendritic networks. *Ecology Letters* 10: 165–175.

Gregory-Eaves, I., & B. E. Beisner, 2011. Palaeolimnological insights for biodiversity science: an emerging field. *Freshwater Biology* 56: 2653–2661.

Griffiths, H. I., & J. A. Holmes, 2000. *Non-marine Ostracods and Quaternary Palaeoenvironments*. QRA Technical Guide.

Grönroos, M., J. Heino, T. Siqueira, V. L. Landeiro, J. Kotanen, & L. M. Bini, 2013. Metacommunity structuring in stream networks: roles of dispersal mode, distance type, and regional environmental context. *Ecology and Evolution* 3: 4473–4487.

Hanski, I., & M. Gilpin, 1991. Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society* 42: 3–16.

Heino, J., 2011. A macroecological perspective of diversity patterns in the freshwater realm. *Freshwater Biology* 56: 1703–1722.

Heino, J., M. Grönroos, J. Soininen, R. Virtanen, & T. Muotka, 2012. Context dependency and metacommunity structuring in boreal headwater streams. *Oikos* 121: 537–544.

Heino, J., A. S. Melo, & L. M. Bini, 2015b. Reconceptualising the beta diversity-environmental heterogeneity relationship in running water systems. *Freshwater Biology* 60: 223–235.

Heino, J., A. S. Melo, T. Siqueira, J. Soininen, S. Valanko, & L. M. Bini, 2015a. Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. *Freshwater Biology* 60: 845–869.

Holmes, J. A., 2001. Ostracoda. In: Smol, J. P., H. J. B. Birks, & W. M. Last (eds), *Tracking Environmental Change Using Lake Sediments*. Kluwer Academic Publishers, Dordrecht: 125–151.

Holyoak, M., M. A. Leibold, N. Mouquet, R. D. Holt, & M. F. Hoopes, 2005. A framework for large-scale community ecology. In: Holyoak, M., M. A. Leibold, & R. D. Holt (eds), *Metacommunities: Spatial Dynamics and Ecological Communities*. University of Chicago Press, Chicago: 1–31.

Horne, D. J., & F. Mezquita, 2008. Palaeoclimatic applications of large databases: developing and testing methods of palaeotemperature reconstruction using nonmarine ostracods. *Senckenbergiana Lethaea* 88: 93–112.

Hubbell, S. P., 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press.

Hulsmans, A., K. Moreau, L. De Meester, B. J. Riddoch, & L. Brendonck, 2007. Direct and indirect measures of dispersal in the fairy shrimp *Branchipodopsis wolfi* indicate a small scale isolation-by-distance pattern. *Limnology and Oceanography* 52: 676–684.

Jackson, D. A., P. R. Peres-Neto, & J. D. Olden, 2001. What controls who is where in freshwater fish communities - the roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 157–170.

Landeiro, V. L., L. M. Bini, A. S. Melo, A. M. O. Pes, & W. E. Magnusson, 2012. The roles of dispersal limitation and environmental conditions in controlling caddisfly (Trichoptera) assemblages. *Freshwater Biology* 57: 1554–1564.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, & A. Gonzalez, 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7: 601–613.

Levin, S. A., 1992. The problem of pattern and scale in ecology. *Ecology* 73: 1943–1967.

Logue, J. B., N. Mouquet, H. Peter, & H. Hillebrand, 2011. Empirical approaches to metacommunities: a review and comparison with theory. *Trends in Ecology & Evolution* 26: 482–491.

MacArthur, R. H., & E. O. Wilson, 1967. *The Theory of Island Biogeography*. Princeton University Press.

Maloney, K. O., & P. Munguia, 2011. Distance decay of similarity in temperate aquatic communities: effects of environmental transition zones, distance measure, and life histories. *Ecography* 34: 287–295.

May, R. M., 1973. *Stability and Complexity in Model Ecosystems*. Princeton University Press.

McCann, K., A. Hastings, & G. R. Huxel, 1998. Weak trophic interactions and the balance of nature. *Nature* 395: 794–798.

Meisch, C., 2000. *Freshwater Ostracoda of Western and Central Europe*. Spektrum Akademischer

Verlag.

Mergeay, J., L. De Meester, H. Eggermont, & D. Verschuren, 2011. Priority effects and species sorting in a long paleoecological record of repeated community assembly through time. *Ecology* 92: 2267–2275.

Mesquita-Joanes, F., A. J. Smith, & F. A. Viehberg, 2012. The ecology of Ostracoda across levels of biological organisation from individual to ecosystem: a review of recent developments and future potential. In: Horne, D., J. A. Holmes, J. Rodríguez-Lázaro, & F. A. Viehberg (eds), *Ostracoda as Proxies for Quaternary Climate Change.* Elsevier, Amsterdam: 15–35.

Mezquita, F., H. I. Griffiths, S. Sanz, J. M. Soria, & A. Piñón, 1999a. Ecology and distribution of ostracods associated with flowing waters in the Eastern Iberian Peninsula. *Journal of Crustacean Biology* 19: 344–354.

Mezquita, F., R. Hernández, & J. Rueda, 1999b. Ecology and distribution of ostracods in a polluted Mediterranean river. *Palaeogeography, Palaeoclimatology, Palaeoecology* 148: 87–103.

Mezquita, F., J. R. Roca, J. M. Reed, & G. Wansard, 2005. Quantifying species–environment relationships in non-marine Ostracoda for ecological and palaeoecological studies: examples using Iberian data. *Palaeogeography, Palaeoclimatology, Palaeoecology* 225: 93–117.

Michelson, A. V., 2012. *Ecological, Taphonomic, and Paleoecological Dynamics of an Ostracode Metacommunity*. Tesi Doctoral, University of Akron, Akron.

Miyazono, S., & C. M. Taylor, 2013. Effects of habitat size and isolation on species immigration–extinction dynamics and community nestedness in a desert river system. *Freshwater Biology* 58: 1303–1312.

Mykrä, H., J. Heino, & T. Muotka, 2007. Scale-related patterns in the spatial and environmental components of stream macroinvertebrate assemblage variation. *Global Ecology and Biogeography* 16: 149–159.

Neale, J. W., 1964. Some factors influencing the distribution of recent British Ostracoda. *Pubblicazioni della Stazione Zoologica di Napoli* 33 (supplement): 247–307.

Ng, I. S. Y., C. M. Carr, & K. Cottenie, 2009. Hierarchical zooplankton metacommunities: distinguishing between high and limiting dispersal mechanisms. *Hydrobiologia* 619: 133–143.

Pimm, S. L., & J. H. Lawton, 1978. On feeding on more than one trophic level. *Nature* 275: 542–544.

Poquet, J. M., & F. Mesquita-Joanes, 2011. Combined effects of local environment and continental biogeography on the distribution of Ostracoda. *Freshwater Biology* 56: 448–469.

Pulliam, H. R., 1988. Sources, sinks, and population regulation. *American Naturalist* 652–661.

Reed, J. M., F. Mesquita-Joanes, & H. I. Griffiths, 2012. Multi-indicator conductivity transfer functions for Quaternary palaeoclimate reconstruction. *Journal of Paleolimnology* 47: 251–275.

Resetarits, W. J., 2001. Colonization under threat of predation: avoidance of fish by an aquatic beetle, *Tropisternus lateralis* (Coleoptera: Hydrophilidae). *Oecologia* 129: 155–160.

Scheiner, S. M., & M. R. Willig. 2011. A general theory of ecology. In: Scheiner, S. M., & M. R. Willig (eds), *The Theory of Ecology*. University of Chicago Press, Chicago: 3–18.

Schulz, G., T. Siqueira, G. Stefan, & F. O. Roque, 2012. Passive and active dispersers respond similarly to environmental and spatial processes: an example from metacommunity dynamics of tree hole invertebrates. *Fundamental and Applied Limnology* 181: 315–326.

Referències

Shmida, A. V. I., & M. V. Wilson, 1985. Biological determinants of species diversity. *Journal of Biogeography* 12: 1–20.

Soininen, J., J. J. Korhonen, J. Karhu, & A. Vetterli, 2011. Disentangling the spatial patterns in community composition of prokaryotic and eukaryotic lake plankton. *Limnology and Oceanography* 56: 508–520.

Thompson, R., & C. Townsend, 2006. A truce with neutral theory: local deterministic factors, species traits and dispersal limitation together determine patterns of diversity in stream invertebrates. *Journal of Animal Ecology* 75: 476–484.

Valls, L., A. Castillo-Escrivà, F. Mesquita-Joanes, & X. Armengol, 2016. Human-mediated dispersal of aquatic invertebrates with waterproof footwear. *Ambio* 45: 99–109.

Van der Gucht, K., K. Cottenie, K. Muylaert, N. Vloemans, S. Cousin, S. Declerck, E. Jeppesen, J. M. Conde-Porcuna, K. Schwenk, G. Zwart, H. Degans, W. Vyverman, & L. D. Meester, 2007. The power of species sorting: Local factors drive bacterial community composition over a wide range of spatial scales. *Proceedings of the National Academy of Sciences* 104: 20404–20409.

Vanschoenwinkel, B., C. De Vries, M. Seaman, & L. Brendonck, 2007. The role of metacommunity processes in shaping invertebrate rock pool communities along a dispersal gradient. *Oikos* 116: 1255–1266.

Vanschoenwinkel, B., S. Gielen, M. Seaman, & L. Brendonck, 2008b. Any way the wind blows - frequent wind dispersal drives species sorting in ephemeral aquatic communities. *Oikos* 117: 125–134.

Vanschoenwinkel, B., S. Gielen, H. Vandewaerde, M. Seaman, & L. Brendonck, 2008a. Relative importance of different dispersal vectors for small aquatic invertebrates in a rock pool metacommunity. *Ecography* 31: 567–577.

Wellborn, G. A., D. K. Skelly, & E. E. Werner, 1996. Mechanisms creating community structure across a freshwater gradient. *Annual Review of Ecology and Systematics* 27: 337–363.

Wiens, J. A., 1989. Spatial scaling in ecology. *Functional Ecology* 3: 385–397.

Williams, D. D., 2006. *The Biology of Temporary Waters*. Oxford University Press, Oxford.

Wilson, D. S., 1992. Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. *Ecology* 1984–2000.

Winegardner, A. K., B. K. Jones, I. S. Y. Ng, T. Siqueira, & K. Cottenie, 2012. The terminology of metacommunity ecology. *Trends in Ecology & Evolution* 27: 253–254.

Zhai, M., O. Nováček, D. Výravský, V. Syrovátka, J. Bojková, & J. Helešic, 2015. Environmental and spatial control of ostracod assemblages in the Western Carpathian spring fens. *Hydrobiologia* 745: 225–239.

Capítol 1

Spatial and environmental analysis of an ostracod metacommunity from endorheic lakes

Nava Grande de Malagón

Aquatic Sciences   CrossMark

RESEARCH ARTICLE

Spatial and environmental analysis of an ostracod metacommunity from endorheic lakes

Andreu Castillo-Escrivà[1] · **Luis Valls**[1] · **Carlos Rochera**[1,2] · **Antonio Camacho**[1] · **Francesc Mesquita-Joanes**[1]

Abstract The metacommunity concept has promoted a new theoretical view of communities that emphasizes their inter-dependence in a multi-scale nature. However, empirical studies testing the proposed mechanisms structuring communities are still scarce. Here we present a multi-scale spatial analysis on the ostracod metacommunity from endorheic lakes in the Central Iberian Peninsula. For this purpose, multivariate ordination, scalograms and variation partitioning analysis were used to identify environmental (i.e. species sorting) and spatial control (i.e. dispersal limitation, mass effects), and their effects on the metacommunity. The results indicate that both species sorting and dispersal processes structure the metacommunity. The main environmental factors contributing to species sorting were salinity and ephemerality. In addition, significant broad-scale spatial components also structure the species assemblages, suggesting ostracod dispersal limitation within the spatial extent considered. Our study confirms the importance of species sorting, but also reveals how dispersal processes play a role in the structure of ostracod metacommunities.

Keywords Species sorting · Dispersal limitation · Passive dispersal · Endorheic lake · Ostracoda

Introduction

The heterogeneous distribution and abundance of species at different locations represent a major concern for ecologists. In this context, community composition has been commonly studied at the local scale, considering sites as isolated systems, with habitat features treated separately for each location (Holyoak et al. 2005). However, other processes operating at regional spatial scales, chiefly dispersal, could also be crucial in determining species assemblages (Levin 1992). The metacommunity concept is based on this multi-scale nature and reveals spatial processes as significant factors to be considered (Wilson 1992). In this framework, empirical studies have mainly focused on disentangling the environmental and spatial mechanisms structuring all sorts of metacommunities (Logue et al. 2011; Heino et al. 2015a).

Many mechanisms structure metacommunities, including species sorting (as local environmental control), dispersal limitation or mass effects (as spatial processes). Species sorting means that environmental conditions filter the local species, which occur at environmentally suitable sites (Leibold et al. 2004). Dispersal can mask species sorting, because low dispersal rates may limit the ability of species to reach all the suitable sites (i.e., dispersal limitation), and high dispersal rates may homogenize the species composition at all the adjacent sites independent of their environmental conditions (i.e., mass effects). Dispersal limitation and mass effects act on different scales (Heino et al. 2015a). Dispersal limitation is relevant at large spatial extents, its effects increasing with geographic distance between sites and the extent of the surveyed area (Verleyen et al. 2009). Contrarily, mass effects play a role at smaller spatial extents (Ng et al. 2009). Furthermore, species

✉ Andreu Castillo-Escrivà
   andreu.castillo@uv.es

1 Cavanilles Institute of Biodiversity and Evolutionary
   Biology, University of Valencia, Catedrático José Beltrán 2,
   46980 Paterna, Spain

2 Regional Centre for Water Studies (CREA), University of
   Castilla-La Mancha, Camilo José Cela s/n,
   13071 Ciudad Real, Spain

Springer

21

Table 1 Lakes sampled and values for the variables selected in RDA

Lake	Code	Conductivity (mS cm^{-1})	LOI$_{550}$ (% DW)	Mean annual rainfall (mm)	Lake surface (ha)
Alcahozo	ALC	25.86	16.93	417	71.60
Almodóvar	ALM	5.99	3.37	497	19.40
Altillo Chica	ATC	29.10	6.16	426	13.79
Altillo Grande	ATR	17.90	8.53	427	20.29
Campo de la Mula	CAM	34.00	8.45	423	29.61
Camino de Villafranca	CAV	23.26	18.49	412	185.00
Caracuel	CRC	0.99	6.04	469	66.70
Camino de Turleque	CTU	5.77	19.36	426	24.33
Grande de Villafranca	GVI	9.00	6.20	418	59.61
Huevero	HUE	3.39	8.00	419	16.17
Larga de Villacañas	LVC	20.70	15.72	420	109.50
Manjavacas	MAN	13.20	10.45	418	152.28
Miguel Esteban	MIG	2.66	18.79	423	55.52
Nava Grande	NGR	1.14	17.70	421	130.05
Pozuelo	POZ	10.02	19.85	430	47.65
Pueblo	PUE	5.20	8.15	416	29.63
Retamar	RET	3.62	9.48	417	51.26
Sánchez Gómez	SGO	10.37	10.33	419	58.46
Salicor	SLC	77.65	2.77	425	60.65
Taray	TAR	1.08	7.37	419	25.21
Tírez	TRZ	37.00	7.18	419	105.89
La Veguilla	VGU	2.63	9.87	412	136.40

sorting may increase with spatial environmental heterogeneity (Heino et al. 2015b).

The role of species sorting and dispersal may also depend on the body size and dispersal mode of the biological group (De Bie et al. 2012). Body size is related to demographic features, such as population size, developmental time and population growth rate (Brown et al. 2004; Jonsson et al. 2005). Small organisms have large populations, and they are more resistant to drift effects and local extinctions (Blackburn and Gaston 1999). They also generate many propagules, therefore increasing the number of potential dispersal events (Fenchel and Finlay 2004). In these cases, it is most likely that dispersal limitation is minimal, and species sorting is most responsible for structuring the metacommunity (Van der Gucht et al. 2007). The relative importance of species sorting and dispersal also depends on the dispersal mode. Passive dispersers need their propagules to be transported by vectors such as animals (Green et al. 2008) or wind (Vanschoenwinkel et al. 2008), and they reduce dispersal limitation by producing high number of propagules, usually associated with high densities and small body size. Contrarily, active dispersers can choose suitable habitats (Resetarits 2001), and be less affected by the problems related to dispersal limitation with big body size (Jenkins et al. 2007; Shurin

et al. 2009). However, for active dispersers dispersal limitation also depends on the mode of locomotion (swimming, flying or terrestrial), the relative barriers and the available connections (Fahrig and Merriam 1994).
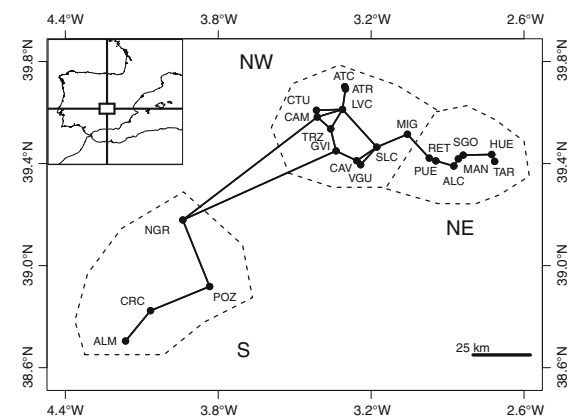

Fig. 1 Map of the study area showing the locations of sampled lakes. Lakes are grouped into three different subregions delimited with a *dashed line* South (S), Northwest (NW) and Northeast (NE). Connection network is plotted as solid lines, following the Gabriel graph criterion. Lake codes as in Table 1

Endorheic lakes, which do not have surface outlets, are interesting ecosystems for testing metacommunity hypotheses because of their hydrological isolation (Löffler 2003). They appear in depressions of the terrain in arid and semiarid regions, when rainfall waters fill the lowest areas of the depression. These water bodies show temporal patterns of flooding and drying out. Their aquatic communities are sometimes simplified but relatively rich in rare taxa, which are usually adapted to temporary waters (Williams 2006) and benefit from the lack of fish predation. Among the dominant invertebrate groups, many microcrustaceans, and Ostracoda in particular, are abundant (e.g., De Deckker 1981; Baltanás et al. 1990; Roca et al. 2000). Ostracods are small bivalved crustaceans, with a body size around 0.5–2.5 mm, and they include many species with passive dispersal strategies and adapted to temporary and often saline waters (Meisch 2000). In the past, researchers have established the relationship of ostracod distribution and abundance to different ranges of environmental variables (e.g., Neale 1964; Forester 1986; Reed et al. 2012) with special focus on reconstructing palaeoenvironments (Holmes 2001). According to these previous works, ostracod species are strongly influenced by environmental factors. Here we present an analysis of ostracods from endorheic lakes in the Central Iberian Peninsula, using both environmental and spatial components to explain their metacommunity structure.

Our aim was to identify the main structuring mechanisms related to both environment and space on lacustrine ostracod metacommunities. We expect that species sorting will be the main mechanism structuring the ostracod metacommunity, due to the sensitivity of these organisms to environmental conditions (Mesquita-Joanes et al. 2012). However, we also envisage that dispersal processes might also affect the local species assemblages, if dispersal rates counteract species sorting, by means of dispersal processes in the regional spatial extent of the study.

Materials and methods

Our focus ecosystems are shallow endorheic lakes from the Biosphere Reserve of La Mancha Húmeda. These lakes have surface areas ranging between 13 and 185 ha, and an average depth less than one meter. This region is considered the main steppic wetland system of Western Europe (Alonso 1998) with a high physiographical and ecological diversity. The lakes surveyed are located on the plains of Castilla-La Mancha (Central Iberian Peninsula; 38.6°–39.8°N, 4.4°–2.6°W; Camacho et al. 2003), organized in three subregions (Fig. 1): South (the region of Campo de Calatrava), Northwest (an area situated between Southeastern Toledo province and Northeastern Ciudad Real

province), and Northeast (the area around Mota del Cuervo). Most of these lakes are temporary isolated systems, characterized by an irregular hydrological regime modified at different intensities by human activities such as water extraction and sewage spills. Ostracods from some of these lakes were previously surveyed by Armengol et al. (1975), Baltanás et al. (1990), Roca et al. (2000) and Schmit et al. (2013).

Sampling was carried out in 22 shallow lakes in May 2013 (Table 1). Ostracods were collected with hand-nets (250 μm mesh) swept over an approximate area of 2 m^2 per lake. Samples were fixed in the field with 4 % formaldehyde. In the laboratory, ostracod species were determined and counted with a stereomicroscope following Meisch (2000) and Baltanás (2001).

We thoroughly characterized the environment of each lake. Conductivity and pH were measured in the field. Surface sediment samples were collected to determine both organic matter and carbonate content by the loss on ignition method (LOI$_{550}$ and LOI$_{950}$ respectively; Heiri et al. 2001). In addition, geographical variables were measured using Quantum GIS version 1.7.5 (QGIS Development Team 2014). Lake surface was determined using images from the web map service interface of the Spanish National Plan of Aerial Orthophotos (PNOA; http://pnoa.ign.es/). Altitude, mean annual rainfall, mean air temperature and annual range of air temperatures were obtained from the WorldClim database version 4.1 (Hijmans et al. 2005). The proportion of surface area dominated by siliceous, carbonate, evaporite and volcanic rocks surrounding the lake (500 m buffer), was extracted from 1:50,000 geological continuum cartography (GEODE). Hydroperiod ephemerality index values were estimated from previous visits: 1 (Permanent, always with water), 2 (Temporary, dried in every summer) and 3 (Ephemeral, filled only for a few months each year).

We carried out a standardized principal components analysis (PCA) to visualize the variation in environmental variables across lakes. We log-transformed conductivity, surface area, mean annual rainfall, mean and range of annual air temperature, and arcsin-transformed LOI$_{550}$ and the proportions of evaporite and volcanic rocks prior to statistical analyses to achieve normality.

Statistical analyses were performed with the matrix of ostracod species abundance for the 22 lakes plus the environmental data matrix for the same sites. First, the species table was transformed with the Hellinger method (Legendre and Gallagher 2001). We then performed a redundancy analysis (RDA) to identify the main structures constrained by the environmental variables, and partial residual analyses (PRA) to check for community structures neglected by environmental variables (which are the residual axes of the same RDA). In RDA, we selected

Table 2 Ostracod species found in the studied lakes from Castilla-La Mancha (Spain)

Species	Code	Lake
Limnocythere inopinata (Baird 1843)	LIN	ALM
Pseudocandona albicans (Brady 1864)	PAL	TAR
Ilyocypris gibba (Ramdohr 1808)	IGI	ALM GVI HUE MAN MIG POZ TAR
Cypris bispinosa Lucas 1849	CBI	CRC NGR
Eucypris virens (Jurine 1820)	EVI	HUE MIG NGR POZ PUE RET TAR VGU
Candelacypris aragonica (Brehm and Margalef 1948)	CAR	ATC SLC
Trajancypris clavata (Baird 1838)	TCL	VGU
Herpetocypris chevreuxi (Sars 1896)	HCH	CRC NGR
Candonocypris novaezelandiae (Baird 1843)	CNO	TAR VGU
Heterocypris incongruens (Ramdohr 1808)	HIN	MAN MIG POZ PUE RET TAR VGU
Heterocypris rotundata (Bronshtein 1928)	HRO	HUE
Heterocypris barbara (Gauthier and Brehm 1928)	HBA	ALC ATC ATR CAM CAV CTU LVC MAN POZ SGO TRZ
Heterocypris salina (Brady 1868)	HSA	CAV MIG POZ PUE
Cypridopsis hartwigi G. W. Müller 1900	CHA	NGR
Plesiocypridopsis newtoni (Brady and Robertson 1870)	PNE	MIG
Sarscypridopsis aculeata (Costa 1847)	SAC	MAN NGR RET VGU
Sarscypridopsis sp.	SAR	ALM CAV VGU
Potamocypris arcuata (Sars 1903)	PAR	MAN MIG VGU

Lake codes as in Table 1

environmental variables with a forward selection procedure. In this selection, we applied a two stopping criteria (Blanchet et al. 2008)—(1) the variance explained by each variable selected had to be significant ($p < 0.05$), and (2) the procedure stops when the adjusted R^2 accumulated by the variables selected exceeds adjusted R^2 of all the explanatory variables considered.

The spatial factors were calculated from site coordinates with Moran Eigenvector Maps (MEMs; Dray et al. 2006). For this purpose, a connection network was built following the Gabriel graph criterion (Dray et al. 2012; Legendre and Legendre 2012). For RDA and PRA, scalograms were used to project the correlation between the site scores of the two first axes of the different ordinations, with the spatial variables (all the 21 MEMs), which represent different spatial scales, from the broadest (MEM1) to the finest scale (MEM21), gradually (Dray et al. 2006, 2012). We avoided aliasing effects presenting a smoothed version with 7 spatial components grouping 3 by 3 successive MEMs. Without spatial structure, the individual R^2 values for each scale group are expected to be equal. In order to test if the highest calculated R^2 is significantly larger than values observed without spatial structure, we used a permutation procedure, with 999 permutations.

Finally, we computed variation partitioning (Borcard et al. 1992; Peres-Neto et al. 2006) of the species table using the environmental, broad-scale and fine-scale variables. As in environmental variables, a forward selection procedure was applied to MEMs. Then, the selected
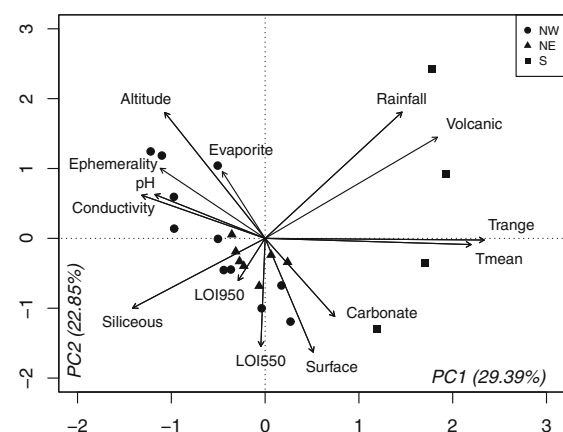
Fig. 2 Ordination plot for the first two axes of a PCA on environmental variables. Points, triangles and squares correspond to lakes from Northwest (NW), Northeast (NE) and South (S) regions respectively. *Tmean* mean annual air temperature, *Trange* annual range of air temperature

MEM components were separated in both broad- and fine-scale space taking into account their associated eigenvalues (positive eigenvalues belong to broad-scale and negative eigenvalues to fine-scale space; Dray et al. 2006).

All analyses were performed with R version 3.0.2 (R Core Team 2013). The R packages spdep (Bivand 2015) and spacemakeR (Dray 2013) were used to obtain MEMs. Multivariate analyses and variation partitioning were

performed with vegan (Oksanen et al. 2015), and packfor was used for the forward selection procedure (Dray et al. 2013). Plots with the scores of the ordination axes represented over a map were obtained with ade4 (Dray and Dufour 2007), and the scalograms were obtained with the scripts from Dray et al. (2012).

Results

We found a total of 18 ostracod species in the 22 sampled lakes (Table 2). Richness ranged from 1 to 7 species per lake, with an average of 2.77 ± 1.93. The most common

Fig. 3 Ordination plot of the first two axes of RDA constrained by the selected environmental variables. Species codes as in Table 2

ostracod was *Heterocypris barbara* (found in 11 lakes), followed by *Eucypris virens* (8 lakes), *Heterocypris incongruens* (7 lakes) and *Ilyocypris gibba* (7 lakes). *Heterocypris barbara* was abundantly collected forming monospecific associations in lakes with high water electrical conductivity values (>9 mS cm^{-1}). *Sarscypridopsis* sp. was previously identified in the Iberian Peninsula by Mezquita et al. (1999) as *Sarscypridopsis* cf. *aculeata*, but it is probably an undescribed *Sarscypridopsis* species, with morphological similarities to the individuals of *Sarscypridopsis* sp. found in Madeira by Fuhrmann and Goth (2011) (Fuhrmann, April 2014, pers. comm.).

A large fraction (52 %) of the environmental variability found in the studied lakes was explained by the first two PCA axes (Fig. 2). PCA-axis 1 was related to climate and related variables, and separated the southern from the northern lakes. The climate in the southern area was warmer and wetter than the northern one, with rainfall being negatively related to lake ephemerality. The first axis suggests therefore a co-variation between environmental and broad-scale spatial variables. PCA-axis 2 was related to geological and sediment-related factors (LOI$_{550}$). This axis separated lakes with a high proportion of carbonate rocks from those with evaporite rocks. The combination of evaporite rocks and dry conditions was related to high water conductivity values, with the northern lakes being more saline than southern ones.

The forward selection procedure for environmental RDA chose electrical conductivity, LOI$_{550}$, mean annual rainfall and lake surface area (Table 3, "Appendix 1"). The selected variables explained 29.81 % (adjusted R^2; $p = 0.001$) of the species variation, but conductivity alone
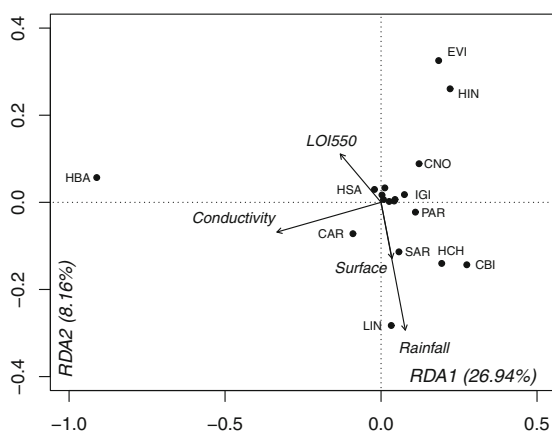
Fig. 4 Maps of the study area showing scores of each site for the environment RDA axis 1 and 2 (**a**, **b**) and PRA axis 1 and 2 (**c**, **d**). *Black circles* indicate positive values and *white circles* negative values of the scores. The size of the circles depends on the absolute value of the score. For each axis, a smoothed scalogram (21 MEMs are split in seven groups) indicates the portion of variance (R^2) explained by each MEM group. The highest R^2 is highlighted in *dark gray*, and *p* values are given. The 95 % confidence limits are also shown by a *pointed line*
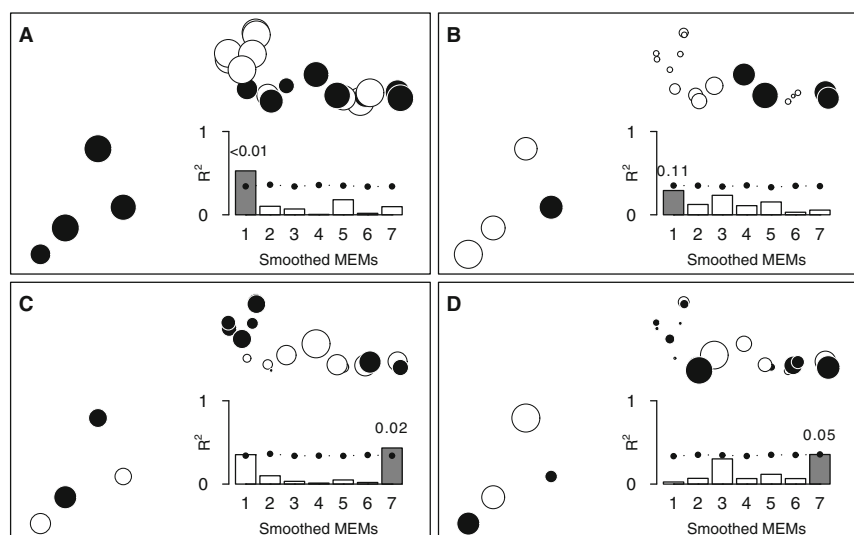
represents half of this percentage (*adjusted R^2 = 0.162; p* = 0.002). RDA-axis 1 (Fig. 3) related *H. barbara* and *Candelacypris aragonica* to high conductivity values, and separated these species from others. The second axis separated *E. virens* and *H. incongruens* from *Cypris bispinosa* and *Herpetocypris chevreuxi*, the latest related positively to rainfall and lake surface area, but negatively to LOI_{550}.

Figure 4 shows the site scores for the first two axes of the previously computed RDA and PRA over a map, and their associated scalograms. In the first axis (Fig. 4a), all the southern lakes had positive scores (black circles), associated with low conductivity values, whereas the most northern lakes showed negative scores (white circles). The scalogram of this first axis (R^2_{max} = 0.53; *p* = 0.004) shows broad-scale spatial effects. However, we did not observe broad-scale spatial differences in the scores of RDA-axis 2 (Fig. 4b), and its correlation with MEMs was not significant (R^2_{max} = 0.29; *p* = 0.109). In contrast, PRA-axis 1 (R^2_{max} = 0.43; *p* = 0.016) and PRA-axis 2 (R^2_{max} = 0.35; *p* = 0.046) present a significant accumulation of explained variance in the fine-scale components (Fig. 4c, d).

The forward selection procedure chose three broad-scale spatial predictors (MEMs 2, 6, 7) and one fine-scale spatial predictor (MEM 20; Table 4, "Appendix 1"). All the selected MEMs explained together a significant fraction of the species variation (*adjusted R^2* = 0.29; *p* = 0.001). Variation partitioning analysis (Fig. 5) identified a significant pure environmental fraction (*adjusted R^2* = 0.17; *p* = 0.001), a significant pure broad-scale spatial fraction (*adjusted R^2* = 0.09; *p* = 0.014) and a significant pure fraction of fine-scale spatial fraction (*adjusted R^2* = 0.09; *p* = 0.003). In addition, the fraction corresponding to the

Fig. 5 Venn diagram of the variation partitioning analysis between environment (E), broad-scale (BS) and fine-scale (FS) MEMs. Adjusted R^2 is shown. Values <0 not shown

interaction between environmental and broad-scale spatial components presented an adjusted R^2 = 0.17. The most inclusive model, with environmental and spatial components, explained 47 % of the variation among communities.

Discussion

Our results indicated that both environment and space affected the ostracod assemblages. Environmental control, as species sorting, was the main structuring mechanism, an expected finding in these organisms traditionally used as paleoenvironmental indicators (Mesquita-Joanes et al. 2012). However, spatial factors also played a role in this metacommunity, as other studies have previously observed in ostracods (Zhai et al. 2014; Escrivà et al. 2015). Our work, together with these previous studies, confirm that the integration of environmental and spatial effects should improve bioassessment with ostracods and other proxies (Heino 2013).

The most influential environmental factor was salt content (as conductivity), previously observed by Roca et al. (2000) and Boronat et al. (2001) for crustaceans in the same region. We found two ostracod species building monospecific ostracod assemblages in the lakes with highest salt content: *H. barbara* and the Iberian endemic *C. aragonica*. Several previous works observed a reduction of species richness with increasing salinity (Baltanás et al. 1990; Williams et al. 1990), but halophilous species benefit from reduced predation and competition in highly saline habitats, although paying an extra metabolic cost (Herbst 2001). Salinity influences the composition and distribution of aquatic organisms (e.g., Horne 1983; Williams et al. 1990; Arribas et al. 2014), because of specific adaptations to particular osmotic conditions. There, the high salinity gradient–in these lakes conductivity ranged from 0.99 to 77.65 mS cm^{-1}–provides a strong barrier between local communities and increases species sorting effects.

Besides salinity, lake hydroperiod also influenced the ostracod assemblages. Lakes with short hydroperiods impose adaptive constraints on their communities, and most ostracods collected from the studied lakes are known to produce drought resistant (diapausing) eggs. Differences between the length of the hydroperiod determined the presence of different ostracods. Some species, such as *H. incongruens* and *E. virens,* occurred in lakes with shorter hydroperiod, as they are often found as pioneer species in recently flooded water bodies (Fryer 1997; Schmit et al. 2013). Otherwise, we found *C. bispinosa* and *H. chevreuxi* in lakes with longer hydroperiod, as Martins et al. (2009) also observed in temporary systems, replacing pioneer
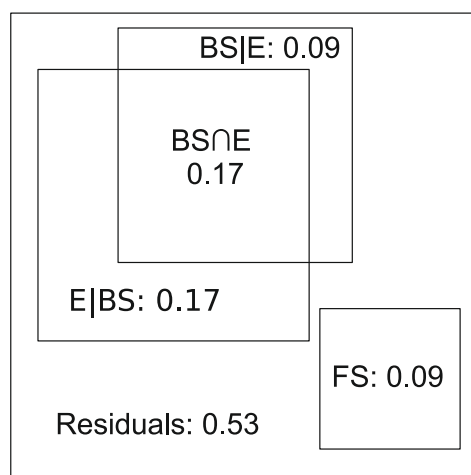
species through the ecological succession of longer lived temporary waters.

On the other hand, human-induced alterations of the hydrological regime, such as pollution and eutrophication, may have modified the dominant ostracod assemblages in the area. The main human effect would be from increased water inputs, which would have maintained some lakes inundated throughout the year and causing drops in their salinity (Roca et al. 2000), allowing generalist species, such as *H. incongruens* to colonize those altered lakes (Fryer 1997). This is related with high values in organic matter in the sediments (LOI_{550}) of the more altered lakes, where we collected *H. incongruens*. The presence of the exotic species *Candonocypris novaezelandiae*, recently cited for the first time in Europe (Valls et al. 2013), is probably related to the artificially elongated hydroperiod in impacted lakes receiving wastewater inputs (e.g., Taray and La Veguilla), a phenomenon already observed in other Mediterranean systems invaded by the same species (Valls et al. 2013; Escrivà et al. 2014). The sensitivity of ostracod species to such changes makes them good indicators of habitat change, especially because their fossil record may help testing hypotheses on past environmental conditions and recent human impacts (e.g., Poquet et al. 2008).

Significant broad-scale spatial effects indicated that species composition varied at large distances. We related these differences mostly to the spatial structure of the environment, corresponding therefore to species sorting effects. Southern and northern lakes differ in climatic and geological features, and these geographical factors determined the conductivity and the ephemerality of the water bodies, making northern lakes more saline and ephemeral than southern lakes. Otherwise, pure broad-scale spatial effects suggested dispersal limitation (species turnover at large distances) and mass effects (similar species composition at short distances), but also historical factors (priority effects limiting colonization after an effective dispersal), or other unmeasured environmental variables with a spatial structure. Dispersal limitation leads to a negative correlation between spatial distance and community similarity (Soininen et al. 2011). Havel and Shurin (2004) noted that the number of propagules of *Daphnia lumholtzi*, a cladoceran with dispersal abilities similar to those of ostracods, significantly decayed by 20–30 km from a source, a separation typical of our studied lakes (averaged distance of 52 ± 39 km). Broad scale spatial factors may also reveal mass effects, because broad-scale MEMs indicate that nearer lakes are similar in species composition. Many works suggest that dispersal between short distances (<10 km) is sufficiently fast to favor mass effects (Brendonck and Riddoch 1999; Bilton et al. 2001; Cohen and Shurin 2003). However, if dispersal of small crustaceans depends on vertebrates (Proctor et al. 1967; Figuerola et al.

2003; Brochet et al. 2010), such as waterfowl, the mobility of dispersers among isolated sites may affect the rates of dispersal, rather than real geographical distances.

On the other hand, fine-spatial scale MEMs pointed to some species turnover at shorter distances, unexplained by the local environmental control. Scalograms related fine scale to PRA, but they have unclear ecological explanation. The explained fraction attributed to fine-scale spatial factors may be associated to other dispersal processes operating at these scales, or non-observed biotic interactions and unmeasured environmental factors, as suggested by Dray et al. (2012).

Environmental factors explained the largest fraction of the metacommunity structure (pure environment 17 %), although another 17 % was shared with broad-scale space. The percentages explained by space were similar altogether, but lower when considered separately depending on spatial scale (broad-scale 9 and 9 % fine-scale space). Consequently, both species sorting and dispersal processes structure the metacommunity. These findings are in partial agreement with other studies carried out comparing the relative importance of environment and space in different taxa (e.g., Cottenie 2005; De Bie et al. 2012; Astorga et al. 2012). The dominance of species sorting over broad scale spatial effects is likely related to the great amount of propagules generated, long-distance passive dispersal provided by vectors, and rapid life cycle in these small crustaceans promoting high dispersal rates, allowing the colonization of environmentally suitable sites, as happens in smaller organisms (e.g., bacteria; Van der Gucht et al. 2007). Yet, barriers and corridors through the dispersal processes can affect the metacommunity organization, as also observed in organisms with the same body size and passive dispersal (e.g., zooplankton; De Bie et al. 2012).

Conclusions

The structuring mechanisms affecting ostracod metacommunities in endorheic lakes point to a combination of species sorting (environmental control) and spatial effects (spatially structured environment and dispersal processes). Regarding the environmental control, salinity and ephemerality were the main factors structuring the communities. Furthermore, spatial processes had significant effects probably related to dispersal limitation, mass effects and resistance of the community to invasion by new species. The use of bio- and palaeoindicators depends on the assumptions that different species hold different niches and that environmental variables control community structure, i.e. a species-sorting view of the metacommunity (Heino 2013). Spatial processes could however provoke misinterpretations of the relationship between analyzed

environmental variables and observed community structure. Therefore, an effort to combine environmental and spatial components is essential to better understanding not only which are the main processes organizing metacommunities but also for the proper implementation of biological assessment programs and unbiased palaeoenvironmental interpretations.

Appendix

See Tables 3 and 4.

Table 3 Forward selection procedure for environmental variables computed by the R-package packfor

Variables	R^2	R^2 cum	Adjusted R^2 cum	F	*p* value
Conductivity	0.202	0.201	0.162	5.053	0.002
LOI550	0.087	0.289	0.214	2.337	0.020
Rainfall	0.071	0.360	0.254	2.000	0.049
Surface	0.072	0.432	0.298	2.144	0.037

Procedure stopped (adjusted R^2 threshold criteria) adjusted R^2 cum = 0.298 with 4 variables (superior to 0.272 with all the variables)

Table 4 Forward selection procedure for spatial variables computed by the R-package packfor

Variables	R^2	R^2 cum	Adjusted R^2 cum	F	*p* value
MEM2	0.184	0.184	0.143	4.497	0.003
MEM 20	0.086	0.269	0.193	2.233	0.040
MEM 6	0.084	0.353	0.245	2.333	0.027
MEM 7	0.076	0.429	0.295	2.260	0.028

Procedure stopped (adjusted R^2 threshold criteria) adjusted R^2 cum = 0.295 with 4 variables (superior to 0.260 with all the variables)

References

Alonso M (1998) Las lagunas de la España peninsular. Limnetica 15:1–176

Armengol J, Estrada M, Guiset A, Margalef R, Planas D (1975) Observaciones limnológicas en las lagunas de La Mancha. Bol Est Cent Ecol 4:11–27

Arribas P, Andújar C, Abellán P, Velasco J, Millán A, Ribera I (2014) Tempo and mode of the multiple origins of salinity tolerance in a water beetle lineage. Mol Ecol 23:360–373

Astorga A, Oksanen J, Luoto M, Soininen J, Virtanen R, Muotka T (2012) Distance decay of similarity in freshwater communities: do macro- and microorganisms follow the same rules? Glob Ecol Biogeogr 21:365–375

Baltanás A (2001) *Candelacypris* n. gen. (Crustacea, Ostracoda): a new genus from Iberian saline lakes, with a redescription of *Eucypris aragonica* Brehm & Margalef, 1948. Bull Soc Nat Luxembourg 101:183–192

Baltanás A, Montes C, Martino P (1990) Distribution patterns of ostracods in iberian saline lakes. Influence of ecological factors. Hydrobiologia 197:207–220

Bilton DT, Freeland JR, Okamura B (2001) Dispersal in freshwater invertebrates. Annu Rev Ecol Syst 32:159–181

Bivand R (2015) spdep: spatial dependence: weighting schemes, statistics and models (Version 0.5-83)

Blackburn TM, Gaston KJ (1999) The relationship between animal abundance and body size: a review of the mechanisms. Adv Ecol Res 28:181–210

Blanchet FG, Legendre P, Borcard D (2008) Forward selection of explanatory variables. Ecology 89:2623–2632

Borcard D, Legendre P, Drapeau P (1992) Partialling out the spatial component of ecological variation. Ecology 73:1045–1055

Boronat L, Miracle MR, Armengol X (2001) Cladoceran assemblages in a mineralization gradient. Hydrobiologia 442:75–88

Brendonck L, Riddoch BJ (1999) Wind-borne short-range egg dispersal in anostracans (Crustacea: Branchiopoda). Biol J Linnean Soc 67:87–95

Brochet AL, Gauthier-Clerc M, Guillemain M, Fritz H, Waterkeyn A, Baltanás Á, Green AJ (2010) Field evidence of dispersal of branchiopods, ostracods and bryozoans by teal (*Anas crecca*) in the Camargue (southern France). Hydrobiologia 637:255–261

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. Ecology 85:1771–1789

Camacho A, Miracle MR, Vicente E (2003) Which factors determine the abundance and distribution of picocyanobacteria in inland waters? A comparison among different types of lakes and ponds. Arch Hydrobiol 157:321–338

Cohen GM, Shurin JB (2003) Scale-dependence and mechanisms of dispersal in freshwater zooplankton. Oikos 103:603–617

Cottenie K (2005) Integrating environmental and spatial processes in ecological community dynamics. Ecol Lett 8:1175–1182

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

De Deckker P (1981) Ostracods of athalassic saline lakes. A review. Hydrobiologia 81:131–144

Dray S (2013) spacemakeR: spatial modelling (Version 0.0-5/r113)

Dray S, Dufour AB (2007) The ade4 package: implementing the duality diagram for ecologists. J Stat Soft 22:1–20

Dray S, Legendre P, Peres-Neto PR (2006) Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecol Mod 196:483–493

Dray S, Pélissier R, Couteron P, Fortin MJ, Legendre P, Peres-Neto PRP, Bellier E, Bivand R, Blanchet FG, De Cáceres M, Dufour AB, Heegard E, Jombart T, Munoz F, Oksanen J, Thioulouse J, Wagner HH (2012) Community ecology in the age of multi-variate multiscale spatial analysis. Ecol Monogr 82:257–275

Dray S, Legendre P, Blanchet FG (2013) packfor: forward selection with permutation (Canoco p.46) (Version 0.0-8/r109)

Escrivà A, Rueda J, Armengol X, Mesquita-Joanes F (2014) Artificial dam lakes as suitable habitats for exotic invertebrates: Ostracoda ecology and distribution in reservoirs of the Eastern Iberian Peninsula. Knowl Manag Aquat Ecosyst 412:09

Escrivà A, Poquet JM, Mesquita-Joanes F (2015) Effects of environmental and spatial variables on lotic ostracod metacommunity structure in the Iberian Peninsula. Inland Waters 5:283–294

Fahrig L, Merriam G (1994) Conservation of fragmented populations. Conserv Biol 8:50–59

Fenchel T, Finlay BJ (2004) The ubiquity of small species: Patterns of local and global diversity. Bioscience 54:777–784

Figuerola J, Green AJ, Santamaría L (2003) Passive internal transport of aquatic organisms by waterfowl in Doñana, south-west Spain. Glob Ecol Biogeogr 12:427–436

Forester RM (1986) Determination of the dissolved anion composition of ancient lakes from fossil ostracodes. Geology 14:796–799

Fryer G (1997) The horse-trough ostracod *Heterocypris incongruens*. Naturalist 122:121–135

Fuhrmann R, Goth K (2011) Neue und weitere bemerkenswerte Ostrakoden aus dem Quartär Mitteldeutschlands. Palaeontogr Abt A 294:95–201

Green AJ, Jenkins KM, Bell D, Morris PJ, Kingsford RT (2008) The potential role of waterbirds in dispersing invertebrates and plants in arid Australia. Freshw Biol 53:380–392

Havel JE, Shurin JB (2004) Mechanisms, effects, and scales of dispersal in freshwater zooplankton. Limnol Oceanogr 49:1229–1238

Heino J (2013) Environmental heterogeneity, dispersal mode, and co-occurrence in stream macroinvertebrates. Ecol Evol 3:344–355

Heino J, Melo AS, Siqueira T, Soininen S, Valanko S, Bini LM (2015a) Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. Freshw Biol 60:845–869

Heino J, Melo AS, Bini LM (2015b) Reconceptualising the beta diversity-environmental heterogeneity relationship in running water systems. Freshw Biol 20:223–235

Heiri O, Lotter AF, Lemcke G (2001) Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. J Paleolimnol 25:101–110

Herbst DB (2001) Gradients of salinity stress, environmental stability and water chemistry as a templet for defining habitat types and physiological strategies in inland salt waters. Hydrobiologia 466:209–219

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978

Holmes JA (2001) Ostracoda. In: Smol JP, Birks HJB, Last WM (eds) Tracking environmental change using lake sediments. Kluwer Academic Publishers, Dordrecht, pp 125–151

Holyoak M, Leibold MA, Mouquet N, Holt RD, Hoopes MF (2005) A framework for large-scale community ecology. In: Holyoak M, Leibold MA, Holt RD (eds) Metacommunities: spatial dynamics and ecological communities. University of Chicago Press, Chicago, pp 1–31

Horne D (1983) Life-cycles of podocopid Ostracoda: a review (with particular reference to marine and brackish-water species). In: Maddoks RF (ed) Applications of Ostracoda. The University of Houston, Houston, pp 238–249

Jenkins DG, Brescacin CR, Duxbury CV, Elliott JA, Evans JA, Grablow KR, Hillegass M, Lyon BN, Metzger GA, Olandese ML, Pepe D, Silvers GA, Suresch HN, Thompson TN, Trexler CM, Williams GE, Williams NC, Williams SE (2007) Does size matter for dispersal distance? Glob Ecol Biogeogr 16:415–425

Jonsson T, Cohen JE, Carpenter SR (2005) Food webs, body size, and species abundance in ecological community description. Adv Ecol Res 36:1–84

Legendre P, Gallagher ED (2001) Ecologically meaningful transformations for ordination of species data. Oecologia 129:271–280

Legendre P, Legendre LF (2012) Numerical ecology, 3rd edn. Amsterdam, Elsevier

Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D, Loreau M, Gonzalez A (2004) The metacommunity concept: a framework for multi-scale community ecology. Ecol Lett 7:601–613

Levin SA (1992) The problem of pattern and scale in ecology. Ecology 73:1943–1967

Löffler H (2003) The origin of lake basins. In: O'Sullivan PE, Reynolds CS (eds) The lakes handbook, vol 1. Blackwell Science Ltd., Oxford, pp 8–60

Logue JB, Mouquet N, Peter H, Hillebrand H (2011) Empirical approaches to metacommunities: a review and comparison with theory. Trends Ecol Evol 26:482–491

Martins MJF, Vandekerkhove J, Mezquita F, Schmit O, Rueda J, Rossetti G, Namiotko T (2009) Dynamics of sexual and parthenogenetic populations of *Eucypris virens* (Crustacea: Ostracoda) in three temporary ponds. Hydrobiologia 636:219–232

Meisch C (2000) Freshwater Ostracoda of western and central Europe. Spektrum Akademischer Verlag, Heidelberg

Mesquita-Joanes F, Smith AJ, Viehberg FA (2012) The ecology of Ostracoda across levels of biological organisation from individual to ecosystem: a review of recent developments and future potential. In: Horne DJ, Holmes JA, Rodríguez-Lázaro J, Viehberg FA (eds) Ostracoda as proxies for quaternary climate change. Elsevier, Amsterdam, pp 15–35

Mezquita F, Tapia G, Roca JR (1999) Ostracoda from springs on the eastern Iberian Peninsula: ecology, biogeography and palaeolimnological implications. Palaeogeogr Palaeoclimatol Palaeoecol 148:65–85

Neale JW (1964) Some factors influencing the distribution of recent British Ostracoda. PSZN 33(supplement):247–307

Ng ISY, Carr CM, Cottenie K (2009) Hierarchical zooplankton metacommunities: distinguishing between high and limiting dispersal mechanisms. Hydrobiologia 619:133–143

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2015) vegan: community ecology package (Version 2.2-1)

Peres-Neto PR, Legendre P, Dray S, Borcard D (2006) Variation partitioning of species data matrices: estimation and comparison of fractions. Ecology 87:2614–2625

Poquet JM, Mezquita F, Rueda J, Miracle MR (2008) Loss of Ostracoda biodiversity in Western Mediterranean wetlands. Aquat Conserv Mar Freshw Ecosyst 18:280–296

Proctor VW, Malone CR, De Vlaming VL (1967) Dispersal of aquatic organisms: viability of disseminules recovered from the interstitial tract of captive killdeer. Ecology 48:672–676

QGIS Development Team (2014) QGIS geographic information system. Open source geospatial foundation project

R Core Team (2013) R: a language and environment for statistical computing (Version 3.02). Vienna: Foundation for Statistical Computing

Reed JM, Mesquita-Joanes F, Griffiths HI (2012) Multi-indicator conductivity transfer functions for Quaternary palaeoclimate reconstruction. J Paleolimnol 47:251–275

Resetarits WJ (2001) Colonization under threat of predation: avoidance of fish by an aquatic beetle, *Tropisternus lateralis* (Coleoptera: Hydrophilidae). Oecologia 129:155–160

Roca JR, Mezquita F, Rueda J, Camacho A, Miracle MR (2000) Endorheic versus karstic lakes: patterns of ostracod distributions and lake typology in a Mediterranean landscape (Castilla—La Mancha, Spain). Mar Freshw Res 51:311–319

Schmit O, Adolfsson S, Vandekerkhove J, Rueda J, Bode SNS, Rossetti G, Michalakis Y, Jokela J, Martens K, Mesquita-Joanes F (2013) The distribution of sexual reproduction of the geographic parthenogen *Eucypris virens* (Crustacea: Ostracoda) matches environmental gradients in a temporary lake. Can J Zool 91:660–671

Shurin JB, Cottenie K, Hillebrand H (2009) Spatial autocorrelation and dispersal limitation in freshwater organisms. Oecologia 159:151–159

Soininen J, Korhonen JJ, Karhu J, Vetterli A (2011) Disentangling the spatial patterns in community composition of prokaryotic and eukaryotic lake plankton. Limnol Oceanogr 56:508–520

Valls L, Rueda J, Mesquita-Joanes F (2013) Dynamics of Ostracoda (Crustacea) assemblages in a Mediterranean pond system (Racó de l'Olla, Albufera Nat. Park) with focus on the exotic species *Candonocypris novaezelandiae* (Baird, 1843). Ann Limnol Int J Limnol 49:237–247

Van der Gucht K, Cottenie K, Muylaert K, Vloemans N, Cousin S, Declerck S, Jeppesen E, Conde-Porcuna JM, Schwenk K, Zwart G, Degans H, Vyverman W, De Meester L (2007) The power of species sorting: local factors drive bacterial community composition over a wide range of spatial scales. Proc Natl Acad Sci 104:20404–20409

Vanschoenwinkel B, Gielen S, Seaman M, Brendonck L (2008) Any way the wind blows: frequent wind dispersal drives species sorting in ephemeral aquatic communities. Oikos 117:125–134

Verleyen E, Vyverman W, Sterken M, Hodgson DA, De Wever A, Juggins S, Van de Vijver B, Jones VJ, Vanormelingen P, Roberts D, Flower R, Kilroy C, Souffreau C, Sabbe K (2009) The importance of dispersal related and local factors in shaping the taxonomic structure of diatom metacommunities. Oikos 118:1239–1249

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

Williams WD, Boulton AJ, Taaffe RG (1990) Salinity as a determinant of salt lake fauna: a question of scale. Hydrobiologia 197:257–266

Wilson DS (1992) Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. Ecology 73:1984–2000

Zhai M, Nováček O, Výravský D, Syrovátka V, Bojková J, Helešic J (2014) Environmental and spatial control of ostracod assemblages in the Western Carpathian spring fens. Hydrobiologia 745:225–239

Capítol 2

Spatial and environmental effects on a rock pool metacommunity depend on landscape setting and dispersal mode

Cocó al Barranc Llarg de Rafelguaraf

Spatial and environmental effects on a rock pool metacommunity depend on landscape setting and dispersal mode

Andreu Castillo-Escrivà, Josep Antoni Aguilar-Alberola & Francesc Mesquita-Joanes

[a] *Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, Catedrático José Beltrán 2, E-46980 Paterna, Spain*.

Summary

1. Empirical studies on structuring mechanisms of metacommunities usually focus on the major roles of environmental filtering and dispersal. Recent works suggest that the relative importance of these structuring mechanisms differs among organisms with different body size, taxonomic affiliation and dispersal abilities, and also depends on regional extent and environmental heterogeneity. However, the effects of connectivity among sites and dispersal mode per se are less commonly considered explicitly in field metacommunity studies.

2. We analyzed a rock pool animal metacommunity, comparing both environmental and spatial effects between a set of pools in a ravine setting, with ephemeral connecting waterways, and another on a hill setting, without such connections. We also analyzed the relative role of structuring mechanisms influencing active vs. passive dispersers in the metacommunity. We used permutational multivariate analysis of variance (NPMANOVA) and analysis of the multivariate homogeneity of group dispersions (PERMDISP) to compare environmental and species variation between landscape settings. Variation partitioning were applied to determine the percentage of the species variation explained by environmental and spatial variables.

3. The effect of the structuring mechanisms depended on both the landscape connectivity context and species dispersal mode. Species sorting drove active disperser metacommunities in both isolated and waterway connected pools, as these organisms can track all the environmentally suitable sites at the spatial extent considered. In addition, beta diversity of active dispersers and species sorting effects were higher in the set of ravine rock pools, with wider environmental heterogeneity and connecting waterways. In contrast, species sorting structured passive dispersers only in the set of pools with connecting waterways, whereas spatial constraints more strongly affected passive dispersers in the more isolated pools at the hill setting.

4. Our findings stress the importance of landscape setting and dispersal mode in rock pool metacommunities at a small spatial extent.

Keywords: Metacommunity; Dispersal mode; Species sorting; Dispersal limitation; Mass effects; Rock pool

Introduction

One of the main issues in community ecology consists in deciphering the mechanisms structuring metacommunities. Among others, scientists have recently focused on species sorting and dispersal processes. Species sorting works by local habitat conditions filtering the community composition, whereby species only inhabit environmentally suitable sites (Leibold *et al.*, 2004). Perfect species sorting needs a relatively moderate dispersal rate to let each species reaching all suitable sites. However, either high or low dispersal rates may overwhelm species sorting (Heino *et al.*, 2015a). High dispersal rates allow species to maintain populations in suboptimal habitat conditions, due to source-sink dynamics, a mechanism called mass effects. By contrast, low dispersal rates hinder species from tracking all suitable sites, a mechanism known as dispersal limitation. Recently, ecologists have tried to disentangle the relative importance of these structuring mechanisms, which in turn depend on the organism groups studied and on the regional context.

Some studies have emphasized that the strength of the different structuring

mechanisms of metacommunities differs among organism traits such as body size (De Bie *et al.*, 2012), taxonomic group (Heino *et al.*, 2012) and potential dispersal distance (Astorga *et al.*, 2012). They concluded that groups with high dispersal abilities can track all the suitable sites, and consequently species sorting drives their community composition. Otherwise, groups with low dispersal abilities exhibit stronger spatial effects. Nonetheless, few studies consider the dispersal mode *per se, e.g.* by splitting organisms between active and passive dispersers (Vanschoenwinkel *et al.*, 2007, Schulz *et al.*, 2012, Grönroos *et al.*, 2013). One could expect that active dispersers display high dispersal abilities and stronger species sorting effects than passive dispersers, whereas spatial effects (*e.g.*, dispersal limitation) might most strongly affect passive dispersers rather than active ones (Vanschoenwinkel et al., 2007).

In addition to species traits, ecologists have increased their interest on the role of the regional context in modulating the processes structuring metacommunities (Heino *et al.*, 2012; Heino *et al.*, 2015b; Grönroos *et al.*, 2013). High environmental heterogeneity -measured as the variability of the environmental conditions among the study sites of a region (Anderson *et al.*, 2006)- results in stronger species sorting effects, as a region with varied niches leads to higher species filtering and beta diversity (Chase & Leibold, 2003). Yet, at a small regional extent, high dispersal rates (*i.e.* mass effects) can homogenize the community composition among sites, whereas low dispersal rates (*i.e.* dispersal limitation) can act at wider extents, hampering the environmental control (Heino *et al.*, 2015b). However, few studies tested the effects of regional habitat connectivity at the landscape scale on metacommunity structure (Vanschoenwinkel *et al.*, 2007, Medley & Havel, 2007, Fernandes *et al.*, 2014).

Connectivity is an essential feature of stream metacommunities (Grönroos *et al.*, 2013, Heino *et al.*, 2015a) and, similarly, overflow may represent an important via to dispersal in small isolated water bodies such as rock pools (Vanschoenwinkel *et al.*, 2008b, Jocque *et al.*, 2010, Pellowe-Wagstaff & Simonis, 2014). The water filling rain-fed rock pools can overflow during heavy rains. The displaced water provokes the leakage of some individuals and propagules into the surrounding landscape matrix. Sometimes, ephemeral waterways may appear connecting the rock pools and dispersing organisms (Brendonck *et*

al., 2010), generating high dispersal rates between the connected pools (Hulsmans *et al*., 2007, Vanschoenwinkel *et al*., 2008b). Consequently, the existence of these connections in the landscape can largely modify the mechanisms that structure rock pool metacommunities (Vanschoenwinkel *et al*., 2007).

At a relatively small spatial extent, we wondered if differences in connectivity among small water bodies might influence the relative importance of species sorting and dispersal on aquatic animal communities. At the small region considered, we expect little dispersal constraints, particularly for actively dispersing animals, and therefore species sorting processes to be the major force, but possibly the most connected sites might experience mass effects, blurring the results of niche filtering.

Methods

Study area

The studied rock pools are located in a low altitude limestone mountain landscape with Mediterranean shrubland vegetation in the municipality of Rafelguaraf (Valencia; Eastern Iberian Peninsula; Fig. 1). The spatial extent of the study area is *c*. 61 ha. These rock pools are small temporary water bodies (ranging from 12 to 250 cm of major axis length), which are filled with rain water (Aguilar-Alberola & Mesquita-Joanes, 2011). We
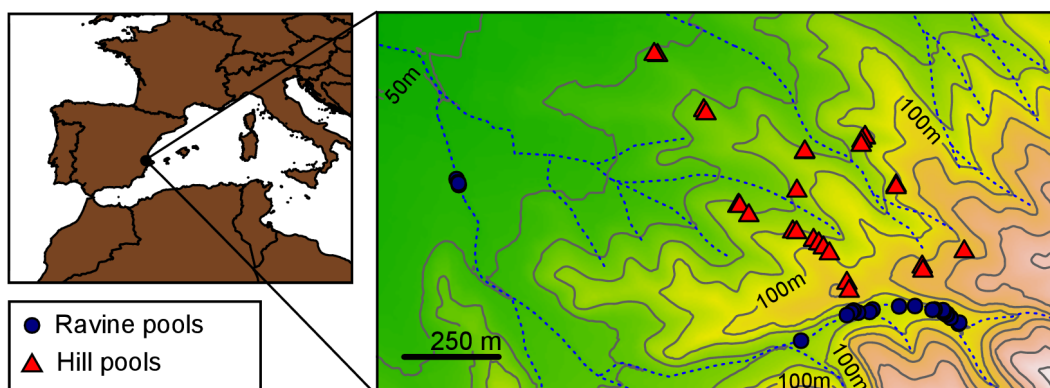
Fig. 1 Map of the study area with the location of the sampled rock pools and symbols according to landscape setting.

subdivided the study area in two sets of sites: ravine and hill rock pools (Fig. 1). In the ravine setting, occasional Mediterranean rainfall results in an ephemeral watercourse, which connect the rock pools located on the ravine bed for a few days. Contrarily, the rock pools on the hill are located beyond the ephemeral watercourses and lack direct connecting waterways among them.

Sampling and dispersal mode groups

We surveyed 53 rock pools from 27 to 29 May 2008. Among them, 25 pools belong to the ravine setting and 28 to the hill setting (Fig. 1). The aquatic fauna was sampled by sweeping a hand-net of 100 μm of mesh and 5 cm of diameter, over a transect of *c*. 25 cm. In the laboratory, we identified and counted the animals (mostly invertebrates) collected using a stereomicroscope. We determined the organisms to species level whenever possible an used informal taxa otherwise in order to attain higher resolution when different morphotypes could be clearly distinguished for a particular taxon. Identification details are summarized in Appendix S1 in Supporting Information. The abundances of identified organisms were summarized into six ordinal categories: 0 for zero individuals, 1 for one individual, 2 for abundances from two to ten individuals, 3 for 11 to 100 ind., 4 for 101 to 1000 ind., and 5 for more than 1000 individuals. Tadpoles were counted in the field (also in abundance categories), and only a few were collected for determination.

Following Jocque *et al*. (2010), we grouped the organisms in active and passive dispersers. We considered as active dispersers those animals with migrant adults that can disperse between pools, by means of terrestrial or aerial movements and, generally, without resistant forms for the dry phase (*i.e.* Ephemeroptera, Diptera, Hemiptera, Coleoptera and Anura). By contrast, passive dispersers produce drought resistant stages, such as resting eggs and encapsulation, and rely on vectors for dispersal, such as water, wind and other animals (*i.e.* Anostraca, Cladocera, Ostracoda, Copepoda and Oligochaeta) (see Williams, 2006).

Environmental and spatial variables

We obtained the geographical coordinates and elevation (m a.s.l.) of each pool with

a GPS. In the field, we measured length (cm), width (cm) and depth (cm) of the pools and from these measures we estimated their surface area (m^2) and volume of water (L). Conductivity (μS cm^{-1}) and pH were determined in the field with portable probes, and we collected water samples to analyze chloride content (mg L^{-1}) and alkalinity (mmol L^{-1}) in the laboratory using standard methods. We used an ordinal index to characterize the amount of substrate at the bottom of the pools, as follows:1 = without substrate (only bare rock), 2 = partially covered with substrate, and 3 = fully covered with substrate; and recorded the presence or absence of leaf litter inside the pools.

We calculated spatial variables as Moran Eigenvector Maps (MEMs) from the geographical coordinates (Dray *et al.*, 2006). The MEMs were calculated with the minimum spanning tree criterion (Legendre & Legendre, 2012), across and within landscape settings (hill / ravine). We used the packages spdep (Bivand & Piras, 2015) and spacemakeR for this purpose (Dray, 2013).

Statistical analyses

We analyzed the differences in environmental characteristics and community composition, and their variability within each of two sets of rock pools according to their position in the landscape (*i.e.* ravine pools / hill pools). First, some environmental variables were log-transformed to achieve normality (Table 1). Distance matrices were computed using the Euclidean distance for the standardized environmental variables, and the Sørensen similarity was used for the whole metacommunity composition and separately for each group of organisms according to dispersal mode (passive / active). We used these two distance matrices to perform principal coordinate analyses (PCoAs), and to visualize the environmental and species variation among sites. Then, a permutational multivariate analysis of variance (NPMANOVA; Anderson, 2001) was performed to determine the differences in the environmental variables and species composition between the hill and ravine settings. The environmental heterogeneity and beta diversity was estimated by calculating the mean distance from each site to the centroid of each group in PCoA (Anderson *et al.*, 2006). The similarity of the environmental and species variations were tested with an analysis of multivariate homogeneity of group dispersions (PERMDISP;

Anderson, 2006). For these analyses, we used all the environmental variables measured.

The relative role of environment and space on community composition was determined with redundancy analysis (RDA) and variation partitioning analysis. We used a series of RDAs and variation partitioning analyses to calculate the proportion explained by pure and shared (as adjusted R^2) environmental and spatial effects on the community structure (Borcard *et al.*, 1992, Peres-Neto *et al.*, 2006). This procedure was applied across and within pool settings, for the whole community and for each dispersal mode separately.

Table 1: Spatial distances among sites, environmental variables and community features of ravine and hill rock pools.

Variables	Ravine (25 pools)			Hill (28 pools)		
	Mean ± sd	Min.	Max.	Mean ± sd	Min.	Max.
Spatial distances (m)	447.2 ± 501.1	1.4	1391.0	344.7 ± 196.4	2.2	997.3
Environmental variables						
Elevation (m a.s.l.)	85.6 ± 14.3	55.0	99.0	90.0 ± 13.3	67.0	115.0
Length* (cm)	78.1 ± 62.6	12.0	250.0	69.0 ± 35.6	25.0	150.0
Width* (cm)	46.6 ± 50.1	8.0	210.0	37.4 ± 12.8	20.0	72.5
Depth* (cm)	8.3 ± 9.3	1.5	49.3	14.4 ± 12.2	2.0	55.5
Area* (m^2)	0.5 ± 1.0	0.0	4.2	0.3 ± 0.2	0.0	1.0
Volume* (L)	103.0 ± 294.1	0.3	1362.2	48.3 ± 77.0	1.8	365.0
Conductivity* (μS cm^{-1})	325.0 ± 117.0	113.0	610.0	283.9 ± 107.8	143.0	615.0
pH	7.6 ± 0.3	7.3	8.3	7.4 ± 0.3	7.1	7.9
Alkalinity* (mmol L^{-1})	4.3 ± 1.5	1.1	7.1	4.4 ± 2.3	2.0	14.4
Cl* (mg L^{-1})	25.8 ± 18.0	8.0	87.0	15.2 ± 5.2	8.0	30.0
Substrate (index 1:3)	2.2 ± 0.6	1.0	3.0	2.8 ± 0.5	1.0	3.0
Leaf litter (index 0:1)	0.8 ± 0.4	0.0	1.0	0.7 ± 0.5	0.0	1.0
Environmental heterogeneity	3.50			2.76		
Species richness						
Whole community	4.9 ± 1.9	2.0	9.0	4.1 ± 1.5	2.0	7.0
Passive dispersers	2.3 ± 1.0	1.0	5.0	2.3 ± 1.0	1.0	4.0
Active dispersers	2.6 ± 1.6	1.0	7.0	1.9 ± 0.8	1.0	4.0
Beta diversity						
Whole community	0.36			0.30		
Passive dispersers	0.38			0.36		
Active dispersers	0.35			0.24		

* These variables were log$_{10}$-transformed for further statistical analyses.

Previously, we applied a forward selection procedure with two stopping criteria to select environmental and spatial variables in each case (Blanchet *et al.*, 2008).

R packages

We performed the statistical analyses by means of R version 3.2.3 (R Development Core Team, 2015). PCoA, NPMANOVA, PERMDISP, RDA and variation partitioning were done with the vegan package (Oksanen *et al.*, 2015) and forward selection with packfor (Dray *et al.*, 2013).

Results

The environmental conditions differed between ravine and hill rock pools (NPMANOVA; $F = 3.26$; $p = 0.015$), mainly due to differences in pool morphometry. The pools with the largest surface area were located in the ravine, whereas the deepest pools appeared on the hill (Table 1; Fig. 2a, b). Water chemistry conditions were similar between
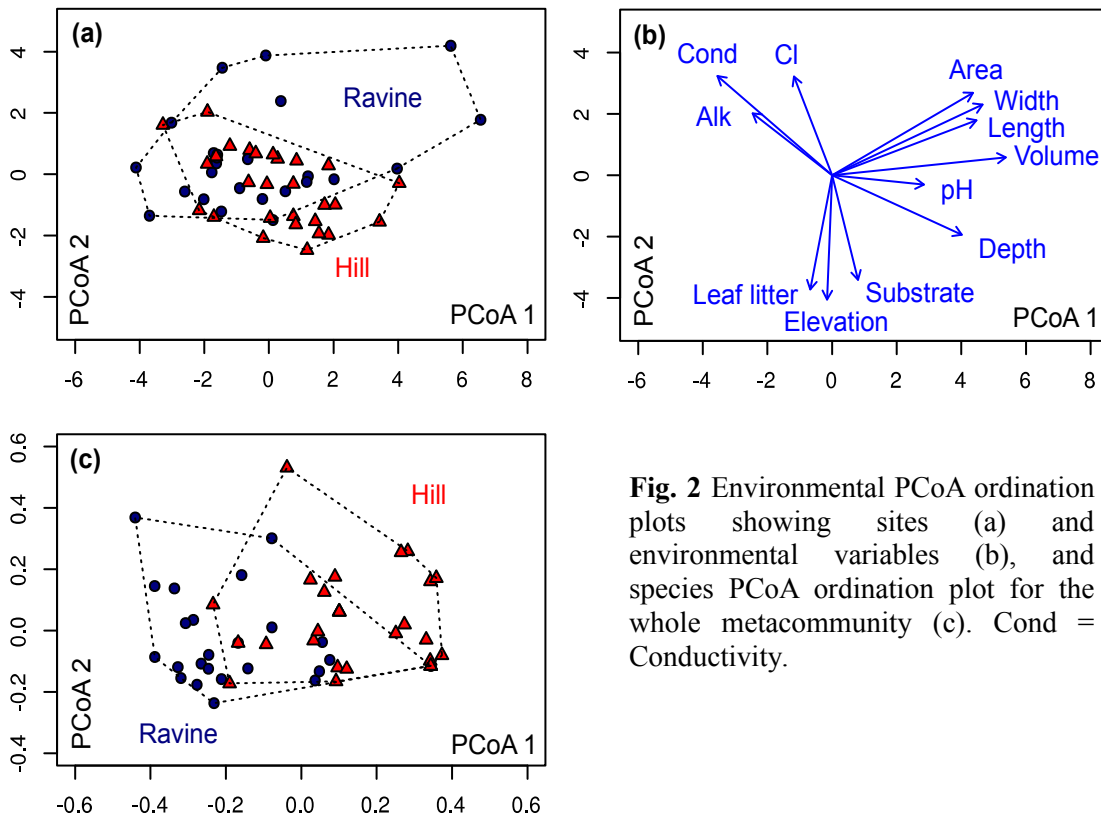
Fig. 2 Environmental PCoA ordination plots showing sites (a) and environmental variables (b), and species PCoA ordination plot for the whole metacommunity (c). Cond = Conductivity.

pool landscape settings. Ravine pools showed higher environmental heterogeneity than hill pools (PERMDISP; F = 5.43; p = 0.023), in accordance to the higher standard deviation of pool surface area (Table 1). Furthermore, we recorded higher mean spatial distances among ravine pools than among hill pools (Table 1).

We identified a total of 20 species; 19 were found in the ravine pools and 15 in hill pools. Out of these, we considered 10 species as active dispersers and 10 as passive dispersers. The community composition differed between the two sets of pools (NPMANOVA; F = 10.68; p = 0.001). We also observed significant differences in community composition when considering separately active (NPMANOVA; F = 5.66; p = 0.002) or passive dispersers (NPMANOVA; F = 14.11; p = 0.001). Beta diversity was higher in the ravine setting than in the hill setting for the whole community (PERMDISP; F = 5.95; p = 0.018). Active dispersers also presented higher beta diversity in the ravine setting (PERMDISP; F = 16.49; p < 0.001), but passive dispersers exhibited similar beta diversity in both sets of pools (PERMDISP; F = 0.182; p = 0.671).

We summarize the selected explanatory variables and RDA results in Appendix S2 in Supporting Information. Across settings (Fig. 3), spatial components explained 21.3% of the whole community variation, whereas environment only contributed to 7.2% of this
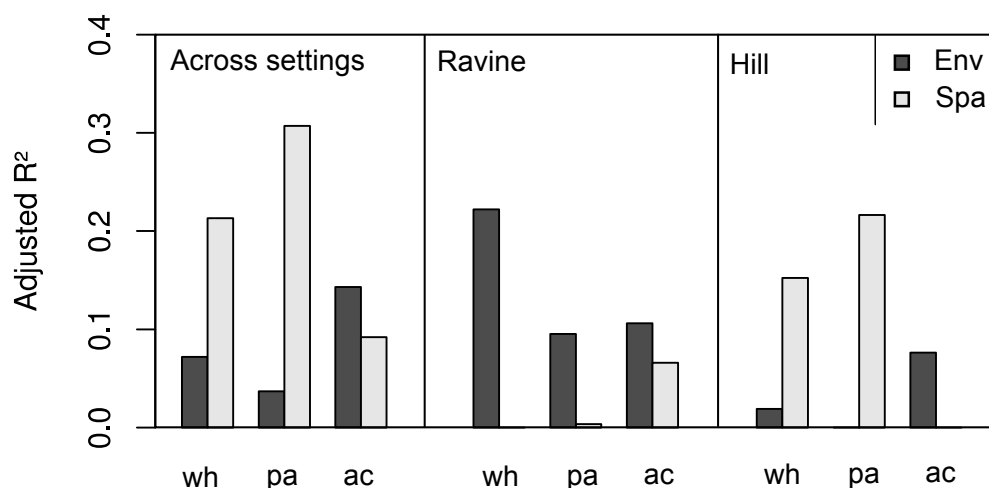
Fig. 3 Pure environmental and spatial fractions of the variation partitioning (as adjusted R^2), for across and within landscape settings. We present results taking into account the whole metacommunity (wh), and separately for active (ac) and passive dispersers (pa).

variation. This pattern was more marked in passive dispersers. In contrast, environmental conditions played a more relevant role for active dispersers than spatial effects. Within the ravine setting, only the environmental part was significant for the whole community. For passive dispersers only environmental components significantly affected the faunal assemblages too, and these effects represented 9.5% of the species variation. For active dispersers, environmental control was also more relevant than spatial drivers, although spatial factors also explained a significant fraction of the species variation. Within the hill setting, spatial effects had a major role for the whole community, and environmental effects were not significant. We observed the same pattern in the passive dispersers. Conversely, only environmental variables were found to significantly relate to active dispersers assemblages, explaining 7.6% of their metacommunity structure.

Discussion

Landscape setting

Our results stress the dependence of metacommunity structuring mechanisms on landscape geographical setting and dispersal mode of organisms. In the ravine setting, environment rather than space conditioned the faunal community composition of rock pools, whereas space was more relevant in the case of the hill setting. We attribute this discrepancy to the existence of ephemeral connecting waterways due to overflows through the ravine, so as their absence on the top of the hill, similarly to the strong effects of connectivity on rock pool metacommunities observed previously by Vanschoenwinkel *et al*. (2007). Some other studies concluded that dispersal via overflow affects propagules and individuals (Hulsmans *et al*., 2007, Vanschoenwinkel *et al*., 2008b), suggesting that these events of high dispersal allow organisms to reach all the connected pools, favoring species sorting and reducing dispersal limitation. Even if hill pools in our study are not connected by waterways, other dispersal mechanisms could play a relevant role, such as active dispersal in invertebrates with flying adults, or passive dispersal by means of wind (Vanschoenwinkel *et al*., 2008a) or other animals (Vanschoenwinkel *et al*., 2008b, Van de Meutter *et al*., 2008). But these mechanisms likely represent lower dispersal rates than

waterways, and dispersal limitation can override species sorting in unconnected rock pools on top of the hill.

Higher environmental heterogeneity could lead to stronger species sorting (Chase & Leibold, 2003). Large environmental gradients may harbor different niches, allowing for stronger species filtering. In accordance, environmental heterogeneity and species sorting were higher in the ravine than in the hill setting. Also, beta diversity was higher in the setting with broader environmental heterogeneity, suggesting that the diversity of niches contributes to the species sorting among sites. Nonetheless, some studies suggested that a positive relationship between environmental heterogeneity, species sorting and beta diversity depends on the spatial extent considered, because dispersal effects can reduce species sorting at either smaller or larger extents (Verleyen *et al.*, 2009; Heino *et al.*, 2015b). The small spatial extent of our sampling area did not prevent to observe spatial effects on metacommunity structure, but it does not allow testing how the observed patterns would possibly change at larger spatial gradients (Heino *et al.*, 2015b).

Dispersal mode

Active dispersers were distributed in accordance to species sorting expectations at all the landscape settings analyzed. Previous studies suggest that active dispersers can track all the pools with suitable environmental conditions, and dispersal limitation would not be able to overwhelm species sorting in that case (*e.g.*, Resetarits, 2001, Shurin *et al.*, 2009, Heino *et al.*, 2012). On the other hand, the structuring mechanisms driving passive dispersers diverged between the landscape settings considered. Species sorting structured passive communities in the ravine setting, because pool overflow leads to high dispersal rates, and organisms can then reach all suitable sites (Cottenie & De Meester, 2003). Space affects passive dispersers on the whole sampling area and in the hill setting, likely due to dispersal limitation (Ng *et al.*, 2009), because the absence of connecting waterways can hamper the movement of passive dispersers among pools (Vanschoenwinkel *et al.*, 2007).

Active dispersers present higher beta diversity and stronger species sorting effects in the ravine setting, associated with broader environmental variation. By contrast, the beta diversity of the passive dispersers was similar in both settings. We associate these

differences between dispersal modes with the species richness recorded for each group of organisms. In active dispersers, species richness was higher in the ravine setting than in the hill setting, and consequently beta diversity could be higher in the ravine setting. In passive dispersers, species richness was similar in both settings. However, the relationship between environmental heterogeneity and beta diversity may also depend on type of organism involved (*e.g.*, habitat generalists *vs*. specialists; Pandit *et al*., 2009), although more research is needed to confirm this in the studied set of rock pools.(but see Astorga *et al*., 2012). In this context, Pandit *et al*. (2009) found that rock-pool specialists were mainly affected by purely environmental factors, suggesting higher dispersal abilities than generalists, whose metacommunity was mainly influenced by purely spatial factors. Conversely, we found more abundance of rock pool specialists in rock pools on the hill (where spatial factors were more determinant) than in the ravine (where environmental effects dominated). For example, the ostracod Heterocypris bosniaca and the anostracan species we found, considered specialists of ephemeral habitats (Aguilar-Alberola & Mesquita-Joanes, 2011; Vanschoenwinkel *et al*., 2010) preferred the hill pools, whereas we abundantly collected Heterocypris incongruens, a generalist ostracod (Fryer, 1997) in the ravine setting. Therefore, this abundance of specialists with rather high dispersal abilities may balance the beta diversity, when compared to another setting with generalist communities connected by overflows (or these relative effects may depend on how specialists and generalists are defined). Finally, the similarity in beta diversity suggests that other structuring mechanisms might be important for passive dispersers. Stochastic colonization and priority effects may affect more strongly passive than active dispersers, because passive dispersers can not determine the direction of the dispersal (they rely on vectors), and priority effects play a relevant role in organisms with drought resistant stages (Chase, 2007).

Disentangling spatial effects

When considering the influence of spatial factors on metacommunity structure, it is difficult to discern between dispersal limitation and mass effects. Anyway, in the case of active dispersers, we related the significant spatial role to dispersal limitation across

landscape settings. Following Ng *et al*. (2009), if mass effects drive the metacommunity across regions -at the largest spatial scale- dispersal rates at the smaller subregions must also be high. Our results do not agree with this assumption for the analyzed metacommunity because within settings -at the smallest spatial scale -we did not determine significant spatial effects; a combination of spatial and environmental effects seem to structure rock pool communities across landscape settings, whereas only species sorting drives them within settings.

Considering passive dispersers, we also associate spatial effects with dispersal limitation across settings, because, as above, space did not affect the metacommunity composition within the ravine set of pools, and only niche-related processes seem to structure the metacommunity at this setting. On the hill, either dispersal limitation or mass effects could be driving the metacommunity, and we would need to study different areas of the hill setting to determine the nature of these spatial effects. We expect that dispersal rates at the top of the hill should be lower than in the ravine, because of connecting waterways in the ravine. In addition, other ecological factors not considered, such as competitive and predation interactions, might be involved among the structuring mechanisms of the metacommunity of these small water bodies (Brendonck *et al*., 2010).

The relative influence of mechanisms structuring the studied rock pool metacommunity depends on landscape setting and dispersal mode. Species sorting drove the community composition of either passive or active dispersers in the ravine setting, where ephemeral waterways facilitate community connectivity among pools. On the other hand, at the hill setting species sorting only affected the community composition of active dispersers, as they can track all the environmentally suitable sites, whereas spatial effects overrode species sorting of passive dispersers, in absence of overflow-mediated dispersal. Rock pools have advantages over other aquatic systems when testing hypotheses on metacommunity organization, due to their small size, a delimited morphology, the relatively high density of sites that can found in a reduced spatial extent, and the widespread presence of these systems around the world (Brendonck *et al*., 2010), being relatively easy to survey. However, we should be careful to extrapolate the conclusions obtained from rock pools to larger aquatic systems, such as lakes. To improve expectations

derived from the study of these systems, future research should also take into account the effects of biotic interactions, such as competition and predator pressure (Vanschoenwinkel *et al.*, 2010), stochastic colonization and priority effects (Chase, 2007) on rock pool metacommunities.

Acknowledgments

References

Aguilar-Alberola, J. A., & F. Mesquita-Joanes, 2011. Population dynamics and tolerance to desiccation in a crustacean ostracod adapted to life in small ephemeral water bodies. *Limnologica* 41: 348–355.

Anderson, M. J., 2006. Distance-based tests for homogeneity of multivariate dispersions. *Biometrics*, 62: 245–253.

Anderson, M. J., K. E. Ellingsen, & B. H. McArdle, 2006. Multivariate dispersion as a measure of beta diversity. *Ecology Letters* 9: 683–693.

Astorga, A., J. Oksanen, L. Luoto, J. Soininen, R. Virtanen, & T. Muotka, 2012. Distance decay of similarity in freshwater communities: do macro- and microorganisms follow the same rules? *Global Ecology and Biogeography* 21: 365–375.

Bivand, R., & G. Piras, 2015. Comparing implemetations of estimation methods for spatial econometrics. *Journal of Statistical Software* 63: 1–36.

Blanchet, F. G., P. Legendre, & D. Borcard, 2008. Forward selection of explanatory variables. *Ecology* 89: 2623–2632.

Borcard, D., P. Legendre, & P. Drapeau, 1992. Partialling out the spatial component of ecological variation. *Ecology* 73: 1045–1055.

Brendonck, L., M. Jocque, A. Hulsmans, & B. Vanschoenwinkel, 2010. Pools "on the rocks": freshwater rock pools as model system in ecological and evolutionary research. *Limnetica* 29: 25–40.

Chase, J. M., 2007. Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences* 104: 17430–17434.

Chase, J. M., & M. A. Leibold, 2003. *Ecological Niches: Linking Classical and Contemporary Approaches*. University of Chicago Press, Chicago.

Cottenie, K., & L. De Meester, 2003. Connectivity and cladoceran species richness in a metacommunity of shallow lakes. *Freshwater Biology* 48: 823–832.

De Bie, T., L. De Meester, L. Brendonck, K. Martens, B. Goddeeris, D. Ercken, H. Hampel, L. Denys, L. Vanhecke, K. Van der Gucht, J. Van Wichelen, W. Vyverman, & S. Declerck, 2012. Body

size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. *Ecology Letters* 15: 740–747.

Dray, S., 2013. spacemakeR: spatial modelling. R package version 0.0-5/r113. http://r-forge.r-project.org/projects/sedar/

Dray, S., P. Legendre, & P. R. Peres-Neto, 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecological Modelling* 196: 483–493.

Dray, S., P. Legendre, & G. Blanchet, 2013. packfor: Forward selection with permutation (Canoco p.46). R package version 0.0-8/r109. http://r-forge.r-project.org/projects/sedar/

Fernandes, I. M., R. Henriques-Silva, J. Penha, J. Zuanon, & P. R. Peres-Neto, 2014. Spatiotemporal dynamics in a seasonal metacommunity structure is predictable: the case of floodplain-fish communities. *Ecography* 37: 464–475.

Fryer, G., 1997. The horse-trough ostracod *Heterocypris incongruens*. *Naturalist* 122: 121–135.

Grönroos, M., J. Heino, T. Siqueira, V. L. Landeiro, L. Kotanen, & L. M. Bini, 2013. Metacommunity structuring in stream networks: roles of dispersal mode, distance type, and regional environmental context. *Ecology and Evolution* 3: 4473–4487.

Heino, J., M. Grönroos, J. Soininen, R. Virtanen, & T. Muotka, 2012. Context dependency and metacommunity structuring in boreal headwater streams. *Oikos* 121: 537–544.

Heino, J., A. S. Melo, T. Siqueira, J. Soininen, S. Valanko, & L. M. Bini, 2015a. Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. *Freshwater Biology* 60: 845-869.

Heino, J., A. S. Melo, & L. M. Bini, 2015b. Reconceptualising the beta diversity-environmental heterogeneity relationship in running water systems. *Freshwater Biology* 60: 223–235.

Hulsmans, A., K. Moreau, L. De Meester, B. J. Riddock, & L. Brendonck, 2007. Direct and indirect measures of dispersal in the fairy shrimp *Branchipodopsis wolfi* indicate a small scale isolation-by-distance pattern. *Limnology and Oceanography* 52: 676–684.

Jocque, M., B. Vanschoenwinkel, & L. Brendonck, 2010. Freshwater rock pools: a review of habitat characteristics, faunal diversity and conservation value. *Freshwater Biology* 55: 1587–1602.

Legendre, P., & L. F. Legendre, 2012. *Numerical ecology*. Elsevier, Amsterdam.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, & A. Gonzalez, 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7: 601–613.

Medley, K. A., & J. E. Havel, 2007. Hydrology and local environmental factors influencing zooplankton communities in floodplain ponds. *Wetlands* 27: 864–872.

Ng, I. S. Y., C. M. Carr, & K. Cottenie, 2009. Hierarchical zooplankton metacommunities: distinguishing between high and limiting dispersal mechanisms. *Hydrobiologia* 619: 133–143.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, & H. Wagner, 2015. vegan: Community Ecology Package (Version 2.2-1). http://CRAN.R-project.org/package=vegan

Pandit, S. N., J. Kolasa, & K. Cottenie, 2009. Contrasts between habitat generalists and specialists: an empirical extension to the basic metacommunity framework. *Ecology* 90: 2253–2262.

Pellowe-Wagstaff, K. E., & J. L. Simonis, 2014. The ecology and mechanisms of overflow-mediated dispersal in a rock-pool metacommunity. *Freshwater Biology* 59: 1161–1172.

Peres-Neto P. R., P. Legendre, S. Dray, & D. A. Borcard, 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* 87: 2614-2625.

R Development Core Team, 2015. *R: A Language and Environment for Statistical Computing*. R foundation for statistical computing. http://www.r-project.org/

Resetarits, W. J., 2001. Colonization under threat of predation: avoidance of fish by an aquatic beetle, *Tropisternus lateralis* (Coleoptera: Hydrophilidae). *Oecologia* 129: 155–160.

Schulz, G., T. Siqueira, G. Stefan, & F. O. Roque, 2012. Passive and active dispersers respond similarly to environmental and spatial processes: an example from metacommunity dynamics of tree hole invertebrates. *Fundamental and Applied Limnology* 181: 315–326.

Shurin, J. B., K. Cottenie, & H. Hillebrand, 2009. Spatial autocorrelation and dispersal limitation in freshwater organisms. *Oecologia* 159: 151–159.

Van de Meutter, F., R. Stocks, & L. De Meester, 2008. Size-selective dispersal of *Daphnia* resting eggs by backswimmers (*Notonecta maculata*). *Biology Letters* 4: 494–496.

Vanschoenwinkel, B., C. De Vries, M. Seaman, & L. Brendonck, 2007. The role of metacommunity processes in shaping invertebrate rock pool communities along a dispersal gradient. *Oikos* 116: 1255–1266.

Vanschoenwinkel, B., S. Gielen, M. Seaman, & L. Brendonck, 2008a. Any way the wind blows - frequent wind dispersal drives species sorting in ephemeral aquatic communities. *Oikos* 117: 125–134.

Vanschoenwinkel, B., S. Gielen, H. Vandewaerde, M. Seaman, & L. Brendonck, 2008b. Relative importance of different dispersal vectors for small aquatic invertebrates in a rock pool metacommunity. *Ecography* 31: 567–577.

Vanschoenwinkel, B., A. Waterkeyn, M. Jocqué, L. Boven, M. Seaman, & L. Brendonck, 2010. Species sorting in space and time—the impact of disturbance regime on community assembly in a temporary pool metacommunity. *Journal of the North American Benthological Society* 29: 1267–1278.

Verleyen, E., W. Vyverman, M. Sterken, D. A. Hodgson, A. De Wever, S. Juggins, B. Van de Vijver, V. J. Jones, P. Vanormelingen, D. Roberts, R. Flower, C. Kilroy, C. Souffreau, & K. Sabbe, 2009. The importance of dispersal related and local factors in shaping the taxonomic structure of diatom metacommunities. *Oikos* 118: 1239–1249.

Williams, D. D., 2006. *The Biology of Temporary Waters*. Oxford University Press, Oxford.

Supporting information

Spatial and environmental effects on a rock pool metacommunity depend on landscape setting and dispersal mode

Appendix S1

<u>Passive dispersers</u>

We found four groups of crustaceans. Anostracans and cladocerans were classified according to Alonso (1996). To identify copepods we used the key of Einsle (1993), together with a review of the *Acanthocyclops robustus* group (Miracle *et al*., 2013). Ostracods were identified following Meisch (2000) and Petkowski *et al*. (2000). *Heterocypris* sp. 1 and *Heterocypris* sp. 2 could not be assigned to any known species, and were left in open nomenclature.

The other passive disperser, the Oligochaeta, were classified to family level following Tachet *et al*. (2000). We provide all the passive disperser taxa found in Table A1.

Table A1: List of passive disperser taxa found in the studied rock pools.

Order / Class	Taxon
Anostraca	*Branchipus shaefferi*
Cladocera	*Ceriodaphnia quadrangula*
Cladocera	*Alona rectangula*
Copepoda	*Acanthocyclops americanus*
Ostracoda	*Heterocypris bosniaca*
Ostracoda	*Heterocypris incongruens*
Ostracoda	*Heterocypris* sp. 1
Ostracoda	*Heterocypris* sp. 2
Ostracoda	*Potamocypris arcuata*
Oligochaeta	Haplotaxidae sp.

<u>Active dispersers</u>

Most active dispersers were insect larvae. For identifications, we followed mostly Tachet *et al*. (2000) to reach family or genus level. Ephemeroptera were classified to species level. We identified Hemiptera to species level from adult individuals, according to

Murillo (1985). Culicidae were classified to species level following Becker *et al.* (2010), and Ceratopogonidae to genus level (Szadziewski *et al.*, 1997). Chironomidae were determined to subfamily level following Tachet *et al.* (2000). We reached the species level for Coleoptera following Millán *et al.* (2014), using both larvae and adult individuals.

Tadpoles were identified as *Epidalea calamita* (Barbadillo *et al.*, 1999). We present all the active disperser taxa found in Table A2.

Table A2: List of active disperser taxa found in the studied rock pools.

Order / Class	Taxon
Ephemeroptera	*Cloeon dipterum*
Hemiptera	*Notonecta maculata*
Diptera	*Dasyhelea* sp.
Diptera	*Culex pipiens*
Diptera	*Culiseta longiareolata*
Diptera	Chironominae sp.
Diptera	Orthocladiinae sp.
Diptera	Tanypodinae sp.
Coleoptera	*Hydroglyphus geminus*
Anura	*Epidalea calamita*

References

Alonso, M., 1996. *Crustacea: Branchiopoda*. Consejo Superior de Investigaciones Cientificas.

Barbadillo, L. J., J. I. Lacomba, V. Pérez-Mellado, V. G. Sancho, & L. F. López-Vallejo, 1999. *Anfibios y Reptiles de la Península Ibérica, Baleares y Canarias*. GeoPlaneta.

Becker, N., D. Petrić, M. Zgomba, C. Boase, M. Madon, C. Dahl, & A. Kaiser, 2010. *Mosquitoes and their Control*. Springer, Heidelberg.

Einsle, U., 1993. *Crustacea Copepoda Calanoida Cyclopoida*. Gustav Fischer Verlag.

Meisch, C., 2000. *Freshwater Ostracoda of Western and Central Europe*. Spektrum Akademischer Verlag.

Millán, A., D. Sánchez-Fernández, P. Abellán, F. Picazo, J. A. Carbonell, J. Lobo, & I. Rivera, 2014. *Atlas de los Coleópteros Acuáticos de España peninsular*. Ministerio de Agricultura y Medio Ambiente.

Miracle, M. R.,V. Alekseev, V. Monchenko, V. Sentandreu, & E. Vicente, 2013. Molecular-genetic-based contribution to the taxonomy of the *Acanthocyclops robustus* group. *Journal of Natural History* 47: 863–888.

Murillo, J., 1985. Clau per a la identificació dels heteròpters aquàtics (Nepomorpha) ibèrics. *Butlletí de la Institució Catalana d'Història Natural* 52: 149–159.

Petkowski, T., B. Scharf, & D. Keyser, 2000. New and little known ostracods of the genus *Heterocypris* (Crustacea, Ostracoda) from the Balkan Peninsula. *Limnologica* 30: 45–57.

Szadziewski R., J. Krzywinsk, W. Gilka, & A. N. Nilsson, 1997. Diptera, Ceratopogonidae, biting midges. In: Nilsson, A. N. (ed), *Aquatic Insects of North Europe - A Taxonomic Handbook*, Apollo Books: 243–263.

Tachet H., P. Richoux, M. Bournaud, & P. Usseglio-Polaterra, 2000. *Invertébrés d'Eau Douce: Systématique, Biologie, Écologie*. CNRS Editions.

Appendix S2

Table A1: Results from RDAs and variation partitioning.

Data	Adj. R^2	P-value	Variables	Data	Adj. R^2	P-value	Variables	Data	Adj. R^2	P-value	Variables
Across settings											
Whole community				**Passive dispersers**				**Active dispersers**			
E	0.160	0.001	Area, Vol, Alt, pH	E	0.093	0.002	pH, Cond	E	0.224	0.001	Area, Cl, Alt
S	0.302	0.001	MEM 3, 1, 4, 10, 5, 7, 2, 6, 14, 48, 46, 45	S	0.363	0.001	MEM 3, 1, 10, 4, 7, 6, 14, 48, 2, 5, 46, 44	S	0.173	0.001	MEM 45, 5, 2, 8, 34
Pure E	0.072	0.001		Pure E	0.037	0.011		Pure E	0.143	0.001	
Shared	0.089			Shared	0.056			Shared	0.081		
Pure S	0.213	0.001		Pure S	0.307	0.001		Pure S	0.092	0.001	
Ravine setting											
Whole community				**Passive dispersers**				**Active dispersers**			
E	0.222	0.001	Area, Cond, Alk, Alt	E	0.144	0.001	Cond, Alk	E	0.332	0.001	Width, Alt, Cl
S	0			S	0.053	0.023	MEM 4	S	0.293	0.001	MEM 3, 23, 1, 6, 18
Pure E	0.222	0.001		Pure E	0.095	0.013		Pure E	0.106	0.009	
Shared	0			Shared	0.049			Shared	0.226		
Pure S	0			Pure S	0.004	0.353		Pure S	0.066	0.091	
Hill setting											
Whole community				**Passive dispersers**				**Active dispersers**			
E	0.138	0.002	Alt, Length	E	0.164	0.002	Alt, Length	E	0.076	0.027	Vol
S	0.271	0.001	MEM 1, 8, 26, 24, 3, 6	S	0.382	0.001	MEM 1, 26, 8, 24, 6, 3, 2	S	0		
Pure E	0.019	0.228		Pure E	-0.002	0.477		Pure E	0.076	0.027	
Shared	0.119			Shared	0.166			Shared	0		
Pure S	0.152	0.003		Pure S	0.217	0.001		Pure S	0		

* Alt = Altitude; Alk = Alkalinity; Cond = Conductivity; Vol = Volume; E = Environment; S = Space; Shared = Fraction shared by environment and space.

Capítol 3

The role of watercourse versus overland dispersal and niche effects on ostracod distribution in Mediterranean streams (eastern Iberian Peninsula)

Riu Millars (Formiche Alto)

Contents lists available at ScienceDirect

Acta Oecologica

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

Original article

The role of watercourse versus overland dispersal and niche effects on ostracod distribution in Mediterranean streams (eastern Iberian Peninsula)

Andreu Castillo-Escrivà [a, *], Juan Rueda [a], Laia Zamora [a], Ramón Hernández [a], Mónica del Moral [b], Francesc Mesquita-Joanes [a]

[a] Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, Catedrático José Beltrán, 2, Paterna, E-46980, Spain
[b] Department of Biology and Geology, IES Violant de Casalduch, Avinguda Castelló s/n, Benicàssim, E-12560, Spain

ARTICLE INFO

ABSTRACT

The processes behind the heterogeneous distribution of species involve a combination of environmental and spatial effects. In the spatial context, stream networks constitute appropriate systems to compare the relative importance of two dispersal modes in aquatic organisms: overland and watercourse dispersal. In the present study, we analyzed the distribution of ostracod species in a river network in the eastern Iberian Peninsula, with variation partitioning between environmental and spatial factors, using Moran and Asymmetric Eigenvector Maps (MEMs, AEMs) as spatial variables. Our aims were to determine the relative importance of environmental and spatial control and to compare the importance of overland and watercourse dispersal for species distribution of passively-dispersing aquatic organisms. Our results suggest that watercourse was the most important dispersal mode, favoring mass-effects. The role of species sorting was significant and related to temperature, stream width and water quality, measured as a biotic index (IBMWP). These results stress the major importance of connectivity, besides niche-related factors, in structuring riverine communities of passively-dispersing aquatic organisms.

© 2016 Elsevier Masson SAS. All rights reserved.

1. Introduction

Classical approaches to study and elucidate factors influencing local community composition focused on environmental effects as drivers, and primarily habitat features were utilized in models explaining species assemblages (Holyoak et al., 2005). However, other processes related to space, such as dispersal, represent important factors determining the distribution of many species, as the metacommunity concept suggests (Holyoak et al., 2005; Leibold et al., 2004). Consequently, ecologists have introduced spatial variables in models to determine the effects of species dispersal on metacommunities (e.g., Cottenie, 2005; Heino et al., 2015; Logue et al., 2011). Recently, metacommunity studies have focused on the relative importance of environmental control (i.e., species sorting), and dispersal in structuring metacommunities (Lindström and Langenheder, 2012). Most past studies on aquatic habitats have focused particularly on lentic systems with clear and discrete

boundaries (Logue et al., 2011), although recently some researchers have also concentrated on streams (Heino et al., 2015). Furthermore, pelagic communities have received more attention than benthic organisms, particularly pelagic bacteria (Logue et al., 2011).

Different aquatic ecosystems (e.g., wetlands, streams, ponds, lakes, estuaries) are structured by different levels of water connectivity. Running waters have a high degree of connectivity between sites, consisting of dendritic networks (Grant et al., 2007). This structure promotes two basic dispersal modes for stream organisms: dispersal within the watercourse (along the network itself), or overland, through the terrestrial landscape (Brown et al., 2011; Fagan, 2002; Urban et al., 2006). In this context, many dispersal strategies have developed in organisms (Heino et al., 2015). They can disperse along the network (1) passively with stream flow (e.g., drift of larval insects) or with animal vectors (e.g., mussels), and (2) actively within streams (e.g., strong swimmers like fishes). Overland dispersal can also be (1) passive, mediated by wind currents (e.g., bacteria, microalgae) or via animal vectors (e.g., bacteria, microcrustaceans, snails), and (2) active, by flying (e.g., winged insects) or via terrestrial movements (e.g., amphibians).

* Corresponding author.
E-mail address: andreu.castillo@uv.es (A. Castillo-Escrivà).

Most empirical studies that have used variation partitioning analysis to study metacommunities have found that environmental control prevails over spatial effects in aquatic environments (De Bie et al., 2012; Padial et al., 2014; Van der Gucht et al., 2007), particularly in streams (Göthe et al., 2013a; Heino and Mykrä, 2008; Landeiro et al., 2011). Comparisons between various organism groups indicate that the importance of species sorting and spatial effects depends on the species body size and dispersal mode (Astorga et al., 2012; Beisner et al., 2006; Maloney and Munguia, 2011). Efficient passive dispersers exhibit stronger environmental control and weaker spatial effects than inefficient passive disperser organisms (Hájek et al., 2011; Rádková et al., 2014). Similarly, efficient active dispersers exhibit stronger environmental control and weaker spatial structuring than inefficient active dispersers (Astorga et al., 2012).

The relative relevance of species sorting and dispersal depends also on the longitudinal position in the stream network. Generally, headwater streams are more isolated compared to the rest of the network because there are little-to-no upstream connections and because few organisms disperse upstream while in their aquatic stage, against the down gradient flow of water, sediment, solutes, and organic debris. Despite this isolation, Brown and Swan (2010) and Göthe et al. (2013a) observed that species sorting prevails over spatial effects in headwaters (whenever a relatively moderate rate of dispersal exists to let the organisms tracking all suitable sites, and avoid dispersal limitation), but dispersal prevails over species sorting in the mainstem, because watercourse dispersal propitiates mass effects (i.e., relative high dispersal rates). The stronger effects of species sorting in headwaters is in accordance with some studies carried out in headwaters (Escrivà et al., 2015) and springs (Hájek et al., 2011; Rádková et al., 2014; Zhai et al., 2015).

In freshwaters, crustaceans are the second most diverse group of invertebrates, after insects (Balian et al., 2008). These two groups strongly differ in their dispersal abilities, as most aquatic insects have a winged adult stage, while the whole life cycle of most crustacean taxa is usually confined to the aquatic habitat. Actually, the migration abilities of freshwater crustaceans depend mostly on passive dispersal (Figuerola et al., 2003; Green et al., 2008; Vanschoenwinkel et al., 2008). Among lotic microcrustaceans, Ostracoda is probably the most diversified group (Dole-Olivier et al., 2000; Martens et al., 2008). Previous studies on ostracods from rivers and brooks (Marmonier and Creuze des Chatelliers, 1992; Mezquita et al., 2001; Poquet and Mesquita-Joanes, 2011), documented the importance of altitude, as surrogate of climatic conditions, and water chemistry variables in explaining ostracod species distribution. But the influence of spatial effects and differential dispersal has been rarely considered when dealing with freshwater microcrustacean metacommunities.

The main aim of this study is to determine the relative importance of species sorting and dispersal in structuring ostracod metacommunities in streams. In addition, we compare the influence of overland and watercourse dispersal. Ostracods, considered relatively small organisms with passive dispersal, likely exhibit a strong influence of watercourse connections and overland dispersal. However, species sorting effects are also expected, as invertebrate aquatic organisms and ostracods in particular are known to present species-specific adaptations to different abiotic niches, mainly related to water flow, temperature and chemistry.

2. Materials and methods

2.1. Study area

The study area is located in the eastern Iberian Peninsula,

encompassing the basins of rivers Millars (156 km long) and Palància (85 km), so as small brooks from the Espadà mountains situated upstream of Veo stream (42 km) basin ($39.5° − 40.5°$ N, $1° − 0°$ W; Fig. 1ab). These basins are immediately adjacent to each other and have similar characteristics (e.g., geographical, physico-chemical, historical). The area is characterized by a Mediterranean climate, with mean annual temperatures varying between 12 and 17 °C, and mean annual precipitation of 400−700 mm, with cool wet winters and hot dry summers (Capel Molina, 2000; Hijmans et al., 2005; Pérez-Cueva, 1994). The altitude of the sampling sites ranged from 50 to 1560 m a.s.l.

2.2. Sampling and datasets

We sampled 39 sites once between 1995 and 2004, always in spring (Appendix A), with a 200 μm mesh size hand-net. Our collection strategy focused on collecting the maximum diversity of ostracods and co-occurring macroinvertebrates in all available habitat types found in the sampling site (e.g., riffle, ditch, macrophyte meadows). Samples were fixed in the field with 70% ethanol and transported to the laboratory for ostracod identification, following mostly Meisch (2000). Species presence-absence was recorded for every site.

During sampling, the following environmental variables were measured in the field (Table 1): altitude (m a.s.l), water electrical conductivity (μS/cm), pH, water temperature (°C), dissolved oxygen concentration (mg/L), flow velocity (1−5 ordinal index), depth (1−4 ordinal index) and width of the stream (1−4 ordinal index). Water samples were also collected to analyze alkalinity and chloride content (meq/L) in the laboratory by means of standard methods (APHA, 1992). Macroinvertebrates accompanying ostracods in the samples were identified under a stereomicroscope up to family level using Tachet et al. (2000). These data were used to calculate the Iberian Bio-Monitoring Working Party Index value (IBMWP; Alba-Tercedor et al., 2002), as a biotic index of water quality. Finally, mean annual temperature, thermal range and mean annual rainfall were obtained from the WorldClim database version 4.1 (Hijmans et al., 2005), using Quantum GIS version 1.7.5 (QGIS Development Team, 2014). Some variables were log-transformed to achieve distributions closer to normality (Table 1).

We considered two sets of spatial variables: overland space (OS), and watercourse space (WS). OS variables were calculated as Moran's Eigenvector Maps (MEMs; Dray et al., 2006) from sites coordinates, creating a connection network according to Gabriel graph criteria, with symmetric links (Dray et al., 2012; Legendre and Legendre, 2012, Fig. 1c), using the R packages spdep (Bivand and Piras, 2015) and spacemakeR (Dray, 2013). OS modeled a spatial network with links throughout the terrestrial landscape, without directionality (i.e., site A and site B were connected by two directions: from A to B and from B to A). Second, WS variables were created as Asymmetric Eigenvector Maps (AEMs; Blanchet et al., 2011, 2008a), by drawing a dendritic system over a real river map with Quantum GIS (Fig. 1d). Fictitious sites were added at each header river site, to impose downstream directionality. Then, we built a sites-by-edges table, giving either 1 or 0 values depending on whether or not the edge affected each site. This table was used to calculate AEMs, with the AEM package (Blanchet et al., 2008a). WS modeled a spatial network with directional links over the stream network (site A and site B were connected in one direction: only from A to B), following the water flow. MEMs can show different spatial scale effects, depending on the eigenvalues associated to each vector or spatial variable. Gradually, MEMs model space from the highest positive (as broad scale) to the lowest negative eigenvalues (as fine scale; Dray et al., 2006). In contrast, all eigenvalues associated to AEMs are positive (Blanchet et al., 2008a), and vectors
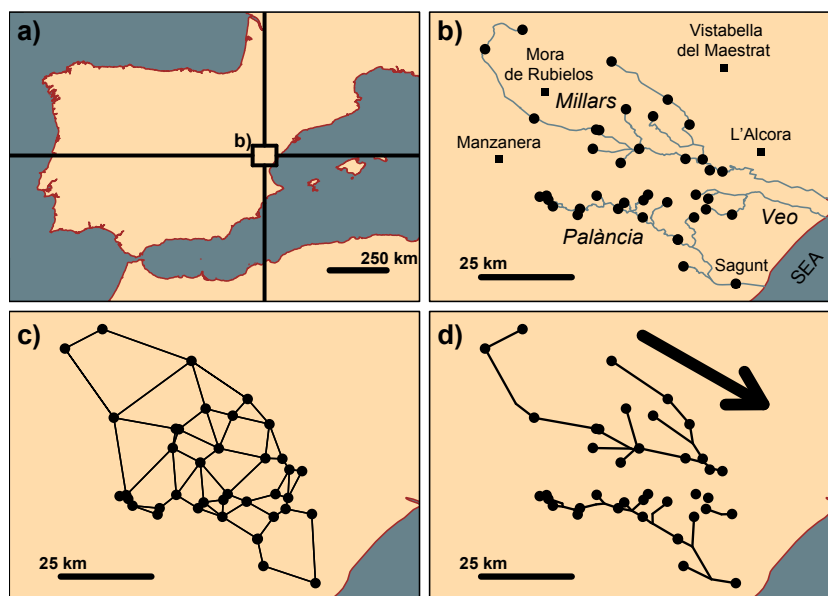
Fig. 1. Location map of the sampling area in the Iberian Peninsula (A) and distribution of sampling points in the three main river basins (B). Connection network with symmetric links as Gabriel graph criteria used for MEMs (overland dispersal) (C) and dendritic networks with asymmetric links for AEMs (watercourse dispersal), with an arrow indicating directionality (D).

Table 1
Environmental variables considered in the study and their (untransformed) mean + SE values.

Name	Description	Type	Transformation	Mean $\pm$ SE
Altitude	Altitude of the site (m a.s.l.)	Continuous	$\log_{10}(x)$	605 $\pm$ 333
Depth	Water depth (1: 0—1 cm; 2: 1—10 cm; 3: 10—50 cm; 4: 50—100 cm; 5: >100 cm)	Ordinal	none	3.23 $\pm$ 0.71
Width	Width of the river (1: 0—1 m; 2: 1—5 m; 3: 5—25 m; 4: >25 m)	Ordinal	none	2.26 $\pm$ 0.82
Velocity	Flow velocity (1: 0—10 cm/s; 2: 10—25 cm/s; 3: 25—50 cm/s; 4: 50—100 cm/s)	Ordinal	none	2.08 $\pm$ 0.92
Twater	Water temperature (ºC)	Continuous	none	14.35 $\pm$ 5.23
Oxygen	Oxygen content (mg/L)	Continuous	none	9.17 $\pm$ 1.60
pH	Negative logarithm of the activity of the hydrogen ions	Continuous	none	8.08 $\pm$ 0.43
Conductivity	Electrical conductivity (μS/cm)	Continuous	none	739 $\pm$ 255
Alkalinity	Alkalinity (meq/L)	Continuous	none	4.41 $\pm$ 0.97
Cl	Chloride concentration (meq/L)	Continuous	$\log_{10}(x)$	0.65 $\pm$ 0.73
Alk/Cl	Ratio Alkalinity/Chloride	Continuous	$\log_{10}(x)$	11.72 $\pm$ 6.65
IBMWP	Iberian Bio-Monitoring Working Party biotic index	Continuous	none	129.3 $\pm$ 55.5
Tmean	Mean annual air temperature (ºC)	Continuous	none	12.02 $\pm$ 1.77
Trange	Annual thermal range (ºC)	Continuous	none	9.19 $\pm$ 0.30
Rainfall	Mean annual rainfall (mm)	Continuous	$\log_{10}(x)$	476.3 $\pm$ 40.7

are not related to spatial scales. The information offered by AEMs allows estimating the influence of a directional process (watercourse) on the species dataset.

2.3. Statistical analyses

Initially, we carried out a Principal Components Analysis (PCA) on environmental variables, in order to summarize the relationships and distribution of environmental features. In this case, we used a correlation matrix as the variables had different variances (Quinn and Keough, 2002). The purpose of this analysis was to show the relationships among the environmental variables and to summarize the local conditions of the sites.

We had four datasets: one with species data and three explanatory datasets (environmental, OS and WS variables). We performed variation partitioning analysis (Borcard et al., 1992), applied

to distance-based Redundancy Analysis (dbRDA), determining the percentage of species variation explained by these three explanatory datasets. First, full dbRDA models were computed for each predictor set, with a selected subset of variables. Selection was done by means of a stepwise procedure with two stopping criteria: an alpha significance level of 0.05 and a threshold of the adjusted R^2 calculated with all the variables of each set separately (Blanchet et al., 2008b). DbRDA used the Jaccard similarity index. Then, four variation partitioning analyses were carried out: environment with OS, environment with WS, OS with WS and a full partitioning with all the three explanatory datasets. The partitioning is based on partial Redundancy Analysis (pRDA), calculating the adjusted R^2 for each fraction (Peres-Neto et al., 2006). Finally, the full dbRDA constrained by environment, with possible masked spatial effects, and the pRDA constrained by environment without spatial effects were computed. All analyses were performed with R version 3.0.2

(R Development Core Team, 2013) and vegan package (Oksanen et al., 2015).

3. Results

We identified 31 species of ostracods in 39 sites (Table 2). The number of species per site ranged from 1 to 8 species, with an average of 3.25 ± 2.00 species per site. *Herpetocypris brevicaudata* and *Potamocypris villosa* were the most common species, found in 12 and 10 sites, respectively, followed by *Cypridopsis vidua* and *Sarscypridopsis lanzarotensis*, distributed in 9 sites each. Conversely, several species only occurred at one site, such as *Tonnacypris lutaria*, *Cryptocandona vavrai* and the exotic *Fabaeformiscandona subacuta* (Escrivà et al., 2012).

The two first axes of the environmental PCA explained 50% of the environmental variation (Fig. 2). This ordination revealed a high correlation between altitude and climate variables; the highest altitude sites were wetter and colder than the lowest altitude sites. In addition, the sites located at highest altitude (headwater) were narrower than those in lowlands. IBMWP was negatively related to conductivity and chloride content. On the other hand, oxygenated waters related to shallow waters, likely with higher water renovation than deep waters. Three environmental variables were selected with the stepwise procedure: mean annual air temperature, stream width and IBMWP. Six OS variables (OS1, OS2, OS6, OS8, OS25 and OS33) and six WS variables (WS1, WS5, WS10, WS14, WS22 and WS26) were also selected. All the selected sets explained a significant fraction of species variation without interaction of sets (Environment: *adjusted* $R^2 = 0.084$, $P = 0.001$; OS:

Table 2
Ostracod species found in the studied streams and frequency of collection (f), i.e., number of sites in which they were collected.

Species	Code	f
Darwinula stevensoni	DST	3
Limnocythere inopinata	LIN	8
Paralimnocythere messanai	PME	2
Ilyocypris gibba	IGI	4
Ilyocypris bradyi	IBR	7
Ilyocypris inermis	IIN	6
Candona neglecta	CNE	4
Pseudocandona albicans	PAL	8
Fabaeformiscandona subacuta	FSU	1
Cryptocandona vavrai	CVA	1
Cyclocypris ovum	COV	5
Cypris sp.[a]	CYP	2
Heterocypris salina	HSA	4
Heterocypris incongruens	HIN	6
Heterocypris reptans	HRE	4
Eucypris virens	EVI	2
Eucypris pigra	EPI	1
Trajancyrpis clavata	TCL	1
Tonnacyrpis lutaria	TLU	1
Notodromas persica	NPE	2
Herpetocypris brevicaudata	HBR	12
Herpetocypris helenae	HHE	2
Herpetocypris intermedia	HNT	7
Cypridopsis hartwigi	CHA	1
Cypridopsis vidua	CVI	9
Cypridopsis elongata	CEL	1
Sarscypridopsis lanzarotensis	SLA	9
Sarscypridopsis sp.[b]	SAR	2
Potamocypris variegata	PVA	1
Potamocypris villosa	PVI	10
Potamocypris zschokkei	PZS	1

[a] *Cypris* sp. did not fit the morphological traits of previously described *Cypris* species found in Europe or Africa (Martens, 1990).
[b] *Sarscypridopsis* sp. was cited by Mezquita et al. (2005) but it is probably an undescribed species found in Madeira by Fuhrmann and Goth (2011) (Fuhrmann, April 2014, pers. comm.).
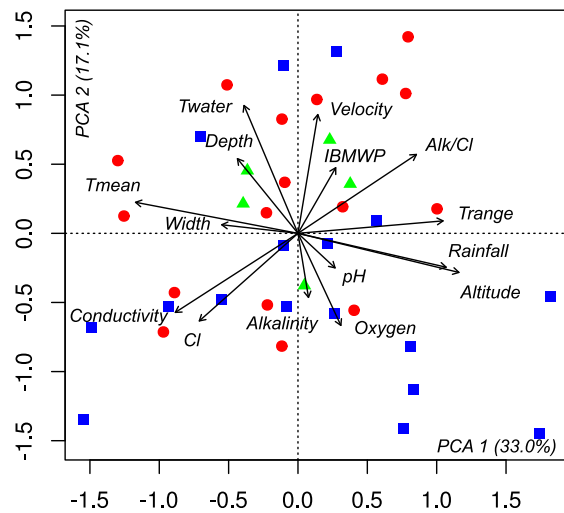

Fig. 2. Ordination plot for the first two axes of PCA on environmental variables. Red circles, green triangles and blue squares correspond to sites in the Palància, Veo and Millars basins, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

adjusted $R^2 = 0.150$, $P = 0.001$; WS: *adjusted* $R^2 = 0.136$, $P = 0.001$).

Variation partitioning helped detecting the shared variance among OS and WS, and therefore pure OS effects were only related to overland dispersal and pure WS effects were related to dispersal along the watercourse. Spatial components (OS or WS) explained larger pure fractions (13.1% and 14.6%, respectively) of the species variation than environment (6.5% and 9.4%, respectively; Table 3). In the model with OS and WS, both sets explained a similar fraction (10.6% and 9.2%, respectively), being weakly higher the percentage explained by OS. However, in the full model the largest fraction was that attributed to WS (8.0%), followed by OS (6.7%) and environment (5.3%). OS had a considerable shared fraction with WS (6.6%) and environment (4.1%).

In the dbRDA of species constrained by environment (Fig. 3a), the first axis was negatively related to temperature, which strongly correlated with altitude ($r = -0.98$; $P < 0.001$). *Herpetocypris brevicaudata*, found in sites with higher annual temperatures, was ordered on the negative side of this axis. *Herpetocypris intermedia* and *Candona neglecta* were associated with lower water temperatures and were therefore located towards the positive side of this axis. Colder sites (Fig. 4a, black circles) mostly corresponded to north and west locations, and warm sites (white circles) were found in the southeast region of our study area. The second axis (Fig. 3a) was negatively correlated with stream width and IBMWP. Several species, such as *Cyclocypris ovum*, *P. villosa* and *Limnocythere inopinata*, were primarily collected in wide mainstem streams that ordinated towards the negative end of the axis. *Herpetocypris brevicaudata, Heterocypris incongruens* and *Paralimnocythere messanai* defined the opposite end of the axis and were primarily collected from narrower, generally headwater streams (black circles in Fig. 4b).

The spatial structure of the environment was clearly detected using variation partitioning, mainly on the first axis. The first axis of the pRDA (Fig. 3b), now excluding spatial effects, was positively related to both stream width and temperature. Most ostracod taxa were associated with the positive side of this axis, suggesting wide streams harbored more species richness (correlation between

Table 3
Variation partitioning results based on partial Redundancy Analysis (pRDA), using ostracod data, with the selected fractions for environment and OS, environment and WS, OS and WS, and, finally, for environment, OS and WS. Fractions as adjusted R^2.

Analysis	Pure fractions			Shared fractions				Residuals
	Env.	OS	WS	Env. + OS	Env. + WS	OS + WS	All	
Env. and OS	0.065*	0.131*		0.019				0.785
Env. and WS	0.094*		0.146*		−0.010			0.770
OS and WS		0.106*	0.092*			0.044		0.758
Env., OS and WS	0.053*	0.067*	0.080*	0.041	0.012	0.066	−0.022	0.705

Env. = environment; OS = overland spatial factors; WS = watercourse spatial factors. Negative values are presented as "-". "*" indicates significance (P < 0.01).
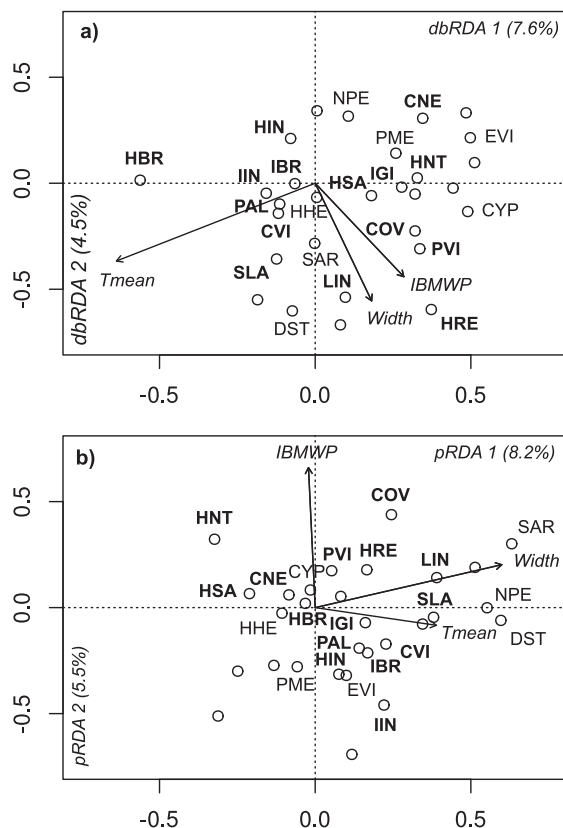

Fig. 3. Ordination biplots of species and selected environmental variables on the first two axes of dbRDA (with possible interacting spatial effects included) (A) and pRDA constrained by environment without spatial effects (B). Species codes are summarized in Table 2. Species found only in one site are not represented, but they were used in the analysis. The species with >3 presences are shown in bold type.

species richness and stream width: $r = 0.34$; $P = 0.01$), whereas *C. neglecta*, *H. brevicaudata* and *H. intermedia* were associated with the negative end of the axis and were collected from narrower and colder streams. In Fig. 4c, when excluding spatial effects, white circles (representing negative values of pRDA Axis 1, i.e., narrow cool sites) were situated generally in headwaters, and not so clearly in the northern area as previously observed (Fig. 4a), and black circles (representing wider, warmer sites) were located in the mainstem, in relation to the presence of *C. ovum*, *C. vidua* and *P. villosa*. The second axis (Figs. 3b and 4d) was positively associated with high IBMWP values corresponding to sites with the presence

of *C. ovum* and *H. intermedia*, whereas other species such as *H. incongruens* and *P. messanai* were found in sites with lower IBMWP values.

4. Discussion

Our findings highlight the importance of dispersal and species sorting as factors influencing the distribution of ostracods, a group of passive dispersers with a completely aquatic life cycle (excluding diapausing eggs in some species). Previous studies also determined significant effects of species sorting and dispersal constraints in ostracod communities from headwaters (Escrivà et al., 2015) and springs (Zhai et al., 2015). These results indicate that dispersal constraints, together with species sorting, play a major role in the distribution of ostracods in streams and springs, structuring mechanisms that have been traditionally neglected. However, our study reveals that dispersal effects can explain a higher amount of variation than species sorting in ostracods from streams, in contrast to more isolated water bodies (Hájek et al., 2011; Rádková et al., 2014; Zhai et al., 2015).

The percent variation explained by the models developed here were relatively low (22−30%), although they were significant. This low explanatory power could be related in part to the use of samples from different years, due to likely changes in climate and water quality that may in some cases drive changes in ostracod assemblage composition. On the other hand, low percentages are shared with other studies developed in streams (Grönroos et al., 2013; Heino et al., 2012; Landeiro et al., 2011) and may suggest that we failed to include other relevant environmental variables or, alternatively, may have resulted from other structuring mechanisms such as priority effects, biotic interactions or stochastic processes (Chase, 2007) that could not be determined by the available dataset of predictors. Alternative reasons for low explanatory power in streams are frequent floods and droughts, which dampen effects of species sorting and increase stochastic processes and random distributions (Miyazono and Taylor, 2013). Floods and droughts in these eastern Iberian streams are in part cyclical but also highly stochastic with high inter-annual climatic/hydrological variation (Bernardo et al., 2003). Therefore, species variation in these systems is expected to be related to apparently random factors, although more studies are required to support this assumption (Datry et al., 2015).

4.1. Environmental versus spatial control

Species composition followed an altitudinal gradient, related to water temperature and stream order. Much of the species variation that was explained by environmental variables was, however, shared with spatial components, suggesting that part of the environmental gradient was spatially structured. Sites situated in the north (mostly belonging to Millars basin) are located at higher altitude than southern sites (belonging to Palància river basin).

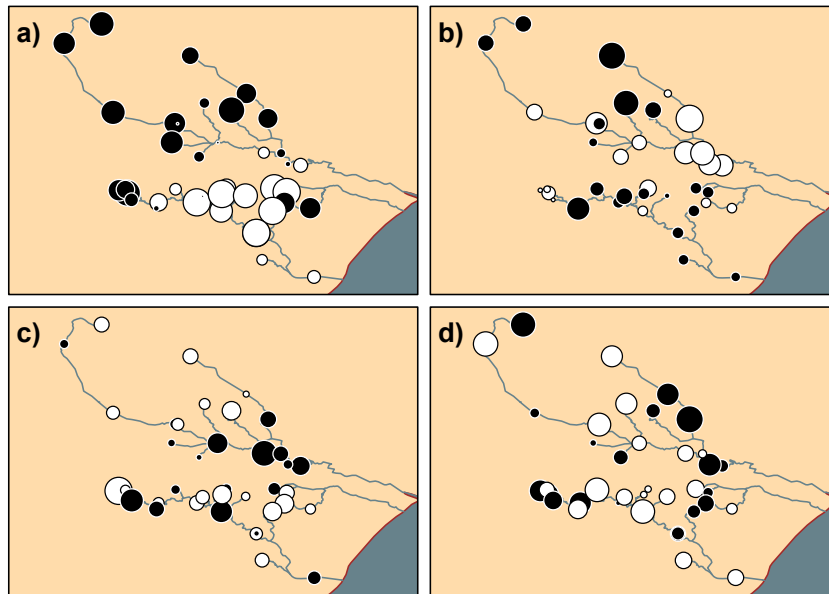Three environmental variables were most important in

Fig. 4. Maps showing the scores of each site for the first two axes (A and B respectively) of the dbRDA constrained by environment, and the first two axes (C and D) of the pRDA constrained by environment after removing the effect of spatial variables. Black dots: positive scores; white dots: negative scores. Symbol size according to absolute value of scores.

explaining variance in species distributions: temperature (strongly related to altitude), stream width and IBMWP (as surrogate of water quality and macroinvertebrate diversity). The effect of temperature on life cycle, growth and final individual size is broadly recognized in many taxa and particularly in ostracods (e.g., Aguilar-Alberola and Mesquita-Joanes, 2014; Cohen and Morin, 1990). These effects on ostracod ecophysiology determine their biogeographic distribution and make them useful indicators in palaeoenvironmental reconstruction (Curry et al., 2012; Horne and Mezquita, 2008). Circum-Mediterranean species, such as *H. brevicaudata* and *S. lanzarotensis*, preferred warm waters at low altitudes, and northern European species (*C. neglecta* and *H. intermedia*) were mostly recorded at high altitudes in the Iberian Peninsula, where temperature is low. This altitude-temperature segregation between regional faunas has been observed in other Mediterranean rivers, such as the Rhône (Marmonier and Creuze des Chatelliers, 1992), some streams in the Betic Ranges (Poquet and Mesquita-Joanes, 2011) and other lotic systems and springs in the eastern Iberian Peninsula (Mezquita et al., 1999a, 1999c). Poquet and Mesquita-Joanes (2011) found relationships between altitudinal and latitudinal distribution throughout Europe in *Potamocypris zschokkei*, *C. ovum*, *C. neglecta* and *H. brevicaudata*, suggesting an important effect of climate on local and continental ostracod species distributions.

The effects of stream width on ostracod assemblages may relate to the variety of microhabitat types inhabited by heterogeneous ostracod communities (Mezquita et al., 2001), and therefore also with higher macroinvertebrate diversity (IBMWP). However, species which are mostly restricted to the widest stream bed locations are usually those with swimming abilities (e.g., *S. lanzarotensis, C. vidua, P. villosa, C. ovum*) whereas headwaters are generally inhabited by crawling species (*H. brevicaudata, H. intermedia, C. neglecta*), which probably represents the shared effect with space (see below).

The pure fractions attributed to space were higher in all the

models than those corresponding to the environment, and so dispersal (in particular watercourse dispersal) effects seem to prevail over species sorting, structuring the local patterns of ostracod diversity in the studied streams. Ostracods, with passive dispersal and relatively intermediate size (ranging broadly between 0.3 and 5 mm; see Baltanás and Danielopol, 2013) are likely more strongly affected by spatial factors than other smaller passive dispersers, such as diatoms and bryophytes (Heino et al., 2012), and larger active dispersers, such as winged insects (Göthe et al., 2013a; Heino et al., 2012; Landeiro et al., 2012), more affected by species sorting. Yet, we may have underestimated the environmental control as we explained above. Furthermore, including a broader geological and geographical extent may capture longer water chemistry gradients, which are known to be instrumental in understanding ostracod species distribution (e.g., Mesquita-Joanes et al., 2012; Poquet and Mesquita-Joanes, 2011), but then, new spatial patterns related not only to recent dispersal constraints but also to colonization history and evolution may become increasingly important, as suggested by the findings of Escrivà et al. (2015) and Baltanás and Danielopol (2013).

4.2. Comparison of overland and watercourse dispersal

Watercourse dispersal prevailed over overland dispersal of ostracod species. Ostracods are strictly aquatic and passive dispersers, so it is likely that their overland dispersal occurs much less frequently than watercourse dispersal driven by passive drifting of individuals and propagules downstream, as Vanschoenwinkel et al. (2008a), observed in rock pools connected by ephemeral watercourses. However, we expected that overland dispersal is also going on, due to the known dispersal abilities shown by ostracods, via animal vectors (Figuerola et al., 2003; Green et al., 2008; Valls et al., 2015) and wind (Vanschoenwinkel et al., 2008b).

Preferences between these two dispersal pathways have been previously analyzed in stream macroinvertebrate communities (see

Kärnä et al., 2015). Although these studies have not demonstrated consistent and clear differences between overland and watercourse dispersal (Landeiro et al., 2011), there is a greater tendency in favor of watercourse dispersal in general (Petersen et al., 2004), although overland dispersal may be more important for insect taxa with winged adults (Heino et al., 2015). Fishes are fully restricted to aquatic habitats and are dependent on watercourse dispersal (Beisner et al., 2006; Maloney and Munguia, 2011; Nabout et al., 2009). Nevertheless, the relative importance between overland and watercourse dispersal could also be related to the position of the studied stream in the whole stream network (Brown and Swan, 2010; Göthe et al., 2013a), where overland dispersal is expected to prevail over watercourse dispersal among certain geographically isolated headwater streams. Our results seem to support this view, as there seem to be not many restrictions to overland dispersal (low percentage explained by spatial patterns), while watercourse dispersal patterns are more clear due to mainstem connections.

Herein, we observed that ostracods collected from narrow headwater streams, were adept crawling species (*H. intermedia* or *C. neglecta*). These organisms should be more resistant to watercourse drift, because they live attached to the substrate. Swimming species (*C. ovum* or *P. villosa*), which we found in wider streams, should be more affected by watercourse, as these prefer lenitic environments (Mezquita et al., 1996). We expect that mass effects (detected here as the influence of AEMs, related to watercourse dispersal) should be stronger in swimming than in crawling species, because swimmers inhabit more time in the water column and can be swept along more easily. This would increase the probabilities of finding swimming species in suboptimal environmental conditions and overall in the larger mainstem rivers, due to mass effects.

Despite stochastic isolation processes, ostracods inhabiting headwaters could have strategies to increase the persistence of their populations and decrease the expected extinction rates. This assumption comes from the observation that many ostracod species found in headwaters in the present study are common inhabitants of spring habitats (*H. intermedia*, *P. messanai* and *C. neglecta*; Meisch, 2000; Mezquita et al., 1999b), where ostracod populations are adapted to isolation conditions, by means reduced population abundances, K-strategies, tolerance to scarcity of resources or adaptation to the absence of predators. This high persistence in headwaters was also observed in spring-adapted fishes of a desert river system (Miyazono and Taylor, 2013). Future studies can compare the relative importance of species sorting and dispersal between these two species traits (swimming and crawling) in streams.

5. Conclusions

Dispersal influenced the studied ostracod stream metacommunity more than species sorting. Among dispersal ways, watercourse dispersal effects were found to be more important than overland dispersal. Watercourse dispersal suggests that mass effects structure species assemblages. However, species-sorting pure effects due to temperature, stream width and water quality also constrained ostracod communities. Similar studies help us to understand a river network as a whole system, adding spatial components to environmental analysis. In the future, we need to study the relationships between dispersal and species traits in ostracods and other taxa (Göthe et al., 2013b; Heino and Peckarsky, 2014), and carry out studies at different spatial and temporal extents, so as in streams with wider environmental gradients and levels of system stability (Datry et al., 2015). This information will be relevant not only for understanding the processes contributing to biodiversity organization in lotic systems, but also for planning

river management and understanding the consequences of habitat fragmentation and connectivity changes for biological communities in running waters.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.actao.2016.02.001.

References

Aguilar-Alberola, J.A., Mesquita-Joanes, F., 2014. Breaking the temperature-size rule: thermal effects on growth, development and fecundity of a crustacean from temporary waters. J. Therm. Biol. 42, 15–24. http://dx.doi.org/10.1016/j.jtherbio.2014.02.016.

Alba-Tercedor, J., Jáimez-Cuéllar, P., Álvarez, M., Avilés, J., Bonada, N., Casas, J., Mellado, A., Ortega, M., Pardo, I., Prat, N., Rieradevall, M., Robles, S., Sáinz-Cantero, C., Sánchez-Ortega, A., Suárez, M.L., Vidal-Abarca, M.R., Vivas, S., Zamora-Muñoz, C., 2002. Caracterización del estado ecológico de ríos mediterráneos ibéricos mediante el índice IBMWP (antes BMWP'). Limnetica 21, 171–185.

APHA, 1992. Standard Methods for the Examination of Water and Wastewater, eighteenth ed. American Public Health Association, Washington D.C.

Astorga, A., Oksanen, J., Luoto, M., Soininen, J., Virtanen, R., Muotka, T., 2012. Distance decay of similarity in freshwater communities: do macro- and microorganisms follow the same rules? Glob. Ecol. Biogeogr. 21, 365–375. http://dx.doi.org/10.1111/j.1466-8238.2011.00681.x.

Balian, E.V., Segers, H., Martens, K., Lévéque, C., 2008. The freshwater animal diversity assessment: an overview of the results. Freshw. Anim. Divers. Assess. 198, 627–637. http://dx.doi.org/10.1007/s10750-007-9246-3.

Baltanás, A., Danielopol, D.L., 2013. Body-size distribution and biogeographical patterns in non-marine ostracods (Crustacea: Ostracoda). Biol. J. Linn. Soc. 109, 409–423. http://dx.doi.org/10.1111/bij.12041.

Beisner, B.E., Peres-Neto, P.R., Lindström, E.S., Barnett, A., Longhi, M.L., 2006. The role of environmental and spatial processes in structuring lake communities from bacteria to fish. Ecology 87, 2985–2991. http://dx.doi.org/10.1890/0012-9658(2006)87[2985:TROEAS]2.0.CO;2.

Bernardo, J.M., Ilhéu, M., Matono, P., Costa, A.M., 2003. Interannual variation of fish assemblage structure in a Mediterranean river: implications of streamflow on the dominance of native or exotic species. River Res. Appl. 19, 521–532. http://dx.doi.org/10.1002/rra.726.

Bivand, R., Piras, G., 2015. Comparing implementations of estimation methods for spatial econometrics. J. Stat. Softw. 63, 1–36.

Blanchet, F.G., Legendre, P., Borcard, D., 2008a. Modelling directional spatial processes in ecological data. Ecol. Model 215, 325–336. http://dx.doi.org/10.1016/j.ecolmodel.2008.04.001.

Blanchet, F.G., Legendre, P., Borcard, D., 2008b. Forward selection of explanatory variables. Ecology 89, 2623–2632. http://dx.doi.org/10.1890/07-0986.1.

Blanchet, F.G., Legendre, P., Maranger, R., Monti, D., Pepin, P., 2011. Modelling the effect of directional spatial ecological processes at different scales. Oecologia 166, 357–368. http://dx.doi.org/10.1007/s00442-010-1867-y.

Borcard, D., Legendre, P., Drapeau, P., 1992. Partialling out the spatial component of ecological variation. Ecology 73, 1045–1055. http://dx.doi.org/10.2307/1940179.

Brown, B.L., Swan, C.M., 2010. Dendritic network structure constrains metacommunity properties in riverine ecosystems. J. Anim. Ecol. 79, 571–580. http://dx.doi.org/10.1111/j.1365-2656.2010.01668.x.

Brown, B.L., Swan, C.M., Auerbach, D.A., Campbell Grant, E.H., Hitt, N.P., Maloney, K.O., Patrick, C., 2011. Metacommunity theory as a multispecies, multiscale framework for studying the influence of river network structure on riverine communities and ecosystems. J. North Am. Benthol. Soc. 30, 310–327. http://dx.doi.org/10.1899/10-129.1.

Capel Molina, J.J., 2000. El clima de la Península Ibérica. Ariel, Barcelona.

Chase, J.M., 2007. Drought mediates the importance of stochastic community assembly. Proc. Natl. Acad. Sci. 104, 17430–17434. http://dx.doi.org/10.1073/pnas.0704350104.

Cohen, A.C., Morin, J.G., 1990. Patterns of reproduction in ostracodes: a review. J. Crustac. Biol. 10, 184–211. http://dx.doi.org/10.2307/1548480.

Cottenie, K., 2005. Integrating environmental and spatial processes in ecological community dynamics. Ecol. Lett. 8, 1175–1182. http://dx.doi.org/10.1111/j.1461-0248.2005.00820.x.

Curry, B.B., Delorne, L.D., Smith, A.J., Palmer, D.F., Stiff, B.J., 2012. The biogeography and physicochemical characteristics of aquatic habitats of freshwater ostracods in Canada and the United States. In: Horne, D., Holmes, J.A., Rodríguez-Lázaro, J., Viehberg, F.A. (Eds.), Ostracoda as Proxies for Quaternary Climate Change. Elsevier, Amsterdam, pp. 85–115. http://dx.doi.org/10.1016/B978-0-444-53636-5.00006-8.

Datry, T., Bonada, N., Heino, J., 2015. Towards understanding the organisation of metacommunities in highly dynamic ecological systems. Oikos. http://dx.doi.org/10.1111/oik.02922 n/a–n/a.

De Bie, T., De Meester, L., Brendonck, L., Martens, K., Goddeeris, B., Ercken, D., Hampel, H., Denys, L., Vanhecke, L., Van der Gucht, K., Van Wichelen, J., Vyverman, W., Declerck, S. a. J., 2012. Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. Ecol. Lett. 15, 740–747. http://dx.doi.org/10.1111/j.1461-0248.2012.01794.x.

Dole-Olivier, M.-J., Galassi, D.M.P., Marmonier, P., Creuzé Des Châtelliers, M., 2000. The biology and ecology of lotic microcrustaceans. Freshw. Biol. 44, 63–91. http://dx.doi.org/10.1046/j.1365-2427.2000.00590.x.

Dray, S., 2013. spacemakeR: Spatial Modelling. R package version 0.0-5/r113. http://R-Forge.R-project.org/projects/sedar/.

Dray, S., Legendre, P., Peres-Neto, P.R., 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecol. Model 196, 483–493. http://dx.doi.org/10.1016/j.ecolmodel.2006.02.015.

Dray, S., Pélissier, R., Couteron, P., Fortin, M.-J., Legendre, P., Peres-Neto, P.R., Bellier, E., Bivand, R., Blanchet, F.G., De Cáceres, M., Dufour, A.-B., Heegaard, E., Jombart, T., Munoz, F., Oksanen, J., Thioulouse, J., Wagner, H.H., 2012. Community ecology in the age of multivariate multiscale spatial analysis. Ecol. Monogr. 82, 257–275. http://dx.doi.org/10.1890/11-1183.1.

Escrivà, A., Poquet, J.M., Mesquita-Joanes, F., 2015. Effects of environmental and spatial variables on lotic ostracod metacommunity structure in the Iberian Peninsula. Inland Waters 5, 283–294. http://dx.doi.org/10.5268/IW-5.3.771.

Escrivà, A., Smith, R.J., Aguilar-Alberola, J.A., Kamiya, T., Karanovic, I., Rueda, J., Schornikov, E.I., Mesquita-Joanes, F., 2012. Global distribution of *Fabaeformiscandona subacuta*: an exotic invasive Ostracoda on the Iberian Peninsula? J. Crustac. Biol. 32, 949–961. http://dx.doi.org/10.1163/1937240X-00002096.

Fagan, W.F., 2002. Connectivity, fragmentation, and extinction risk in dendritic metapopulations. Ecology 83, 3243–3249. http://dx.doi.org/10.1890/0012-9658(2002)083 [3243:CFAERI]2.0.CO;2.

Figuerola, J., Green, A.J., Santamaría, L., 2003. Passive internal transport of aquatic organisms by waterfowl in Doñana, south-west Spain. Glob. Ecol. Biogeogr. 12, 427–436. http://dx.doi.org/10.1046/j.1466-822X.2003.00043.x.

Fuhrmann, R., Goth, K., 2011. Neue und weitere bemerkenswerte Ostrakoden aus dem Quartär Mitteldeutschlands. Palaeontogr. Abt. A 294, 95–201.

Göthe, E., Angeler, D.G., Gottschalk, S., Löfgren, S., Sandin, L., 2013a. The influence of environmental, biotic and spatial factors on diatom metacommunity structure in swedish headwater streams. PLoS One 8, e72237. http://dx.doi.org/10.1371/journal.pone.0072237.

Göthe, E., Angeler, D.G., Sandin, L., 2013b. Metacommunity structure in a small boreal stream network. J. Anim. Ecol. 82, 449–458. http://dx.doi.org/10.1111/1365-2656.12004.

Grant, E.H.C., Lowe, W.H., Fagan, W.F., 2007. Living in the branches: population dynamics and ecological processes in dendritic networks. Ecol. Lett. 10, 165–175. http://dx.doi.org/10.1111/j.1461-0248.2006.01007.x.

Green, A.J., Jenkins, K.M., Bell, D., Morris, P.J., Kingsford, R.T., 2008. The potential role of waterbirds in dispersing invertebrates and plants in arid Australia. Freshw. Biol. 53, 380–392. http://dx.doi.org/10.1111/j.1365-2427.2007.01901.x.

Grönroos, M., Heino, J., Siqueira, T., Landeiro, V.L., Kotanen, J., Bini, L.M., 2013. Metacommunity structuring in stream networks: roles of dispersal mode, distance type, and regional environmental context. Ecol. Evol. 3, 4473–4487. http://dx.doi.org/10.1002/ece3.834.

Hájek, M., Roleček, J., Cottenie, K., Kintrová, K., Horsák, M., Poulíčková, A., Hájková, P., Fránková, M., Dítě, D., 2011. Environmental and spatial controls of biotic assemblages in a discrete semi-terrestrial habitat: comparison of organisms with different dispersal abilities sampled in the same plots. J. Biogeogr. 38, 1683–1693. http://dx.doi.org/10.1111/j.1365-2699.2011.02503.x.

Heino, J., Grönroos, M., Soininen, J., Virtanen, R., Muotka, T., 2012. Context dependency and metacommunity structuring in boreal headwater streams. Oikos 121, 537–544. http://dx.doi.org/10.1111/j.1600-0706.2011.19715.x.

Heino, J., Melo, A.S., Siqueira, T., Soininen, J., Valanko, S., Bini, L.M., 2015. Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. Freshw. Biol. 60, 845–869. http://dx.doi.org/10.1111/fwb.12533.

Heino, J., Mykrä, H., 2008. Control of stream insect assemblages: roles of spatial configuration and local environmental factors. Ecol. Entomol. 33, 614–622. http://dx.doi.org/10.1111/j.1365-2311.2008.01012.x.

Heino, J., Peckarsky, B.L., 2014. Integrating behavioral, population and large-scale approaches for understanding stream insect communities. Curr. Opin. Insect Sci. Ecol. 2, 7–13. http://dx.doi.org/10.1016/j.cois.2014.06.002.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978. http://dx.doi.org/10.1002/joc.1276.

Holyoak, M., Leibold, M.A., Mouquet, N., Holt, R.D., Hoopes, M.F., 2005. A framework for large-scale community ecology. In: Holyoak, M., Leibold, M.A., Holt, R.D. (Eds.), Metacommunities: Spatial Dynamics and Ecological Communities. University of Chicago Press, Chicago, pp. 1–31.

Horne, D.J., Mezquita, F., 2008. Palaeoclimatic applications of large databases:

developing and testing methods of palaeotemperature reconstruction using nonmarine ostracods. Senckenberg. Lethaea 88, 93–112. http://dx.doi.org/10.1007/BF03043981.

Kärnä, O., Grönroos, M., Antikainen, H., Hjort, J., Ilmonen, J., Paasivirta, L., Heino, J., 2015. Inferring the effects of potential dispersal routes on the metacommunity structure of stream insects: as the crow flies, as the fish swims or as the fox runs? J. Anim. Ecol. 84, 1342–1353. http://dx.doi.org/10.1111/1365-2656.12397.

Landeiro, V.L., Bini, L.M., Melo, A.S., Pes, A.M.O., Magnusson, W.E., 2012. The roles of dispersal limitation and environmental conditions in controlling caddisfly (Trichoptera) assemblages. Freshw. Biol. 57, 1554–1564. http://dx.doi.org/10.1111/j.1365-2427.2012.02816.x.

Landeiro, V.L., Magnusson, W.E., Melo, A.S., Espírito-Santo, H.M.V., Bini, L.M., 2011. Spatial eigenfunction analyses in stream networks: do watercourse and overland distances produce different results? Freshw. Biol. 56, 1184–1192. http://dx.doi.org/10.1111/j.1365-2427.2010.02563.x.

Legendre, P., Legendre, L.F., 2012. Numerical Ecology. Elsevier, Amsterdam.

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., Gonzalez, A., 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecol. Lett. 7, 601–613. http://dx.doi.org/10.1111/j.1461-0248.2004.00608.x.

Lindström, E.S., Langenheder, S., 2012. Local and regional factors influencing bacterial community assembly. Environ. Microbiol. Rep. 4, 1–9. http://dx.doi.org/10.1111/j.1758-2229.2011.00257.x.

Logue, J.B., Mouquet, N., Peter, H., Hillebrand, H., 2011. Empirical approaches to metacommunities: a review and comparison with theory. Trends Ecol. Evol. 26, 482–491. http://dx.doi.org/10.1016/j.tree.2011.04.009.

Maloney, K.O., Munguia, P., 2011. Distance decay of similarity in temperate aquatic communities: effects of environmental transition zones, distance measure, and life histories. Ecography 34, 287–295. http://dx.doi.org/10.1111/j.1600-0587.2010.06518.x.

Marmonier, P., Creuze des Chatelliers, M., 1992. Biogeography of the benthic and interstitial living ostracods (Crustacea) of the Rhone river (France). J. Biogeogr. 19, 693–704. http://dx.doi.org/10.2307/2845710.

Martens, K., 1990. Taxonomic revision of African Cypridini. Part I. The genera *Cypris* O. F. Müller, *Pseudocypris* Daday and *Globocypris* Klie. Bull. Van Het K. Belg. Inst. Voor NatuurwetenschappenBiologie 60, 127–172.

Martens, K., Schön, I., Meisch, C., Horne, D.J., 2008. Global diversity of ostracods (Ostracoda, Crustacea) in freshwater. Hydrobiologia 595, 185–193. http://dx.doi.org/10.1007/s10750-007-9245-4.

Meisch, C., 2000. Freshwater Ostracoda of Western and Central Europe. Spektrum Akademischer Verlag.

Mesquita-Joanes, F., Smith, A.J., Viehberg, F.A., 2012. The ecology of Ostracoda across levels of biological organisation from individual to ecosystem: a review of recent developments and future potential. In: Horne, David J., H., J.A., Rodriguez-Lazaro, Julio, Viehberg, Finn A. (Eds.), Developments in Quaternary Sciences, Ostracoda as Proxies for Quaternary Climate Change. Elsevier, pp. 15–35.

Mezquita, F., Griffiths, H.I., Dominguez, M.I., Lozano-Quilis, M.A., 2001. Ostracoda (Crustacea) as ecological indicators : a case study from Iberian Mediterranean brooks. Arch. Für Hydrobiol. 150, 545–560.

Mezquita, F., Griffiths, H.I., Sanz, S., Soria, J.M., Piñón, A., 1999a. Ecology and distribution of ostracods associated with flowing waters in the Eastern Iberian Peninsula. J. Crustac. Biol. 19, 344–354. http://dx.doi.org/10.2307/1549241.

Mezquita, F., Hernández, R., Rueda, J., 1999b. Ecology and distribution of ostracods in a polluted Mediterranean river. Palaeogeogr. Palaeoclimatol. Palaeoecol. 148, 87–103. http://dx.doi.org/10.1016/S0031-0182(98)00177-1.

Mezquita, F., Roca, J.R., Reed, J.M., Wansard, G., 2005. Quantifying species–environment relationships in non-marine Ostracoda for ecological and palaeoecological studies: examples using Iberian data. Palaeogeogr. Palaeoclimatol. Palaeoecol. 225, 93–117. http://dx.doi.org/10.1016/j.palaeo.2004.02.052.

Mezquita, F., Sanz-Brau, A., Miracle, M.R., 1996. New data on freshwater ostracod assemblages (Crustacea, Ostracoda) from Cuenca (Central Spain). Bull. Soc. Nat. Luxemb. 97, 239–247.

Mezquita, F., Tapia, G., Roca, J.R., 1999c. Ostracoda from springs on the eastern Iberian Peninsula: ecology, biogeography and palaeolimnological implications. Palaeogeogr. Palaeoclimatol. Palaeoecol. 148, 65–85. http://dx.doi.org/10.1016/S0031-0182(98)00176-X.

Miyazono, S., Taylor, C.M., 2013. Effects of habitat size and isolation on species immigration–extinction dynamics and community nestedness in a desert river system. Freshw. Biol. 58, 1303–1312. http://dx.doi.org/10.1111/fwb.12127.

Nabout, J.C., Siqueira, T., Bini, L.M., Nogueira, I. de S., 2009. No evidence for environmental and spatial processes in structuring phytoplankton communities. Acta Oecol. 35, 720–726. http://dx.doi.org/10.1016/j.actao.2009.07.002.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2015. Vegan: Community Ecology Package. R package version 2.3-1. http://CRAN.R-project.org/package=vegan.

Padial, A.A., Ceschin, F., Declerck, S.A.J., De Meester, L., Bonecker, C.C., Lansac-Tôha, F.A., Rodrigues, L., Rodrigues, L.C., Train, S., Velho, L.F.M., Bini, L.M., 2014. Dispersal ability determines the role of environmental, spatial and temporal drivers of metacommunity structure. PLoS One 9, e111227. http://dx.doi.org/10.1371/journal.pone.0111227.

Peres-Neto, P.R., Legendre, P., Dray, S., Borcard, A., Daniel, A., 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. Ecology 87, 2614–2625. http://dx.doi.org/10.1890/0012-9658(2006)87 [2614:

VPOSDM]2.0.CO;2.

Pérez-Cueva, A., 1994. Atlas Climático de la Comunidad Valenciana. Consellería de Territori i Habitatge. Generalitat Valenciana, Valencia.

Petersen, I., Masters, Z., Hildrew, A.G., Ormerod, S.J., 2004. Dispersal of adult aquatic insects in catchments of differing land use. J. Appl. Ecol. 41, 934–950. http://dx.doi.org/10.1111/j.0021-8901.2004.00942.x.

Poquet, J.M., Mesquita-Joanes, F., 2011. Combined effects of local environment and continental biogeography on the distribution of Ostracoda. Freshw. Biol. 56, 448–469. http://dx.doi.org/10.1111/j.1365-2427.2010.02511.x.

QGIS Development Team, 2014. QGIS Geographic Information System. Open Source Geospatial Foundation Project.

Quinn, G.P., Keough, M.J., 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press.

Rádková, V., Bojková, J., Křoupalová, V., Schenková, J., Syrovátka, V., Horsák, M., 2014. The role of dispersal mode and habitat specialisation in metacommunity structuring of aquatic macroinvertebrates in isolated spring fens. Freshw. Biol. 59, 2256–2267. http://dx.doi.org/10.1111/fwb.12428.

R Development Core Team, 2013. R: a Language and Environment for Statistical Computing. R foundation for statistical computing, Vienna.

Tachet, H., Richoux, P., Bournaud, M., Usseglio-Polaterra, P., 2000. Invertébrés d'Eua Douce: systématique, biologie, écologie. CNRS Editions, Paris.

Urban, M.C., Skelly, D.K., Burchsted, D., Price, W., Lowry, S., 2006. Stream communities across a rural–urban landscape gradient. Divers. Distrib. 12, 337–350. http://dx.doi.org/10.1111/j.1366-9516.2005.00226.x.

Valls, L., Castillo-Escrivà, A., Mesquita-Joanes, F., Armengol, X., 2015. Human-mediated dispersal of aquatic invertebrates with waterproof footwear. Ambio. http://dx.doi.org/10.1007/s13280-015-0689-x.

Van der Gucht, K., Cottenie, K., Muylaert, K., Vloemans, N., Cousin, S., Declerck, S., Jeppesen, E., Conde-Porcuna, J.-M., Schwenk, K., Zwart, G., Degans, H., Vyverman, W., Meester, L.D., 2007. The power of species sorting: local factors drive bacterial community composition over a wide range of spatial scales. Proc. Natl. Acad. Sci. 104, 20404–20409. http://dx.doi.org/10.1073/pnas.0707200104.

Vanschoenwinkel, B., Gielen, S., Seaman, M., Brendonck, L., 2008a. Any way the wind blows - frequent wind dispersal drives species sorting in ephemeral aquatic communities. Oikos 117, 125–134. http://dx.doi.org/10.1111/j.2007.0030-1299.16349.x.

Vanschoenwinkel, B., Gielen, S., Vandewaerde, H., Seaman, M., Brendonck, L., 2008b. Relative importance of different dispersal vectors for small aquatic invertebrates in a rock pool metacommunity. Ecography 31, 567–577. http://dx.doi.org/10.1111/j.0906-7590.2008.05442.x.

Zhai, M., Nováček, O., Výravský, D., Syrovátka, V., Bojková, J., Helešic, J., 2015. Environmental and spatial control of ostracod assemblages in the Western Carpathian spring fens. Hydrobiologia 745, 225–239. http://dx.doi.org/10.1007/s10750-014-2104-1.

Appendix A

Supplementary data

The role of watercourse versus overland dispersal and niche effects on

ostracod distribution in Mediterranean streams (eastern Iberian

Peninsula)

List of sampling sites (locality, river basin, coordinates and altitude). Mean annual temperature, stream width and IBMWP values are also shown.

Locality	Basin	Longitude (°)	Latitude (°)	Altitude (m)	T. mean (°C)	Width	IBMWP
Sueras	Veo	-0.368	39.940	400	12.4	2	175
Alcudia de Veo	Veo	-0.337	39.928	350	13.4	2	174
Ahín	Veo	-0.343	39.897	520	12.5	2	200
Artana	Veo	-0.278	39.882	280	13.0	2	180
Cedrillas	Millars	-0.797	40.419	1458	7.6	2	218
Formiche Alto	Millars	-0.890	40.362	1200	8.6	3	116
Mora de Rubielos	Millars	-0.769	40.161	840	10.7	3	149
Puebla de Arenoso	Millars	-0.615	40.129	620	11.9	3	163
Montanejos	Millars	-0.508	40.073	460	12.8	3	115
Torrechiva	Millars	-0.383	40.044	300	13.5	3	108
Fanzara	Millars	-0.302	40.007	200	14.3	4	130
Puebla de Arenoso	Millars	-0.607	40.127	625	11.7	1	174
Fuente la Reina	Millars	-0.623	40.073	820	10.9	2	117
Montán	Millars	-0.554	40.032	560	12.2	3	152
Cortes de Arenoso	Millars	-0.541	40.188	1000	9.9	1	98
Espadilla	Millars	-0.333	40.011	280	13.9	2	154
Linares de Mora	Millars	-0.576	40.326	1560	8.1	1	14
Villahermosa	Millars	-0.437	40.216	780	11.0	3	151
Castillo de Villamalefa	Millars	-0.383	40.143	580	12.0	3	231

Locality	Basin	Longitude (º)	Latitude (º)	Altitude (m)	T. mean (ºC)	Width	IBMWP
Argelita	Millars	-0.351	40.042	280	13.8	3	182
Villahermosa	Millars	-0.474	40.167	940	10.0	2	36
Bejís	Palància	-0.733	39.925	820	10.3	2	228
Teresa	Palància	-0.655	39.898	632	12.2	2	154
Jérica	Palància	-0.560	39.899	440	13.2	2	91
Navajas	Palància	-0.500	39.874	400	13.4	2	82
Soneja	Palància	-0.413	39.809	280	14.2	2	74
Sot de Ferrer	Palància	-0.412	39.810	220	14.2	3	70
Sagunt	Palància	-0.269	39.671	50	15.3	4	5
El Toro 1	Palància	-0.754	39.934	1000	9.8	2	179
El Toro 2	Palància	-0.738	39.936	844	10.6	3	109
Bejís	Palància	-0.722	39.906	740	11.2	2	184
Teresa	Palància	-0.660	39.881	688	11.6	1	50
Viver	Palància	-0.614	39.937	655	11.9	2	137
Jérica	Palància	-0.546	39.916	502	13.0	1	91
Gaibiel 1	Palància	-0.486	39.939	539	12.6	2	123
Gaibiel 2	Palància	-0.497	39.923	490	12.8	1	144
Algimia de Almonacid	Palància	-0.439	39.917	480	12.6	2	95
Azuébar	Palància	-0.372	39.874	560	11.7	1	128
Torres Torres	Palància	-0.398	39.731	215	14.3	2	63

Metacommunity dynamics of Ostracoda in temporary lakes: overall strong niche effects except at the onset of the flooding period

Llacuna d'Alcahozo

Metacommunity dynamics of Ostracoda in temporary lakes: overall strong niche effects except at the onset of the flooding period.

Andreu Castillo-Escrivà[a], Luis Valls[a], Carlos Rochera[a,b], Antonio Camacho[a], Francesc Mesquita-Joanes[a]

[a] *Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, Catedrático José Beltrán 2, E-46980 Paterna, Spain.*

[b] *Regional Centre for Water Studies (CREA), University of Castilla-La Mancha, Camilo José Cela s/n, E-13071, Ciudad Real, Spain.*

Abstract

Metacommunity research usually focuses on the structure of species assemblages and their influencing factors, chiefly environment and space. However, the temporal dynamics of metacommunities and their structuring processes are rarely investigated. Here, we analyze the temporal variations in a metacommunity of ostracods from temporary shallow lakes of the Iberian Peninsula. Our aims were to determine the variability of the ostracod assemblages throughout a hydrological cycle by means of partial triadic analysis (PTA), and to analyze the response of these communities to both environmental and spatial variables. The metacommunity was moderately stable through the study period, with larger variability between sites than between months. However, the metacommunity structure at the beginning of the hydroperiod was notably different from the rest of months. Species sorting was the predominant mechanism structuring the metacommunity through monthly samples, establishing a conspicuous separation between species that inhabit saline lakes and those preferring freshwater bodies. Spatial processes were negligible. Our results show the strength of a temporal approach in the study of metacommunities, against a single

snapshot, stressing differences at the onset and the end of hydroperiod in temporary water bodies, but still surpassed by species sorting effects under a steep environmental gradient.

Keywords: Niche effects; Dispersal limitation; Metacommunities; Ostracods; Shallow lakes

Introduction

Research in metacommunity ecology has recently focused on the study of community patterns and their relationship with underlying mechanisms, such as species sorting and dispersal processes (Heino *et al*., 2015). Although these patterns may vary through time, most studies have analyzed metacommunities at a single point in time, with a few exceptions (*e.g.*, Erős *et al*., 2012; Fernandes *et al*., 2014; Korhonen *et al*., 2013). As a result, ecologists may find inconsistent conclusions using only a snapshot, because the same study carried out at different occasions could provide different results.

The variability of the results on community organization through time may strongly depend on the life history of the studied organisms and the frequency at which a system is visited. In fact, a single snapshot approach could be adequate for groups of organisms with low dispersal capacity and slow population dynamics (*e.g.*, shrub communities). Yet, it could be markedly inefficient in other organisms with high temporal variations, for instance, animals with active dispersal capacities (*e.g.*, stream fishes; Fernandes *et al*., 2014) or organisms with passive dispersal, small body size, high population densities and fast population dynamics (*e.g.*, bacteria; Langenheder *et al*., 2012). In addition, metacommunity variability can also be related to different habitat conditions, for instance, Korhonen *et al*. (2013) found differences in temporal variation of diatom metacommunities among eutrophic, mesotrophic and oligotrophic streams, being the latest more stable than others.

Previous studies suggest that the relevance of species sorting may increase during periods with high environmental heterogeneity (*e.g.*, Chase & Leibold, 2003; Heino *et al*., 2012; Langenheder *et al*., 2012). Large environmental gradients are often related to extreme events. For instance, the invertebrate communities of boreal streams relate more tightly to environmental conditions in spring, when flood events cause environmental

extremes (*e.g.*, a marked decrease in pH), than in autumn (Göthe *et al.*, 2013). In fact, extreme events lead to strong species sorting because only a fraction of the community can inhabit the newly established conditions (Chase, 2007; Lepori & Malmqvist, 2009; Vanschoenwinkel *et al.*, 2010). On the other hand, spatial control also varies in importance through time. In the above mentioned boreal streams example, space was also more relevant in spring than in autumn, because floods favoured dispersal processes (Göthe *et al.*, 2013). In this line, Fernandes *et al.* (2014) suggested that connectivity is only important at the beginning of the flooding season in a metacommunity of fishes of a floodplain in South America. Therefore, the cycle of wetting and drying can promote changes in the relative importance of species sorting and dispersal through time (Medley & Havel, 2007).

Here, we analyzed the variation in a set of ostracod communities from shallow temporary lakes throughout one hydrological cycle, and their relationship with environmental and spatial variables. Ostracods are small crustaceans with passive dispersal, which can be transported among these lakes by wind (Vanschoenwinkel *et al.*, 2008) or other animals (Green *et al.*, 2008), decreasing dispersal limitation. On the other hand, the ostracods that inhabit these temporary lakes have developed many strategies in order to maintain their populations in these kind of habitats, such as production of diapausing eggs (Meisch, 2000). A recent snapshot study (Castillo-Escrivà *et al.*, 2016) of an ostracod metacommunity in these lakes in spring stressed the major importance of species sorting, chiefly by salinity and hydroperiod, besides spatial effects. However, taking into account the successional changes in ostracod community composition that may happen in temporary habitats (McLay, 1978), we expect to find also variations in the relative influence of structuring factors of such type of metacommunities through time, unless there was a tight biotic response to environmental variation.

Material and methods

Study area

The studied shallow lakes are situated in the Biosphere Reserve of La Mancha

Húmeda, on the plains of Castilla – La Mancha (Central Iberian Peninsula; 38.6º - 39.8º N, 4.4º - 2.6º W; Camacho *et al.*, 2003). These lakes are hydrologically isolated systems, surrounded by an arid landscape, which represent the main steppic wetland of Western Europe (Alonso, 1998). They are mostly temporary, and generally fill up during fall and dry out in late spring (April - June), although in some lakes the flooding period has been reduced due to aquifer overexploitation (*i.e.* more ephemeral) or increased as a consequence of sewage spills (*i.e.* more permanent waters). In this dry landscape, there is a wide salinity variation among lakes, from fresh to hypersaline waters (Table 1).

Table 1. Lakes sampled, their location and average values of the measured environmental variables in the study period.

Code	Lake	Long (°)	Lat (°)	Cond	pH	Oxy	Chla	NO3	NH4	TP	LOI$_{550}$	LOI$_{950}$
ALC	Alcahozo	-2.88	39.39	28.6	8.0	9.3	12.1	1.1	0.5	0.3	16.9	2.5
ALM	Almodóvar	-4.16	38.70	7.8	9.2	5.9	7.7	2.8	0.0	6.8	3.4	5.1
CAV	Camino de Villafranca	-3.41	39.58	30.2	8.8	9.1	143.0	2.0	0.4	0.8	18.5	3.7
CRC	Caracuel	-4.07	38.82	1.5	8.5	10.1	4.	1.0	0.3	0.2	6.0	0.8
LVC	Larga de Villacañas	-3.31	39.61	32.3	9.3	14.1	461.1	3.6	0.3	1.6	15.7	6.3
MAN	Manjavacas	-2.86	39.42	7.0	8.3	10.2	28.0	0.6	0.3	0.4	10.5	11.7
NGR	Nava Grande	-3.94	39.18	2.1	8.0	12.1	1.0	1.1	0.2	0.2	17.7	4.7
POZ	Pozuelo	-3.83	38.92	12.0	8.3	10.5	6.4	2.0	0.8	0.5	19.9	6.9
SLC	Salicor	-3.18	39.46	73.0	8.7	6.4	82.7	1.7	0.3	1.0	2.8	4.1
VGU	La Veguilla	-3.24	39.40	2.6	8.3	10.4	7.9	1.0	0.4	0.7	9.9	7.5

Long = longitude; Lat = latitude; Cond = water electrical conductivity (mS cm^{-1}); concentrations in water of; Oxy = dissolved oxygen (mg L^{-1}), Chla = chlorophyll-*a* (µg L^{-1}), NO3 = nitrate (mg L^{-1}), NH4 = ammonium (mg L^{-1}), and TP = total phosphorus (mg L^{-1}); LOI$_{550}$ = percent of the organic matter content in the sediments (%); LOI$_{950}$ = percent of the carbonate content (%) in the sediments.

Sampling and data sets

We sampled 10 lakes monthly, from December 2012 to May 2013 (60 samples). The lakes were flooded in November 2012, and most were already dry in June 2013. At each sampling occasion, we collected ostracod samples with a hand net (250 µm mesh size) over an approximate area of 2 m^2, and fixed them in situ with formaldehyde 4%. In the laboratory, ostracods were identified to species level following Meisch (2000), counted and stored in 70% ethanol.

We measured 9 environmental variables: water electrical conductivity (mS cm^{-1}), pH and dissolved oxygen concentration (mg L^{-1}) were measured in the field using portable probes, and water samples were gathered for subsequent analyses of the concentrations of nitrate (mg L^{-1}), ammonium (mg L^{-1}) and total phosphorus content (mg L^{-1}) following Golterman *et al*. (1978). Water samples were filtered through Whatman GF/F glass fibre filters to extract Chlorophyll a with acetone (DMSO 1:1 v/v; Shoaf & Lium, 1976) and determine its concentration (μg L^{-1}) with a spectrophotometer according to Jeffrey and Humphrey (1975). In addition, we obtained surface sediment samples in order to determine the organic matter (LOI$_{550}$) and carbonate proportion (LOI$_{950}$) in the lake sediment, by means of the loss on ignition method (Heiri *et al*., 2001).

Moran Eigenvector Maps (MEMs; Dray *et al*., 2006) were used as spatial variables. MEMs were calculated from lake geographical coordinates, from a connection network drawn according to the Gabriel graph criterion (Legendre & Legendre, 2012). We used spdep (Bivand & Piras, 2015) and spacemakeR packages (Dray, 2013) for spatial modeling.

Statistical analyses

We performed partial triadic analysis (PTA; Erős *et al*., 2012; Thioulouse & Chessel, 1987; Thioulouse *et al*., 2004) to compare the ostracod assemblage variation among lakes and determine the temporal stability of this structure. PTA allows to analyze three-way data tables (*i.e.* a data cube), such as a species matrix (lakes x species) with a third dimension representing time (months). The analysis consists of two main steps called interstructure and compromise. The interstructure provides the contribution of individual species matrices to the common ecological structure through time and gives a weight to each matrix according to their importance. The compromise calculates an average matrix (*i.e.* a compromise table), with a weighed mean of the different species matrices. The compromise table offers a common structure among sampling periods. After this, the species (abundance) matrices were Hellinger transformed (Legendre & Gallagher, 2001).

PTA provides three useful values to interpret the results: RV coefficients, table weights and cos^2 values. RV coefficients are the pairwise vectorial correlations between

individual matrices and determine the similarity between the different data matrices (Robert & Scourfier, 1976). Table weights are a measure of the contribution of each matrix to the constructed compromise table (Thioulouse *et al*., 2004). $\cos^2$ values indicate the how much information of each matrix is represented by the compromise table.

On the other hand, we determined the relative contribution of both environmental and spatial data sets to the different species matrices and the compromise table. We used variation partitioning analyses (Borcard *et al.*, 1992), which separate the pure fraction of the species matrix variation explained by the environmental data set from the pure spatial fraction. These fractions correspond to the adjusted R^2 of redundancy analysis (RDA; Peres-Neto *et al.*, 2006). Previously, we selected the best combination of variables in each explanatory set, using forward selection with a second stopping criterion (*i.e.* final models retain variables with a p < 0.05 and the final adjusted R2 is not higher than global models built with all the variables; Blanchet *et al*., 2008). As supporting information, we computed the environmental heterogeneity of each month as an average Euclidean distance from sites to a region unit centroid, using the standardized environmental variables (Anderson *et al*., 2006; Heino *et al*., 2015). RDA and variation partitioning were performed using the vegan R package (Oksanen *et al*., 2015) and PTA with ade4 (Dray & Dufour, 2007). All the analyses were carried out with R version 3.0.2 (R Development Core Team, 2013).

Results

We gathered a total of 21 species of ostracods (Table 2). The species richness in each sample was 2.71 ± 2.07 species, and reached a maximum of 7 species in lakes Almodóvar (December) and La Veguilla (April). In these two lakes up to 10 species were recorded through the hydrological cycle, accounting for the highest species richness among studied lakes. The most common species was *Eucypris virens* (21 samples; 5 lakes), followed by *Heterocypris barbara* (20 samples; 5 lakes) and *Heterocypris incongruens* (18 samples; 5 lakes). However, there were some differences in species occurrence among months (Table 1). *Tonnacypris lutaria* and *Ilyocypris biplicata* var. *anomala* were only observed in December, and *Plesiocypridopsis newtoni* only in May. Other species were recorded each month, including *H. barbara*, *H. incongruens* and *Herpetocypris chevreuxi*.

Table 2. List of ostracod species identified in the study and months when they were collected. In parenthesis the number of species found in the ten lakes in each month.

Species	Code	Dec (18)	Jan (11)	Feb (14)	Mar (14)	Apr (15)	May (12)
Tonnacypris lutaria	TLU	x					
Ilyocypris biplicata var. *anomala*	IBI	x					
Candonocypris novaezelandiae	CNO	x				x	
Cypridopsis vidua	CVI	x			x		
Eucypris virens	EVI	x	x	x	x	x	
Candelacypris aragonica	CAR	x	x	x	x	x	
Trajancypris clavata	TCL	x	x		x	x	
Cypridopsis parva	CPA	x		x			x
Heterocypris salina	HSA	x			x	x	x
Limnocythere inopinata	LIN	x		x	x	x	x
Sarscypridopsis sp.[a]	SAR	x	x	x		x	x
Ilyocypris gibba	IGI	x	x	x	x	x	x
Cypris bispinosa	CBI	x	x	x	x	x	x
Herpetocypris chevreuxi	HCH	x	x	x	x	x	x
Heterocypris incongruens	HIN	x	x	x	x	x	x
Heterocypris barbara	HBA	x	x	x	x	x	x
Sarscypridopsis aculeata	SAC	x	x	x	x	x	x
Potamocypris arcuata	PAR	x	x	x	x	x	x
Cypridopsis hartwigi	CHA			x	x	x	
Heterocypris sp.[b]	HET			x			
Plesiocypridopsis newtoni	PNE						x

[a]*Sarscypridopsis* sp. is an undescribed *Sarscypridopsis* species, with morphological similarities to other *Sarscypridopsis* sp. found in Madeira by Fuhrmann and Goth (2011) (Fuhrmann, April 2014, pers. comm.), previously identified as *Sarscypridopsis* sp. by Mezquita, Roca, Reed and Wansard (2005).
[b]*Heterocypris* sp. could not be assigned to any known species, and was left in open nomenclature.

The temporal interstructure of the PTA separated December, at the beginning of the flooding period, from the other months (Fig. 1a). Overall, December and May were widely separated. The table weights were similar, ranging from 0.32 to 0.45 (Fig. 1b). However, December and May showed values slightly lower than other months (0.32 and 0.36, respectively). The cos^2 values also revealed that the compromise table was moderately representative of the individual matrices (varied between 0.61 and 0.80), being again
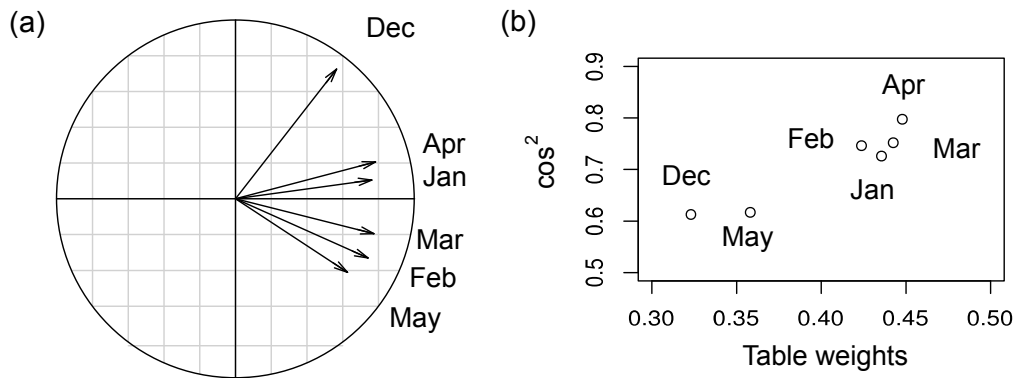
Fig. 1. Interstructure month ordination from RV coefficients (a), and table weights and cos^2 values for each month represented in a scatter plot (b).

having the lowest values found in December and May (Fig. 1b). Therefore, these values indicated that ostracod assemblages varied moderately among the months, but December the first sampling through the hydrological cycle was slightly more different than others as compared to the compromise results. May values were also showing to have a great dissimilarity with December.

Environmental variables influenced the community structure more than spatial variables (Table 3). Indeed, only one spatial variable was selected in February, March and April, being only significant in March after variation partitioning. No variables (neither environmental nor spatial) were selected in December, the first month of the study. Pure environmental control contributed differently to the assemblages from January to May. The pure percentage explained by these variables reached the highest explanation percentage in January (59%), but it was lower in other months, varying between 22% and 37%. Conductivity had a key role among environmental variables, particularly in January (18%) and May (24%). LOI950 and conductivity were selected in the compromise table, explaining 23% of the compromise table variation. We did not find a significant correlation between environmental heterogeneity (Table 3) neither with whole environmental effects (without space; r = 0.55; p = 0.25), nor pure environmental effects (r = 0.67; p = 0.15). December was the month with the lowest environmental heterogeneity.

The first two axes of the PCA of the compromise table and its related RDA with the selected environmental variables showed the same ordination (Fig. 2 a,b). Both ordinations

Table 3. Variation partitioning between environmental (E) and spatial (S) variables, selected by means of forward selection, of each month species matrix and the compromise table. We also provide the selected variables with their explained percentage and the environmental heterogeneity (EH) values as average euclidean distance to centroid. *Com* stands for compromise.

Data set	Pure E Adj. R^2	F	P	Pure S Adj. R^2	F	P	Shared Adj. R^2	Total Adj. R^2	Selected variables E	S
Dec	-	-	-	-	-	-	-	-	-	-
Jan	0.588	4.807	0.001	-	-	-	-	0.588	Cond (18%), LOI_{550} (15%), LOI_{950} (9%)	-
Feb	0.356	2.996	0.003	0.172	2.607	0.081	-0.063	0.465	Cond (8%), Chla (7%)	M7 (11%)
Mar	0.222	2.249	0.016	0.126	2.218	0.050	0.030	0.378	Cond (11%), LOI_{550} (10%)	M8 (16%)
Apr	0.374	2.815	0.009	0.124	2.288	0.114	0.021	0.519	Cond (11%), LOI_{550} (10%), NO3 (8%)	M8 (15%)
May	0.240	3.558	0.004	-	-	-	-	0.240	Cond (24%)	-
Com	0.232	2.356	0.002	-	-	-	-	0.232	Cond (10%), LOI_{950} (11%)	-

present a clear separation between two groups of communities. The first type corresponded to saline lakes (i.e. with high water electrical conductivity), such as Salicor and Alcahozo, situated to the top-left corner of the ordination graph, where we collected the halophilous species *H. barbara* and *Candelacypris aragonica*. The other group correspond to communities of slightly saline and freshwater lakes. Among these, the lakes with the lowest carbonate content (as LOI_{950}) in the sediment (*i.e.* Caracuel and Nava Grande) were ordered to the bottom of the graph. In these lakes, we recorded *H. chevreuxi* and *Cypris bispinosa*, which prefer slightly saline waters of lakes with a relatively long hydroperiod. On the other hand, Manjavacas and La Veguilla, which had the highest content of carbonates in their sediments, were ordered to the right side of the graph. In these lakes, we mainly observed generalist species, typical of temporary waters, such as *H. incongruens* and *E. virens*.

Discussion

Generally, all monthly data sets contributed equally to the compromise table, indicating low variation among months, with the exception of the first sampling campaign
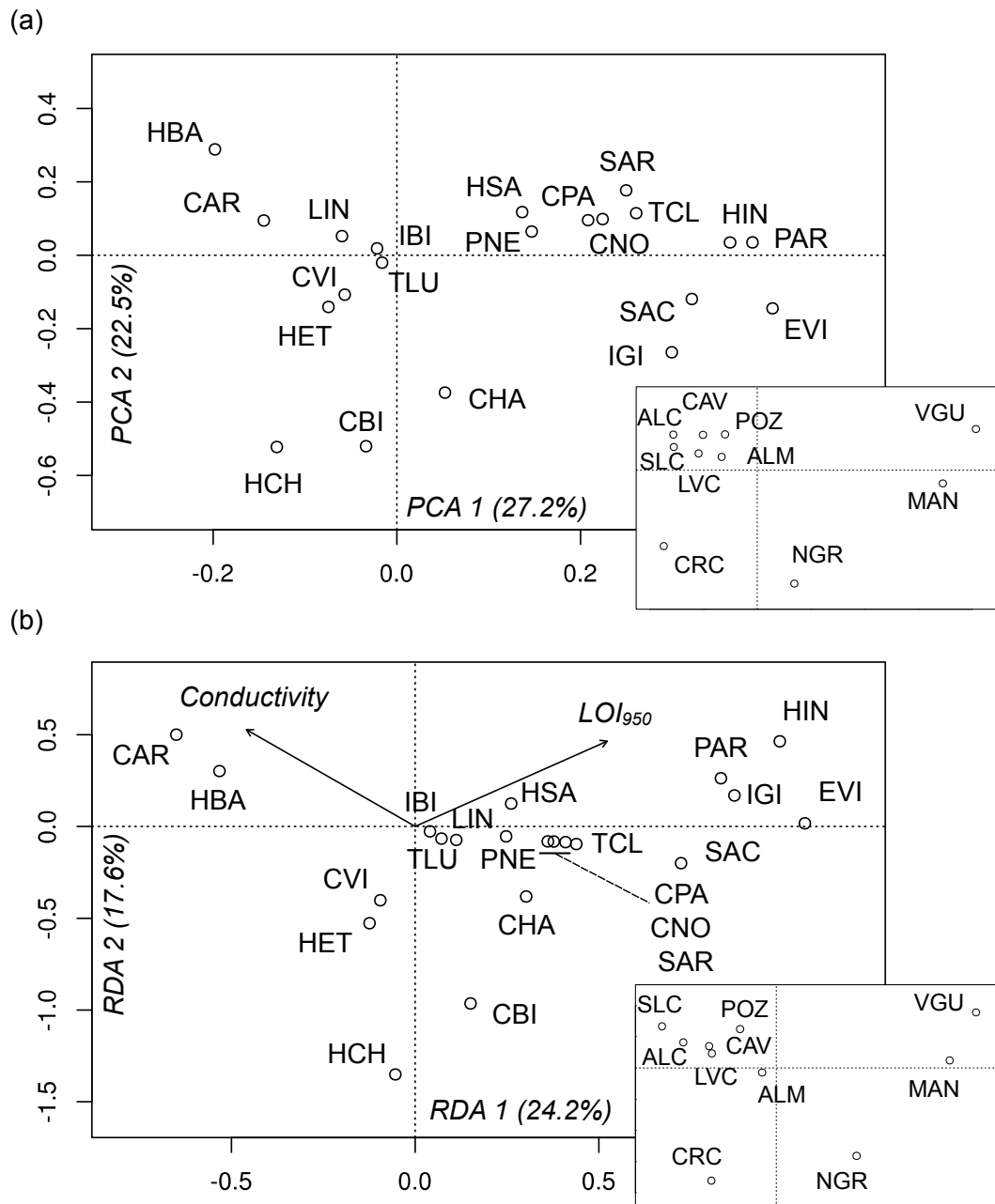
(a)

(b)

Fig. 2. Ordination plots of the first two axes of the PCA of the compromise table (a) and the RDA constrained by selected environmental variables (b). Lake and species codes as in Table 1 and 2, respectively.

in December. Furthermore, variation partitioning determined a general pattern of dominance of environmental effects. Spatial components were less influential in this study. The selected MEMs were related to fine-scale spatial effects (they were associated to negative eigenvalues; Dray *et al*., 2006), and likely correspond to local effects of unmeasured variables, and not to specific spatial processes related to dispersal. The prevalence of species sorting as a structuring mechanism is in agreement with the hypothesis that small organisms with passive dispersal can reach all the environmentally suitable locations, due to a high density of propagules transported by animals (Finlay, 2002; Fenchel & Finlay, 2004), so as with the recognized species-specific water chemistry requirements of Ostracoda (Neale, 1964; Mezquita, 2005; Mesquita-Joanes *et al*., 2012). However, when considering a slightly higher number of sites in the same area, Castillo-Escrivà *et al*. (2016) found spatial effects to be also significant when explaining an ostracod metacommunity, therefore stressing the relevance of spatial gradients and extent considered.

The general structure of the metacommunity separated lakes with halophilous species from others, maintaining their community composition throughout the study. In fact, ionic content (measured as electrical conductivity) was the main environmental variable, and contributed as a strong differentiating factor between different communities. Hence, assemblage composition varied more among sites than among months, as $\cos^2$ values higher than 0.60 indicated good concordance between compromise and individual tables, revealing stability in the metacommunity structure among months, and maintaining the differences in community composition among sites. A similar pattern of a strong environmental limitation maintained through time was observed by Korhonen *et al*. (2013) in diatom communities inhabiting streams with different trophic levels.

December was a singular month because no measured explanatory variable was associated to the ostracod metacommunity structure. The absence of environmental control could be generated by three reasons. First, perhaps we did not measure all appropriate factors. However, some measured variables were selected in other months, and especially conductivity was observed as a relevant factor in these systems (Roca *et al*., 2000). Second, the inundation of the lakes at the beginning of the wet period could lead to a

homogenization of the environmental conditions (Heino *et al*., 2015), in agreement with the lowest environmental heterogeneity in this month. Third, we associate the absence of environmental influence in December mainly to a fast hatching response to inundation from the complex egg bank at the beginning of the wet period, previously observed in ostracods that inhabit temporary waters (Aguilar-Alberola & Mesquita-Joanes, 2011). We envisage in that way an abundant hatching of many opportunistic species, leading to almost random species assemblages, (*i.e.* some species seek their opportunity in suboptimal local conditions), diminishing species sorting effects. In support of this view, December was the month with the highest species richness (18 species). Among them, *T. lutaria* and *I. biplicata* var. *anomala* were only collected in December. Both species are usually recorded in seasonal ponds at the beginning of the rainy season, when water bodies are filled up and temperatures are cold (Coviaga *et al*., 2015; Escrivà *et al*., 2010). These species have therefore evolved r-strategies, under unpredictable hydroperiods (Mesquita-Joanes *et al*., 2012; Stearns, 1976). On the other side, the highest explanatory power of environmental variables in January is likely a consequence of a strong species sorting process, when those individuals suboptimally adapted to local environmental conditions are removed or even later eliminated by the presence of predators (Vanschoenwinkel *et al*., 2010), together with a decrease in hatching as expected from diapausing strategies (Alekseev, 2007).

Conclusions

The ostracod metacommunity structure of the studied lakes was rather stable throughout the study time span, showing more differences between sites than between months. Furthermore, species sorting was the main structuring mechanism, driven by the large salinity range of the lakes.. However, at the beginning of the wet period, no environmental variables were related to the species assemblages, likely because of random structures generated by an abundant hatching of opportunistic species from accumulated egg banks and because of reduced environmental heterogeneity. Our study reveals the potential information acquired from a temporal approach to the metacommunity, improving that obtained from a single snapshot.

Acknowledgements

References

Aguilar-Alberola, J. A., & F. Mesquita-Joanes, 2011. Population dynamics and tolerance to desiccation in a crustacean ostracod adapted to life in small ephemeral water bodies. *Limnologica* 41: 348–355.

Alekseev, V. R., 2007. Diapause in crustaceans: peculiarities of induction. In: Alekseev, V.R., B. T. De Stasio, & J. J. Gilbert, (eds), *Diapause in Aquatic Invertebrates, Theory and Human Use*. Springer Netherlands: 29–64.

Alonso, M., 1998. Las lagunas de la España peninsular. *Limnetica* 15: 1–176.

Anderson, M. J., K. E. Ellingsen, B. H. McArdle, 2006. Multivariate dispersion as a measure of beta diversity. *Ecology Letters* 9: 683–693.

Bivand, R., & G. Piras, 2015. Comparing implementations of estimation methods for spatial econometrics. *Journal of Statistical Software* 63: 1–36.

Blanchet, F. G., P. Legendre, & D. Borcard, 2008. Forward selection of explanatory variables. *Ecology* 89: 2623–2632.

Borcard, D., P. Legendre, & P. Drapeau, 1992. Partialling out the spatial component of ecological variation. *Ecology* 73: 1045–1055.

Camacho, A., M. R. Miracle, E. Vicente, 2003. Which factors determine the abundance and distribution of picocyanobacteria in inland waters? A comparison among different types of lakes and ponds. *Archiv für Hydrobiologie* 157: 321–338.

Castillo-Escrivà, A., L. Valls,,A. Camacho, C. Rochera, & F. Mesquita-Joanes, 2016. Spatial and environmental analysis of an ostracod metacommunity from endorheic lakes. *Aquatic Sciences* 78: 707–716.

Chase, J. M., 2007. Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences* 104: 17430–17434.

Chase, J. M, & M. A. Leibold, 2003. *Ecological Niches: Linking Classical and Contemporary Approaches*. University of Chicago Press, Chicago.

Coviaga, C., G. Cusminsky, N. Baccalá, & A. P. Pérez, 2015. Dynamics of ostracod populations from shallow lakes of Patagonia: life history insights. *Journal of Natural History* 49: 1023–1045.

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

Dray, S., 2013. spacemakeR: spatial modelling (Version 0.0-5/r113).

Dray, S., & A. B. Dufour, 2007. The ade4 package: implementing the duality diagram for ecologists. *Journal of Statistical Software* 22: 1–20.

Dray, S., P. Legendre, & P. R. Peres-Neto, 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecological Modelling* 196: 483–493.

Erős, T., P. Sály, P. Takács, A. Specziár, & P. Bíró, 2012. Temporal variability in the spatial and environmental determinants of functional metacommunity organization – stream fish in a human-modified landscape. *Freshwater Biology* 57: 1914–1928.

Escrivà, A., X. Armengol, & F. Mezquita, 2010. Microcrustacean and rotiferan communities of two close Mediterranean mountain ponds, Lagunas de Bezas and Rubiales (Spain). *Journal of Freshwater Ecology* 25: 427–435.

Fenchel, T., & B. J. Finlay, 2004. The ubiquity of small species: patterns of local and global diversity. *BioScience* 54: 777–784.

Fernandes, I. M., R. Henriques-Silva, J. Penha, J. Zuanon, & P. R. Peres-Neto, 2014. Spatio-temporal dynamics in a seasonal metacommunity structure is predictable: the case of floodplain-fish communities. *Ecography* 37: 464–475.

Finlay, B. J., 2002. Global dispersal of free-living microbial eukaryote species. *Science* 296: 1061–1063.

Fuhrmann, R., & K. Goth, 2011. Neue und weitere bemerkenswerte Ostrakoden aus dem Quartär Mitteldeutschlands. *Palaeontographica Abteilung A* 294: 95–201.

Göthe, E., D. G. Angeler, & L. Sandin, 2013. Metacommunity structure in a small boreal stream network. *Journal of Animal Ecology* 82: 449–458.

Golterman, H. L., R. S. Clymo, & M. A. M. Ohnstad, 1978. *Methods for Physical and Chemical Analysis of Freshwaters. IBP Handbook No. 8*. Blackwell Science Publications, Oxford.

Green, A. J., K. M. Jenkins, D. Bell, P. J. Morris, & R. T. Kingsford, 2008. The potential role of waterbirds in dispersing invertebrates and plants in arid Australia. *Freshwater Biology* 53: 380–392.

Heino, J., A. S. Melo, & L. M. Bini, 2015. Reconceptualising the beta diversity-environmental heterogeneity relationship in running water systems. *Freshwater Biology* 60: 223–235.

Heino, J., A. S. Melo, T. Siqueira, J. Soininen, S. Valanko, & L. M. Bini, 2015. Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. *Freshwater Biology* 60: 845–869.

Heino, J., J. Soininen, R. Virtanen, & T. Muotka, 2012. Context dependency and metacommunity structuring in boreal headwater streams. *Oikos* 121: 537–544.

Heiri, O., A. F. Lotter, & G. Lemcke, 2001. Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. *Journal of Paleolimnology* 25: 101–110.

Jeffrey, S. W., & G. F. Humphrey, 1975. New spectrophotometric equation for determining chlorophylls a, b, c1 and c2 in higher plants, algae and natural phytoplankton. *Biochemie und Physiologie del Pflanzen* 167: 191–194.

Korhonen, J. J., P. Köngäs, & J. Soininen, 2013. Temporal variation of diatom assemblages in oligotrophic and eutrophic streams. *European Journal of Phycology* 48: 141–151.

Langenheder, S., M. Berga, Ö. Östman, & A. J. Székely, 2012. Temporal variation of β-diversity and assembly mechanisms in a bacterial metacommunity. *ISME Journal* 6: 1107–1114.

Legendre, P., & E. D. Gallagher, 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129: 271–280.

Legendre, P., & L. F. Legendre, 2012. *Numerical Ecology*. Elsevier, Amsterdam.

Lepori, F., & B. Malmqvist, 2009. Deterministic control on community assembly peaks at intermediate levels of disturbance. *Oikos* 118: 471–479.

McLay, C. L., 1978. Comparative observations on the ecology of four species of ostracods living in a temporary freshwater puddle. *Canadian Journal of Zoology* 56: 663–675.

Medley, K. A., & J. E. Havel, 2007. Hydrology and local environmental factors influencing zooplankton communities in floodplain ponds. *Wetlands* 27: 864–872.

Meisch, C., 2000. *Freshwater Ostracoda of Western and Central Europe*. Spektrum Akademischer Verlag, Heidelberg.

Mesquita-Joanes, F., A. J. Smith, & F. A. Viehberg, 2012. The ecology of Ostracoda across levels of biological organisation from individual to ecosystem: a review of recent developments and future potential. In: Horne, D.J., J. A. Holmes, J. Rodríguez-Lázaro, & F. A. Viehberg, (eds), *Ostracoda as Proxies for Quaternary Climate Change*. Elsevier, Amsterdam: 15–35.

Mezquita, F., J. R. Roca, J. M. Reed, & G. Wansard, 2005. Quantifying species–environment relationships in non-marine Ostracoda for ecological and palaeoecological studies: Examples using Iberian data. *Palaeogeography, Palaeoclimatology, Palaeoecology* 225: 93–117.

Mezquita, F., G. Tapia, & J. R. Roca, 1999. Ostracoda from springs on the eastern Iberian Peninsula: ecology, biogeography and palaeolimnological implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 148: 65–85.

Neale, 1964. Some factors influencing the distribution of recent British Ostracoda. *Pubblicazioni della Stazione Zoologica di Napoli* 33 (supplement): 247–307.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, & H. Wagner, 2015. vegan: Community Ecology Package (Version 2.2-1). http://CRAN.R-project.org/package=vegan

Peres-Neto, P. R., P. Legendre, S. Dray, & D. Borcard, 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* 87: 2614–2625.

R Development Core Team, 2013. *R: A Language and Environment for Statistical Computing* (Version 3.02). R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org

Robert, P., & Y. Scourfier, 1976. A unifying tool for linear multivariate statistical methods: the RV-

coefficient. *Applied Statistics* 25: 257–265.

Roca, J. R., F. Mezquita, J. Rueda, A. Camacho, & M. R. Miracle, 2000. Endorheic versus karstic lakes: patterns of ostracod distributions and lake typology in a Mediterranean landscape (Castilla - La Mancha, Spain). *Marine and Freshwater Research* 51: 311–319.

Shoaf, W. T., & B. W. Lium, 1976. Improved extraction of chlorophyll-a and b from algae using dimethyl sulfoxide. *Limnology and Oceanography* 21: 926–928.

Stearns, S. C., 1976. Life-history tactics: a review of the ideas. *The Quarterly Review of Biology* 51: 3–47.

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

Thioulouse, J., M. Simier, & D. Chessel, 2004. Simultaneous analysis of a sequence of paired ecological tables. *Ecology* 85: 272–283.

Vanschoenwinkel, B., A. Waterkeyn, M. Jocqué, L. Boven, M. Seaman, & L. Brendonck, 2010. Species sorting in space and time—the impact of disturbance regime on community assembly in a temporary pool metacommunity. *Journal of the North American Benthological Society* 29: 1267–1278.

Vanschoenwinkel, B., S. Gielen, M. Seaman, & L. Brendonck, 2008. Any way the wind blows - frequent wind dispersal drives species sorting in ephemeral aquatic communities. *Oikos* 17: 125–134.

Disentangling environmental, spatial, and historical effects on ostracod communities in shallow lakes
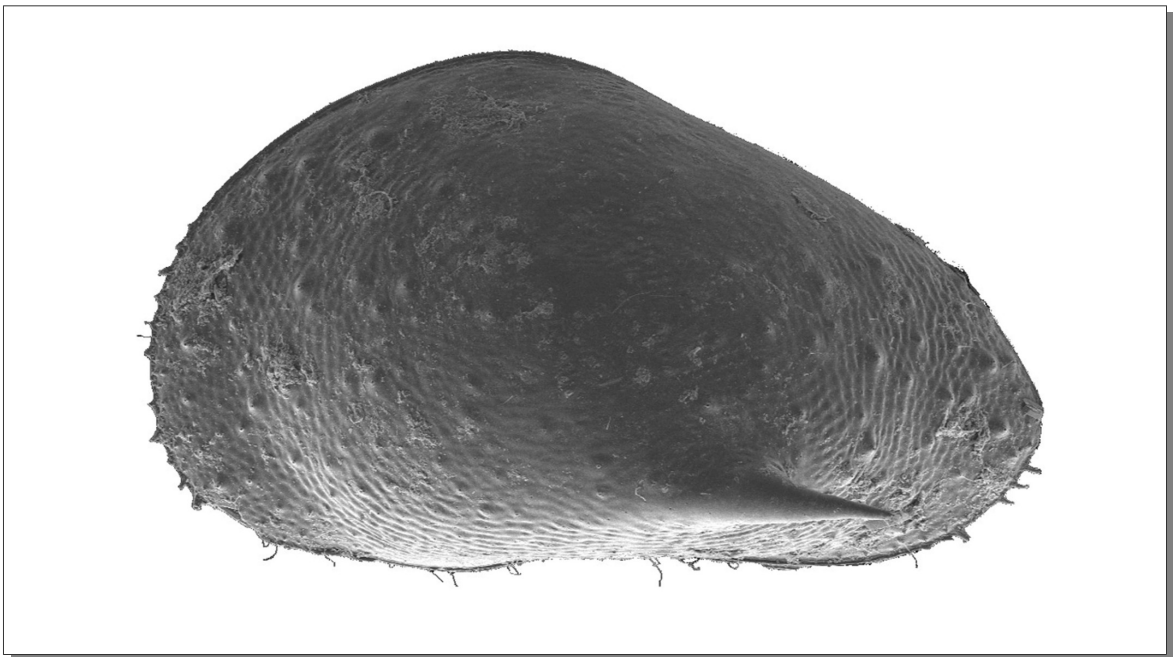
Valva esquerra d'un juvenil de Cypris bispinosa *de Nava Grande de Malagón*

CrossMark

PRIMARY RESEARCH PAPER

Disentangling environmental, spatial, and historical effects on ostracod communities in shallow lakes

Andreu Castillo-Escrivà · Luis Valls · Carlos Rochera · Antonio Camacho · Francesc Mesquita-Joanes

Abstract Community structure is determined by a variety of ecological mechanisms, including environmental control, dispersal, and historical contingency. Recently, many studies have focused on the relative relevance of environment and dispersal in shaping metacommunities. Historical contingency (e.g., priority effects) rarely has been considered, although it could have a key role. In this context, the use of paleoecological methods could help assess the influence of past events on the present-day communities. In this survey, we compare living ostracod assemblages (i.e., biocoenoses) and subfossil assemblages (i.e., taphocoenoses) from 22 steppic shallow lakes and determine the relative contribution of environmental and spatial components on both assemblages. In addition, we estimate the role of putative priority effects of past assemblages on contemporary ones. Our results indicate a high concordance between both assemblages (Procrustes analysis; $r = 0.877$; $P = 0.001$). However, environment dominates over space in explaining the biocoenoses, whereas in taphocoenoses space dominates over environment. Furthermore, the contemporary metacommunity structure was related not only to pure environmental and spatial effects (suggesting species sorting and dispersal constraints) but also notably to pure historical effects, suggesting a significant major role of earlier habitat occupation in these ecosystems.

Keywords Metacommunity · Species sorting · Priority effects · Lakes · Ostracoda

Handling editor: Luis Mauricio Bini

A. Castillo-Escrivà (✉) · L. Valls · C. Rochera · A. Camacho · F. Mesquita-Joanes
Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, Catedrático José Beltrán, 2, 46980 Paterna, Spain
e-mail: andreu.castillo@uv.es

C. Rochera
Regional Centre for Water Studies (CREA), University of Castilla-La Mancha, Ciudad Real, Spain

Introduction

Ecological communities vary in space and time. Their structure is modeled by a complex combination of abiotic factors (e.g., local environmental conditions), biotic factors (e.g., competition or predation pressure), historical contingency (e.g., priority effects) and dispersal processes (Leibold et al., 2004). Disentangling the relative importance of these factors is a major concern in the field of metacommunity ecology (Heino, 2013; Holyoak et al., 2005). Ecologists have carried out numerous surveys focusing on the structuring mechanisms of metacommunities, especially

Ⓐ Springer

87

dedicated to the relative importance of species sorting and dispersal (e.g., Logue et al., 2011; Heino et al., 2015). Recently, an increasing interest has arisen in long-term approaches in aquatic systems (Heino, 2009). Paleoecological methods may be providential in understanding contemporary ecological patterns by allowing understanding past dynamics of species distributions and their environments (Davis, 1994; Rull, 2010). Indeed, the integration of paleolimnological approaches in studies of contemporary aquatic diversity may be more efficient than extensive neolimnological surveys, because sediments commonly accumulate organisms over time and space (Gregory-Eaves & Beisner, 2011).

Paleolimnology has been focused on analyzing long-term environmental changes (Cohen, 2003; Birks & Birks, 2006). Nonetheless, studies using subfossil assemblages, particularly from lake sediments, can also be applied to contemporary ecological questions (Gregory-Eaves & Beisner, 2011; Seddon et al., 2014), such as response to nutrient reduction (Battarbee et al., 2005), introduction of exotic species (Hawryshyn et al., 2012), and other recent human disturbances on aquatic systems (Jeppesen et al., 2001; Poquet et al., 2008; Michelson & Park, 2013). In addition, these approaches can also contribute to the understanding of metacommunity processes, by comparing the mechanisms structuring contemporary (i.e., biocoenoses) and past (i.e., thanato- or taphocoenoses) assemblages and determining the relative contribution of environmental and spatial drivers to both data sets (Verleyen et al., 2009; Levi et al., 2014; Winegardner et al., 2015).

Empirical studies showed that environmental variables explained similarly the variation of subfossil and living assemblages of cladocerans (Çakıroğlu et al., 2014), macrophytes (Levi et al., 2014) and diatoms (Winegardner et al., 2015). Moreover, environmental control seems to be more important in subfossil diatom assemblages than spatial factors (Verleyen et al., 2009, Winegardner et al., 2015). However, the relevance of dispersal processes could be higher at larger scales (Bennett et al., 2010) and could depend on the organisms' dispersal mode and body size (Cottenie, 2005; Astorga et al., 2012; De Bie et al., 2012).

The differences between past and present communities provide information about the effects of past events on the existing community assemblage (i.e., priority effects) that can be essential in understanding metacommunity organization (Fukami, 2015). In temporary water bodies, early colonizers may inhibit—or facilitate—the colonization by other species, as they may monopolize the resources or modify the local conditions (De Meester et al., 2002; Louette & De Meester, 2007; Urban & De Meester, 2009). In these systems, the organisms' remains represent part of the community that previously inhabited the site. Therefore, high levels of concordance between the biocoenoses and taphocoenoses in a water body can be related to priority effects of the communities, although a fraction of these effects may interact with other structuring mechanisms, such as species sorting. In this way, Mergeay et al. (2011) studied the role of species sorting and priority effects on *Daphnia* assemblages in a fluctuating tropical lake, by means of a long paleolimnological record. These authors showed that the best predictor of the community composition was the prior community composition, when the lake was in transition from low to a high water level, by observing a temporal lag until the community changed in response to the change in environmental conditions.

Due to the adequate preservation of shell remains, ostracods are excellent model organisms to perform these studies. Ostracods are small bivalved crustaceans, known to live in all types of water bodies, presenting large population densities and showing high species-specific sensitivity to environmental variation (Holmes, 2001). These features led to the establishment of strong relationships between environmental variables and ostracod species distributions (e.g., Neale, 1964; Forester, 1986; Mesquita-Joanes et al., 2012). However, other structuring mechanisms, such as dispersal and historical contingency, are usually neglected in these studies. Ostracods are passively dispersed by several vectors, such as wind (Vanschoenwinkel et al., 2008) and animals (Brochet et al., 2010; Valls et al., 2016a). Given that these factors may be relevant to the community composition, including them in the ecological analyses may improve the performance of bioassessment programs (Heino, 2013), too often based only on the abiotic environmental influence on species distribution, and not so much on dispersal ways or connectivity, which would allow for instance the (re-)colonization by extirpated native species or by new exotic invaders.

In the present study, we compare the species composition of ostracod taphocoenoses and

biocoenoses from Mediterranean shallow lakes in Central Spain and determine the environmental and spatial contribution to both datasets. In addition, we test the influence of historical contingency (i.e., previous community composition) on present biocoenoses and its interaction with environmental and spatial effects on the ostracod metacommunity.

## Materials and methods

Study area

The study was carried out in a set of shallow lakes from the Biosphere Reserve of La Mancha Húmeda (Camacho et al., 2003), on the plains of Castilla-La Mancha (Central Iberian Peninsula; 38.6°–39.8°N, 2.6°–4.4°W; Fig. 1). The mean annual temperature in this region is 12 °C with high variability among seasons, with extreme values reaching more than 40 °C in summer and down to less than 0 °C in winter. Rainfall (427 mm of mean annual precipitation) occurs mainly in fall and spring, when many ephemeral lakes are inundated. These lakes are mostly endorheic, the majority of which also lack surface inlets, so they are isolated water bodies. The average distance between the studied lakes is 52.3 ± 38.9 km (range 1.1–148.4 km). The lakes have an average depth less than 1 m, and surface areas ranging between 13 and 185 ha. There is a wide diversity of environmental features among lakes, from fresh (1.0 mS cm^{-1}) to hypersaline waters (77.7 mS cm^{-1}) and from ephemeral to permanent waters. Generally, these conditions are modified at different intensities by humans, mainly due to aquifer exploitation and sewage spills. Despite these threats, these systems are unique biodiversity reservoirs, and the region is considered the main steppic wetland system of Western Europe (Alonso, 1998).

Sampling and datasets

We sampled 22 shallow lakes in spring 2013 (Fig. 1; see Appendix I in Electronic Supplementary Material). Benthic samples were collected with a hand net (250 μm mesh size), over an approximate area of 2 m^2. The hand net filtered the water, but also approximately the first 2 cm of the surface sediment, where we collected living ostracods and shell remains. This methodology follows common techniques used in ostracod research (e.g., Holmes, 2001; Danielopol et al., 2002), so as particular studies carried out in the same area and type of systems (Roca et al., 2000), or in other shallow lakes but comparing tapho- and biocoenoses using the same semiquantitative sampling strategy with hand nets (Valls et al., 2013). Previous studies suggested an approximate sedimentation rate of 0.10 cm year^{-1} in Camino de Villafranca lake (García-Roger, 2006), so a sediment depth of ~2 cm is estimated to represent about 20 years of sedimentary history in the lakes studied. The samples were fixed in situ with formaldehyde 4%. In the laboratory, we used a stereomicroscope to identify and count ostracods to species level following Meisch (2000). We recorded all the complete ostracods captured alive, so as their shell remains (disarticulated valves and empty carapaces). The two resulting sets of species matrices were called biocoenoses, for living ostracods, and taphocoenoses, for ostracod remains. The biocoenosis assemblages were previously analyzed in another study, where both environmental and spatial components were found significant in structuring the

Fig. 1 Map showing the location of the studied lakes (*gray circles*). Lake codes as in Appendix I in Electronic Supplementary Material
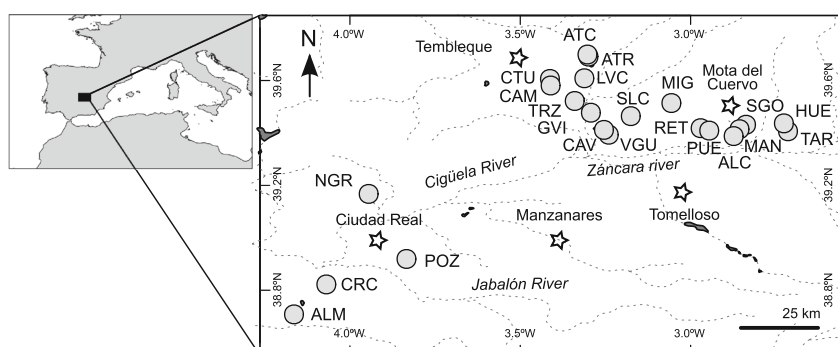
metacommunity (Castillo-Escrivà et al., 2015). However, in the present survey, we also used the taphocoenoses to consider also historical effects.

Fourteen environmental variables were used in this study (Table 1). Conductivity (resolution: 0.01 mS cm^{-1}) and pH (resolution: 0.01 pH units) were measured in the field using WTW portable probes. Surface sediment samples were collected to determine both organic matter and carbonate content by the loss on ignition method (LOI$_{550}$ and LOI$_{950}$, respectively; Heiri et al., 2001). Ephemerality index values were estimated from previous periodic visits: 1 (Permanent, always with water), 2 (Temporary, dried in summer), and 3 (Ephemeral, filled only from a few days to a maximum of 4 months). Lake surface area, elevation, and climatic and geological variables were calculated using Quantum GIS version 1.7.5 (QGIS Development Team, 2014). Lake surface area (ha) was measured using images from the web map service interface of the Spanish National Plan of Aerial Orthophotos (PNOA; http://www.pnoa.ign.es). Elevation, mean annual rainfall, and mean, minimum, and maximum annual temperature were obtained from the WorldClim database version 4.1 (Hijmans et al., 2005). The proportion of surface area dominated by siliceous, carbonated, evaporitic, and volcanic rocks surrounding the lake (500 m buffer) was extracted from 1:50,000 geological continuum cartography (GEODE, 2011). Local geological conditions can determine the hydrochemistry of the lakes, and ostracods are known to respond to water hydrochemistry (Forester, 1986).

Spatial variables were obtained by means of Moran Eigenvector Maps (MEMs; Dray et al., 2006). We used the Gabriel graph criterion (Dray et al., 2012; Legendre & Legendre, 2012), creating a connection network among lakes, using the spdep R package (Bivand & Piras, 2015) and then MEMs were calculated with the spacemakeR package (Dray, 2013).

Statistical analyses

We compared biocoenoses and taphocoenoses with each other, and with the ecological variables that may affect them. Both species matrices (abundances) were transformed with the Hellinger method (Legendre & Gallagher, 2001). Species distribution was first analyzed with principal component analysis (PCA). After that, we applied redundancy analysis (RDA) to determine the role of both environmental and spatial variables on both assemblages. Some environmental variables were transformed to achieve normality (Table 1). For RDAs, we selected the best environmental variables and MEMs by means of a forward selection procedure with two stopping criteria (Blanchet et al., 2008). Variation partitioning (Borcard et al., 1992) was used to determine the relative contribution of selected environmental and spatial variables to the variation of each species dataset, using adjusted R^2 (Peres-Neto et al., 2006).

Table 1 Mean, maximum, and minimum values of the environmental variables recorded

Variable	Mean $\pm$ SE	Minimum	Maximum
Conductivity (mS cm^{-1}; log*)	15.7 $\pm$ 17.8	1.0	77.7
pH	8.3 $\pm$ 0.6	7.2	9.2
LOI$_{550}$ (proportion; asin*)	0.11 $\pm$ 0.05	0.03	0.20
LOI$_{950}$ (proportion; asin)	0.07 $\pm$ 0.05	0.00	0.19
Ephemerality (index)	2.3 $\pm$ 0.8	1.0	3.0
Surface area (ha; log)	66.8 $\pm$ 49.0	13.8	185.0
Elevation (m a.s.l.)	666 $\pm$ 20	624	693
Mean annual temperature (°C; log)	12.5 $\pm$ 0.2	12.2	13.0
Annual temperature range (°C; log)	12.2 $\pm$ 0.3	11.8	12.8
Mean annual rainfall (mm; log)	426 $\pm$ 19	412	497
Siliceous rocks (proportion)	0.51 $\pm$ 0.28	0.07	0.92
Carbonated rocks (proportion; asin)	0.12 $\pm$ 0.10	0.00	0.35
Evaporite rocks (proportion; asin)	0.10 $\pm$ 0.20	0.00	0.67
Volcanic rocks (proportion; asin)	0.06 $\pm$ 0.19	0.00	0.81

* Log indicate the variables were log$_{10}$-transformed and asin indicates they were arcsine transformed [$arcsin(\sqrt{x})$]

We determined the concordance between bio-coenoses and taphocoenoses, with a procrustes test of the first two axes of PCA and RDA ordinations (Peres-Neto & Jackson, 2001). In RDA, we used both environmental and spatial variables selected. The procrustes statistic is m^2, which in the "protest" function of vegan is the residual sum of squares (Oksanen et al., 2015). The function "protest" provides also the r statistic as $r = \sqrt{1 - m^2}$. The r statistic is positively related to the concordance of two matrices (being $r = 1$ the maximum value of concordance), and vegan allows testing this statistic by permutation (999 permutations in our study), following Jackson (1995).

In addition, we tested which fraction of the biocoenoses variation could be explained by environment, space, or history, using RDA and variation partitioning as described above. We used the first two axes of the taphocoenoses PCA as variables related to historical contingency.

All the statistical analyses were carried out with R version 3.0.2 (R Development Core Team, 2013). We used the vegan package for PCA, RDA, variation partitioning, and procrustes test (Oksanen et al., 2015). Forward selection procedure was performed with packfor (Dray et al., 2013).

Results

We collected a total of 20 species of ostracods from the biocoenoses and taphocoenoses (Table 2). The total number of species found in the biocoenoses was similar to that of the taphocoenoses, i.e., 17 and 19 species, respectively. A large proportion of the biocoenoses and taphocoenoses species composition was shared in each lake (Table 2). Despite this, the taphocoenoses provided 24 new locations for species not recorded in the biocoenoses; among these, three species were not collected alive (*Ilyocypris biplicata* var. *anomala*, *Eucypris mareotica*, and *Cypridopsis parva*) in any of the sampled lakes. In contrast, *Pseudocandona albicans* was recovered only as living individuals. The species PCA ordinations in both sets of dead and living assemblages were similar (Fig. 2a, b, respectively; see Appendix II in Electronic Supplementary Material for lake labels), i.e., *Heterocypris barbara* was separated from other species in the

negative side of the first axis in both PCAs. This species was mainly collected in monospecific associations. The second axis ordered *Eucypris virens* and *Heterocypris incongruens* on its positive part, separated from *Cypris bispinosa* and *Herpetocypris chevreuxi*.

In biocoenoses, forward selection chose four significant environmental variables (conductivity, LOI_{550}, surface area, and annual rainfall) and four spatial components (MEMs 2, 6, 7, and 20; Table 3). The analysis of taphocoenoses selected only conductivity as significant environmental variable, plus MEMs 1, 2, 6, 16, 19, and 20. Variation partitioning determined a significant 17.5% of pure environmental effects and 17.3% of pure space for biocoenoses. In contrast, in the taphocoenoses, the spatial components (27.9%) played a more relevant role than environmental effects (7.6%) (Table 3).

The two RDAs constrained by the selected environmental variables indicated that the first axis was negatively related to conductivity, as a surrogate for salinity, in both sets of assemblages (Fig. 2c, d). *Heterocypris barbara* was collected in lakes with high conductivity values (>9 mS cm^{-1}). The second axis of the biocoenoses RDA was associated with surface area and rainfall (Fig. 2c), considered surrogate for hydroperiod. The axis related *H. chevreuxi* and *C. bispinosa* to long hydroperiods and low LOI_{550}, and *E. virens* and *H. incongruens* to lakes with short hydroperiods.

Procrustes analyses indicated a high concordance between biocoenoses and taphocoenoses species composition in the first two axes of both sets of PCAs ($r = 0.877$; $P = 0.001$), and RDAs with environmental and spatial variables ($r = 0.853$; $P = 0.001$). Procrustean analyses showed a marked separation between lakes dominated by *H. barbara* (situated in the negative side of the first axis) from other lakes in both PCA and RDA procrustes (Fig. 3a), not crossing their arrows (arrow lengths correspond to the residual values, or the distance between biocoenoses and taphocoenoses, for each lake).

The two first axes of taphocoenoses PCA (i.e., surrogate for historical contingency) explained 38.0% of the total variation of the biocoenoses. This percentage was reduced to a significant pure historical fraction of 10.3% in variation partitioning analysis (Fig. 4). We also determined a significant 10.1% corresponding to pure environmental variables and

Table 2 Ostracod species found in the studied lakes

Species	Lake
Limnocythere inopinata	**ALM**, *POZ*
Pseudocandona albicans	TAR
Ilyocypris gibba	**ALM**, GVI, **HUE**, **MAN**, **MIG**, *NGR*, **POZ**, TAR
Ilyocypris biplicata var. *anomala*	*ALM*
Cypris bispinosa	**CRC**, **NGR**
Eucypris virens	**HUE**, *MAN*, **MIG**, **POZ**, **PUE**, **RET**, **TAR**, VGU
Eucypris mareotica	*MAN*
Candelacypris aragonica	**ATC**, **SLC**
Trajancypris clavata	**VGU**
Herpetocypris chevreuxi	**CRC**, **NGR**
Candonocypris novaezelandiae	**TAR**, **VGU**
Heterocypris incongruens	*ALM*, *CAV*, **MAN**, **MIG**, **POZ**, **PUE**, **RET**, **TAR**, **VGU**
Heterocypris rotundata	**HUE**
Heterocypris barbara	**ALC**, *ALM*, ATC, **ATR**, CAM, **CAV**, *CTU*, *GVI*, **LVC**, MAN, **POZ**, **SGO**, **TRZ**
Heterocypris salina	**CAV**, *LVC*, *MAN*, **MIG**, **POZ**, **PUE**
Cypridopsis parva	*ALM*
Plesiocypridopsis newtoni	**MIG**, *POZ*, *PUE*, *RET*, *VGU*
Sarscypridopsis aculeata	**MAN**, NGR, *POZ*, **RET**, *SGO*, *SLC*, VGU,
Sarscypridopsis sp.*	**ALM**, **CAV**, **VGU**
Potamocypris arcuata	*ALM*, **MAN**, **MIG**, *POZ*, *PUE*, *RET*, **VGU**

Lake codes in regular type correspond to lakes with the presence of living individuals (i.e., biocoenoses), in italics correspond to ostracod remains (i.e., taphocoenoses) and in bold correspond to both assemblages. Lake codes as in Appendix I in Electronic Supplementary Material

* We referred *Sarscypridopsis* sp. to an undescribed species identified as *Sarscypridopsis* cf. *aculeata* by Mezquita et al. (1999), and *Sarscypridopsis* sp. by Mezquita et al. (2005), with morphological similarities to the individuals found in Madeira by Fuhrmann & Goth (2011) (Fuhrmann, April 2014, pers. comm.)

7.6% of pure spatial effects. We obtained a 7.4% of the variation associated with the combination of environment and historical contingency, plus 9.7% shared between space and history, and 10.6% between environment, space, and history.

Discussion

Our results showed a high concordance between ostracod biocoenoses and taphocoenoses composition in the studied set of shallow lakes. The tight correspondence of the two types of records in ostracods was also observed by Michelson & Park (2013) and Valls et al. (2016b), demonstrating the high fidelity of the ostracod remains to the active communities in the mid-term (decades) and consequently the

relevance of ostracod metacommunity resilience. However, other studies have also emphasized the importance of recent ecological changes that may distort the relationship between past and present metacommunities. Indeed, Poquet et al. (2008), in a study carried out in Mediterranean wetlands suffering recent increasing eutrophication or modifications of their hydrological regime, showed that ostracod taphocoenoses had much higher species richness than their corresponding biocoenoses. These findings support the idea that ostracods are excellent proxies to estimate past environmental changes and their effects on diversity (Horne et al., 2012).

The match between past and present assemblages in the studied shallow lakes may have several explanations. The concordance observed may be related to low variation in species composition in

Fig. 2 Ordination plots for the first two axes of biocoenoses PCA (**a**), taphocoenoses PCA (**b**), biocoenoses RDA (**c**), and taphocoenoses RDA (**d**) constrained by selected environmental variables. *Circles* and *crosses* represent lakes and species, respectively. *HBA Heterocypris barbara, HIN Heterocypris incongruens, EVI Eucypris virens, HCH Herpetocypris chevreuxi, CBI Cypris bispinosa*
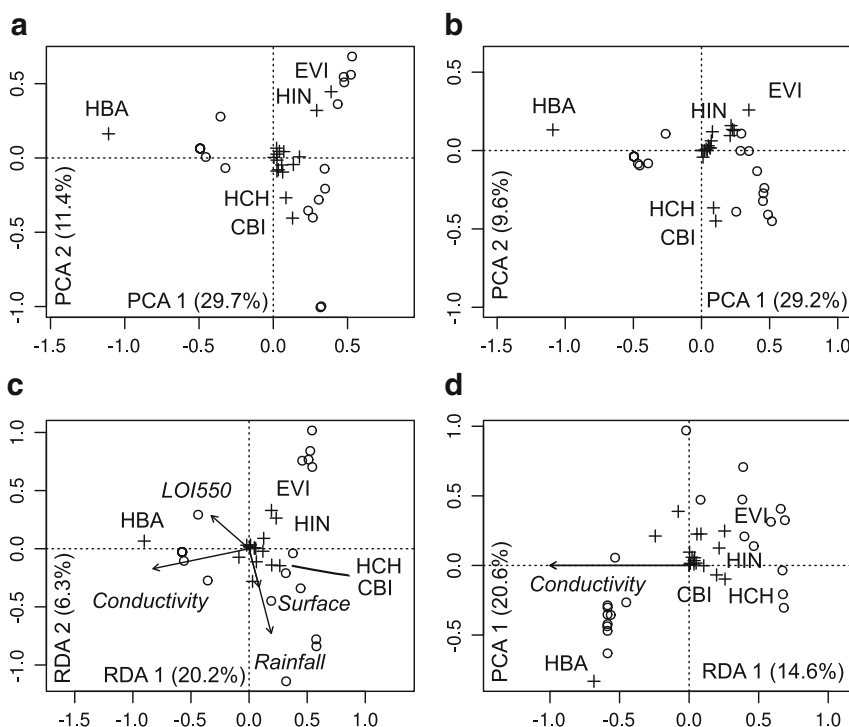

Table 3 Results of RDA for ostracod biocoenoses and taphocoenoses, with environmental (E) and spatial (S) selected factors

Predictor dataset	Adjusted R^2	P value	Selected factors
Biocoenoses			
E	0.296	0.001	Conductivity, LOI_{550}, surface, rainfall
S	0.295	0.001	MEM2, 6, 7, 20
Pure E	0.175	0.001	
Shared	0.121		
Pure S	0.173	0.001	
Taphocoenoses			
E	0.158	0.002	Conductivity
S	0.360	0.002	MEM1, 2, 6, 16, 19, 20
Pure E	0.076	0.003	
Shared	0.081		
Pure S	0.279	0.001	

Pure and shared fractions were calculated by means of pRDA

these lakes, as sediment samples usually recover the annual species succession in a snapshot, and even a time-averaged community through multiple years (Brothers et al., 2008). This explanation may hold in saline and/or ephemeral lakes, where few species tolerate extreme levels of salinity (Williams et al., 1990) and the time of water permanence is short, avoiding species turnover because of the short time of ecological succession.

The correspondence between dead and living assemblages was observed in other shallow Mediterranean lakes in the case of macrophytes (Levi et al., 2014) and littoral cladocerans, but not in pelagic cladocerans in the same systems (Çakıroğlu et al., 2014). The difference between benthic and pelagic organisms was attributed to a general inadequate preservation of remains of pelagic organisms, being particularly very reduced in some cladocerans (e.g.,
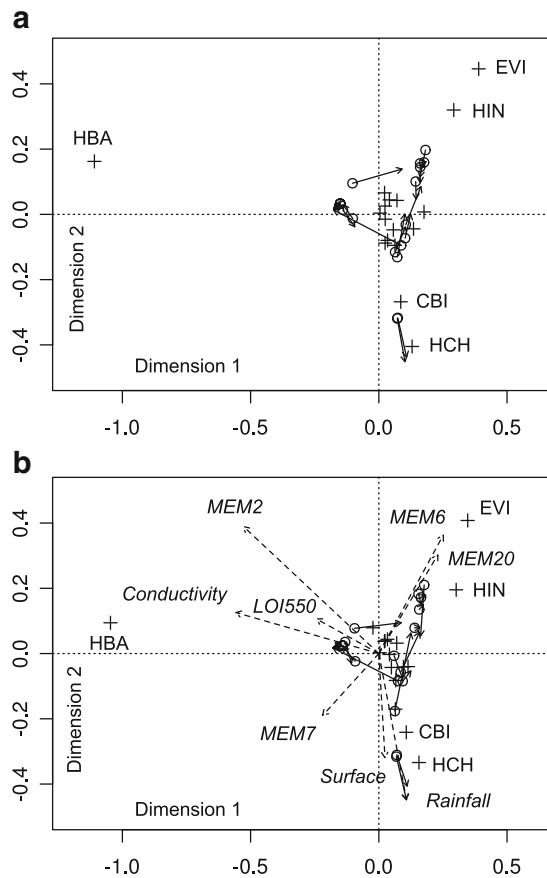
Fig. 3 Procrustean plots comparing the PCAs (**a**) and RDAs constrained by selected environmental and spatial variables (**b**). *Circles* represent the rotated matrix (taphocoenoses), and the heads of the *arrows* represent the target matrix (biocoenoses). The lengths of the *arrows* are proportional to the procrustean residuals (*long arrow*-high residual-low concordance). We also represent the biocoenoses species PCA scores (**a**) and the selected environmental and spatial variables of the biocoenoses RDA (**b**). Species codes as in Fig. 2. *Circles* and *crosses* represent lakes and species, respectively

Fig. 4 Venn diagram of the variation partitioning analysis of the effects on the biocoenoses corresponding to environment, space, and first two axes of taphocoenoses (history). Adjusted R^2 values are also shown

found differences in the relative importance of environment and space. Environment dominates over space in biocoenoses, whereas space dominates over environment in taphocoenoses. Other studies found more concordance in the effects of both environmental and spatial effects in cladocerans (Çakıroğlu et al., 2014) and macrophytes (Levi et al., 2014) of other shallow Mediterranean lakes, and also in diatoms of deeper lakes (Winegardner et al., 2015). Likely, in our study, taphocoenoses are less related to environmental factors because of the temporal species integration of the taphocoenoses, which allows the presence of species that inhabited different past local conditions, indicating certain seasonal or annual changes in community composition and environment. Conversely, taphocoenoses are more closely related to spatial variables, because these better reflect the potential spatial distribution of species and dispersal events. Nonetheless, this spatial fraction might be related to other spatially structured environmental variables that were not included in the final model, such as unmeasured past environmental conditions.

We found that environmental, spatial, and historical components largely drove the living ostracod metacommunity. Indeed, an important fraction was explained by historical components, suggesting few changes in ostracod communities in the last few years. This could be due to several reasons, including weak environmental changes with respect to the main structuring environmental factors (i.e., salinity), priority effects of the ostracods that previously occupied each lake, or community resistance (and/or resilience)

Diaphanosoma sp. and *Macrothrix* sp.) with soft-shelled chitinous body parts (Rautio et al., 2000). Several works carried out in deeper lakes support that taphocoenoses are more similar to benthic than to pelagic biocoenoses, as observed in cladocerans (Davidson et al., 2007) and diatoms (Winegardner et al., 2015). Indeed, freshwater ostracods are benthic organisms with calcified valves, which are usually well preserved in the sediment.

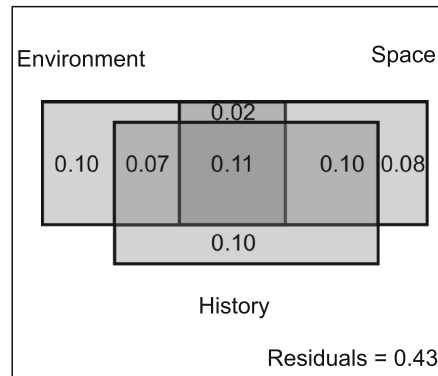Despite the similarity in species composition between past and present ostracod assemblages, we

to minor environmental changes. In these temporary habitats, many species produce dormant propagules which, when the lakes dry out, remain in the resting egg bank waiting a new inundation period. Therefore, when the lakes are refilled, offering an empty habitat, the first colonizers or founders come from the egg bank, a type of colonization over time. As a consequence, these founders obtain more advantages over later colonizers, monopolizing the resources with fast population growth, profiting from more time to local adaptation, and creating a new egg bank (De Meester et al., 2002). These priority effects decrease the invasiveness of communities and reduce the chance of structural changes. In addition, the short inundation period and salinity of many of these lakes may difficult the substitution of founders and therefore an ecological succession to proceed, thus increasing priority effects. In the study lakes, the dominance of pioneer taxa, such as ostracods of the genera *Heterocypris* and *Eucypris*, suggests priority effects of these r-strategists (Fryer, 1997; Meisch, 2000; Mesquita-Joanes et al., 2012).

On a broader time-scale and within a wider ecological gradient, an increase of environmental changes may reduce the priority effects and increase the invasiveness of the metacommunity, because new conditions might be more unsuitable for founders, providing a chance for other colonizers better adapted to the new environments (Davis et al., 2000; Strecker & Arnott, 2010; Symons & Arnott, 2014). Wide environmental variations could be found when increasing the temporal window, by older subfossil assemblages (Mergeay et al., 2011), allowing to infer the period of time when recent communities became established. Therefore, priority effects might be important under more stable conditions, but prolonged disturbances over time could also provide more opportunities for species sorting. It would be interesting to widen our temporal view to over hundreds of years, and study the fluctuations of environmental conditions to achieve a better understanding of the variability and processes structuring lake metacommunities.

Environmental control in our survey was predominantly associated with conductivity (as surrogate of salinity). This variable was also a strong determinant of ostracod and cladoceran communities in previous studies carried out in this region (Roca et al., 2000; Boronat et al., 2001), and within the Mediterranean

basin (Reed et al., 2012; Çakıroğlu et al., 2014; Levi et al., 2014). Salinity is considered an essential factor influencing ostracod distribution (Neale, 1964; Horne, 1983), as in other aquatic organisms (Williams et al., 1990; Arribas et al., 2014). We found two ostracod species, *H. barbara* and *C. aragonica* to be dominant in saline lakes. These species were previously reported in other steppic shallow lakes of the Iberian Peninsula, always at the highest salinities (Baltanás et al., 1990).

Dispersal-related effects contribute significantly to species distribution in our systems. The fraction explained by the spatial components could be related to dispersal limitation, due to a lower dispersal rate between the more distant lakes (Heino et al., 2015), although we must be cautious when associating spatial components with dispersal processes, as these factors might also be related to unmeasured environmental variables. Dispersal limitation was observed in other microcrustaceans with similar body size, such as cladocerans and copepods (Ng et al., 2009; Soininen et al., 2011; De Bie et al., 2012). However, other organisms with different body size and dispersal mode could be differently affected by dispersal (and also by environment; De Bie et al., 2012). For instance, Finlay (2002) suggested that small organisms (such as bacteria) are less affected by dispersal limitation, due to the straightforward passive dispersal (i.e., small body size, high population abundance, and propagules). On the other hand, big animals with active dispersal can track all the environmentally suitable sites (Resetarits, 2001), decreasing the spatial effects too. These hypotheses should be tested in future studies with other organisms (e.g., bacteria, cladocerans, macroinvertebrates) in these water bodies.

Our results showed a relationship between ostracod biocoenoses and taphocoenoses in shallow lakes, although both assemblages did not share the same dominant structuring mechanisms. We reveal the importance of not only species sorting but also spatial and historical effects. The present study stresses the importance of considering historical processes in metacommunities and highlights the potential of paleoecological tools in neoecology (Gregory-Eaves & Beisner, 2011). The integration of spatial and historical ecological processes in metacommunity studies, together with classical environmental effects, provides more realistic results and improves future

applications of this knowledge in bioassessment and conservation biology (Heino, 2013).

References

Alonso, M., 1998. Las lagunas de la España peninsular. Limnetica 15: 1–176.

Arribas, P., C. Andújar, P. Abellán, J. Velasco, A. Millán & I. Ribera, 2014. Tempo and mode of the multiple origins of salinity tolerance in a water beetle lineage. Molecular Ecology 23: 360–373.

Astorga, A., J. Oksanen, M. Luoto, J. Soininen, R. Virtanen & T. Muotka, 2012. Distance decay of similarity in freshwater communities: do macro- and microorganisms follow the same rules? Global Ecology and Biogeography 21: 365–375.

Baltanás, A., C. Montes & P. Martino, 1990. Distribution patterns of ostracods in iberian saline lakes. Influence of ecological factors. Hydrobiologia 197: 207–220.

Battarbee, R. W., N. J. Anderson, E. Jeppesen & P. R. Leavitt, 2005. Combining palaeolimnological and limnological approaches in assessing lake ecosystem response to nutrient reduction. Freshwater Biology 50: 1772–1780.

Bennett, J. R., B. F. Cumming, B. K. Ginn & J. P. Smol, 2010. Broad-scale environmental response and niche conservatism in lacustrine diatom communities. Global Ecology and Biogeography 19: 724–732.

Birks, H. H. & H. J. B. Birks, 2006. Multi-proxy studies in palaeolimnology. Vegetation History and Archaeobotany 15: 235–251.

Bivand, R. & G. Piras, 2015. Comparing implementations of estimation methods for spatial econometrics. Journal of Statistical Software 63: 1–36.

Blanchet, F. G., P. Legendre & D. Borcard, 2008. Forward selection of explanatory variables. Ecology 89: 623–2632.

Borcard, D., P. Legendre & P. Drapeau, 1992. Partialling out the spatial component of ecological variation. Ecology 73: 1045–1055.

Boronat, L., M. R. Miracle & X. Armengol, 2001. Cladoceran assemblages in a mineralization gradient. Hydrobiologia 442: 75–88.

Brochet, A. L., M. Gauthier-Clerc, M. Guillemain, H. Fritz, A. Waterkeyn, Á. Baltanás & A. J. Green, 2010. Field evidence of dispersal of branchiopods, ostracods and bryozoans by teal (*Anas crecca*) in the Camargue (southern France). Hydrobiologia 637: 255–261.

Brothers, S., J. C. Vermaire & I. Gregory-Eaves, 2008. Empirical models for describing recent sedimentation rates in lakes distributed across broad spatial scales. Journal of Paleolimnology 40: 1003–1019.

Çakıroğlu, Aİ., Ü. N. Tavşanoğlu, E. E. Levi, T. A. Davidson, T. Bucak, A. Örzen, G. K. Akyıldız, E. Jeppesen & M. Beklioğlu, 2014. Relatedness between contemporary and sub-fossil cladoceran assemblages in Turkish lakes. Jounal of Paleolimnology 52: 367–383.

Camacho, A., M. R. Miracle & E. Vicente, 2003. Which factors determine the abundance and distribution of pico-cyanobacteria in inland waters? A comparison among different types of lakes and ponds. Archiv für Hydrobiologie 157: 321–338.

Castillo-Escrivà, A., L. Valls, C. Rochera, A. Camacho & F. Mesquita-Joanes, 2015. Spatial and environmental analysis of an ostracod metacommunity from endorheic lakes. Aquatic Sciences. doi:10.1007/s00027-015-0462-z.

Cohen, A. S., 2003. Paleolimnology: The History and Evolution of Lake Systems. Oxford University Press, New York.

Cottenie, K., 2005. Integrating environmental and spatial processes in ecological community dynamics. Ecology Letters 8: 1175–1182.

Danielopol, D. L., E. Ito, G. Wansard, T. Kamiya, T.M. Cronin & A. Baltanás, 2002. Techniques for the collection and study of Ostracoda. In: J. Holmes & A. Chivas (eds) Applications of the Ostracoda in Quaternary Research. Geophysical Monograph Series, 131: 65–97.

Davidson, T. A., C. D. Sayer, M. R. Perrow, M. Bramm & E. Jeppesen, 2007. Are the controls of species composition similar for contemporary and sub-fossil cladoceran assemblages? A study of 39 shallow lakes of contrasting trophic status. Journal of Paleolimnology 38: 117–134.

Davis, M. A., J. P. Grime & K. Thompson, 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88: 528–534.

Davis, M. B., 1994. Ecology and paleoecology begin to merge. Trends in Ecology & Evolution 9: 357–358.

De Bie, T., L. De Meester, L. Brendonck, K. Martens, B. Godeeris, D. Ercken, H. Hampel, L. Denys, L. Vanhecke, K. Van der Gucht, J. Van Wichelen, W. Vyverman & S. A. J. Declerck, 2012. Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. Ecology Letters 15: 740–747.

De Meester, L., A. Gómez, B. Okamura & K. Schwenk, 2002. The monopolization hypothesis and the dispersal–gene flow paradox in aquatic organisms. Acta Oecologica 23: 121–135.

Dray, S., 2013. spacemakeR: spatial modelling. R package version 0.0-5/r113. http://r-forge.r-project.org/projects/sedar/.

Dray, S., P. Legendre & P. R. Peres-Neto, 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecological Modelling 196: 483–493.

Dray, S., R. Pélissier, P. Couteron, M. J. Fortin, P. Legendre, P. R. Peres-Neto, E. Bellier, R. Bivand, F. G. Blanchet, M. De Cáceres, A. B. Dufour, E. Heegaard, T. Jombart, F. Munoz, J. Oksanen, J. Thioulouse & H. H. Wagner, 2012. Community ecology in the age of multivariate multiscale spatial analysis. Ecological Monographs 82: 257–275.

Dray, S., P. Legendre & F. G. Blanchet, 2013. packfor: Forward selection with permutation (Canoco p. 46). R package version 0.0-8/r109. http://R-Forge.R-project.org/projects/sedar/.

Finlay, B. J., 2002. Global dispersal of free-living microbial eukaryote species. Science 296: 1061–1063.

Forester, R. M., 1986. Determination of the dissolved anion composition of ancient lakes from fossil ostracodes. Geology 14: 796–799.

Fryer, G., 1997. The horse-trough ostracod *Heterocypris incongruens*. Naturalist 122: 121–135.

Fukami, T., 2015. Historical contingency in community assembly: integrating niches, species pools, and priority effects. Annual Review of Ecology, Evolution, and Systematics 46: 1–23.

Fuhrmann, R. & K. Goth, 2011. Neue und weitere bemerkenswerte Ostrakoden aus dem Quartär Mitteldeutschlands. Palaeontographica Abteilung A 294: 95–201.

García-Roger, E. M., 2006. Análisis demográfico de bancos de huevos diapáusicos de rotíferos, Unpublished PhD, Universitat de València, València.

GEODE, 2011. Mapa Geológico Digital continuo de España [en línea]. Sistema de Información Geológica Continua: SIGECO. IGME. http://cuarzo.igme.es/sigeco/.

Gregory-Eaves, I. & B. E. Beisner, 2011. Palaeolimnological insights for biodiversity science: an emerging field. Freshwater Biology 56: 2653–2661.

Hawryshyn, J., K. M. Rühland, M. Julius & J. P. Smol, 2012. Absence of evidence is not evidence of absence: is *Stephanodiscus binderanus* (Bacillariophyceae) an exotic species in the Great Lakes Region? Journal of Phycology 48: 270–274.

Heino, J., 2009. Species co-occurrence, nestedness and guild–environment relationships in stream macroinvertebrates. Freshwater Biology 54: 1947–1959.

Heino, J., 2013. The importance of metacommunity ecology for environmental assessment research in the freshwater realm. Biological Reviews 88: 166–178.

Heino, J., A. S. Melo, T. Siqueira, J. Soininen, S. Valanko & L. M. Bini, 2015. Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. Freshwater Biology 60: 845–869.

Heiri, O., A. F. Lotter & G. Lemcke, 2001. Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. Journal of Paleolimnology 25: 101–110.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones & A. Jarvis, 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25: 1965–1978.

Holmes, J. A., 2001. Ostracoda. In Smol, S. P., H. J. B. Birks & W. M. Last (eds), Tracking Environmental Change Using Lake Sediments. Kluwer Academic Publishers, Dordrecht: 125–151.

Holyoak, M., M. A. Leibold, N. M. Mouquet, R. D. Holt & F. Hoopes, 2005. A framework for large-scale community ecology. In Holyoak, M., M. A. Leibold & R. D. Holt (eds), Metacommunities: Spatial Dynamics and Ecological Communities. University of Chicago Press, Chicago: 1–31.

Horne, D., 1983. Life-cycles of podocopid Ostracoda—a review (with particular reference to marine and brackish-water species). In Madokks, R. F. (ed.), Application of Ostracoda. The University of Houston, Houston: 238–249.

Horne, D., J. Holmes, J. Rodríguez-Lázaro & F. Viehberg, 2012. Ostracoda as Proxies for Quaternary Climate Change. Elsevier, Amsterdam.

Jackson, D. A., 1995. Protest: a procrustean randomization test of community environment concordance. Écoscience 2: 297–303.

Jeppesen, E., P. Leavitt, L. De Meester & J. P. Jensen, 2001. Functional ecology and palaeolimnology: using cladoceran remains to reconstruct anthropogenic impact. Trends in Ecology and Evolution 16: 191–198.

Legendre, P. & E. D. Gallagher, 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129: 271–280.

Legendre, P. & L. F. Legendre, 2012. Numerical Ecology, 3rd ed. Elsevier, Amsterdam.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau & A. Gonzalez, 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7: 601–613.

Levi, E. E., Aİ. Çakıroğlu, T. Bucak, B. V. Odgaard, T. A. Davidson, E. Jeppesen & M. Bekİİoğlu, 2014. Similarity between contemporary vegetation and plant remains in the surface sediment in Mediterranean lakes. Freshwater Biology 59: 724–736.

Logue, J. B., N. Mouquet, P. Hannes, H. Hillebrand & The Metacommunity Working Group, 2011. Empirical approaches to metacommunities: a review and comparison with theory. Trends in Ecology Evolution 26: 482–491.

Louette, G. & L. De Meester, 2007. Predation and priority effects in experimental zooplankton communities. Oikos 116: 419–426.

Meisch, C., 2000. Freshwater Ostracoda of Western and Central Europe. Spektrum Akademischer Verlag, Heidelberg.

Mergeay, J., L. De Meester, H. Eggermont & D. Vershuren, 2011. Priority effects and species sorting in a long paleoecological record of repeated community assembly through time. Ecology 92: 2267–2275.

Mesquita-Joanes, F., A. J. Smith & F. A. Viehberg, 2012. The Ecology of Ostracoda Across Levels of Biological Organisation from Individual to Ecosystem: A Review of Recent Developments and Future Potential. In Horne, D. J., J. A. Holmes, J. Rodriguez-Lázaro & F. A. Viehberg (eds), Developments in Quaternary Sciences. Ostracoda as Proxies for Quaternary Climate Change. Elsevier, Amsterdam: 15–35.

Mezquita, F., G. Tapia & J. R. Roca, 1999. Ostracoda from springs on the eastern Iberian Peninsula: ecology, biogeography and palaeolimnological implications. Palaeogeography, Palaeoclimatolology, Palaeoecology 148: 65–85.

Mezquita, F., J. R. Roca, J. Reed & G. Wansard, 2005. Quantifying species–environment relationships in non-marine Ostracoda for ecological and palaeoecological studies: examples using Iberian data. Palaeogeography, Palaeoclimatology, Palaeoecology 225: 93–117.

Michelson, A. V. & L. E. Park, 2013. Taphonomic dynamics of lacustrine ostracodes on San Salvador Island, Bahamas: high fidelity and evidence of anthropogenic modification. Palaios 28: 129–135.

Neale, J. W., 1964. Some factors influencing the distribution of recent British Ostracoda. Pubblicazioni Della Stazione Zoologica di Napoli 33(supplement): 247–307.

Ng, I. S. Y., C. M. Carr & K. Cottenie, 2009. Hierarchical zooplankton metacommunities: distinguishing between high and limiting dispersal mechanisms. Hydrobiologia 619: 133–143.

Oksanen, J., G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. R. Stevens & H. Wagner, 2015. vegan: Community Ecology Package. R package version 2.2-1. http://CRAN.R-project.org/package=vegan.

Peres-Neto, P. R. & D. A. Jackson, 2001. How well do multivariate data sets match? The advantages of a Procrustean superimposition approach over the Mantel test. Oecologia 129: 169–178.

Peres-Neto, P. R., P. Legendre, S. Dray & D. A. Borcard, 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. Ecology 87: 2614–2625.

Poquet, J. M., F. Mezquita, J. Rueda & M. R. Miracle, 2008. Loss of Ostracoda biodiversity in Western Mediterranean wetlands. Aquatic Conservation: Marine and Freshwater Ecosystems 18: 280–296.

QGIS Development Team, 2014. QGIS geographic information system. Open source geospatial foundation project. http://qgis.osgeo.org/.

Rautio, M., S. Sorvari & A. Korhola, 2000. Diatom and crustacean zooplankton communities, their seasonal variability and representation in the sediments of subarctic Lake Saanajärvi. Journal of Limnology 59: 81–96.

R Development Core Team, 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing. http://www.R-project.org/.

Reed, J. M., F. Mesquita-Joanes & H. I. Griffiths, 2012. Multi-indicator conductivity transfer functions for Quaternary palaeoclimate reconstruction. Journal of Paleolimnology 47: 251–275.

Resetarits, W. J., 2001. Colonization under threat of predation: avoidance of fish by an aquatic beetle, *Tropisternus lateralis* (Coleoptera: Hydrophilidae). Oecologia 129: 155–160.

Roca, J. R., F. Mezquita, J. Rueda, A. Camacho & M. R. Miracle, 2000. Endorheic versus karstic lakes: patterns of ostracod distributions and lake typology in a Mediterranean landscape (Castilla - La Mancha, Spain). Marine and Freshwater Research 51: 311–319.

Rull, V., 2010. Ecology and palaeoecology: two approaches, one objective. Open Ecology Journal 3: 1–5.

Seddon, A. W. R., A. W. Mackay, A. G. Backer, H. J. B. Birks, E. Breman, C. E. Buck, E. C. Ellis, et al., 2014. Looking forward through the past: identification of 50 priority research questions in palaeoecology. Journal of Ecology 102: 256–267.

Soininen, J., J. J. Korhonen, J. Karu & A. Vetterli, 2011. Disentangling the spatial patterns in community composition of prokaryotic and eukaryotic lake plankton. Limnology and Oceanography 56: 508–520.

Strecker, A. L. & S. E. Arnott, 2010. Complex interactions between regional dispersal of native taxa and an invasive species. Ecology 91: 1035–1047.

Symons, C. C. & S. E. Arnott, 2014. Timing is everything: priority effects alter community invasibility after disturbance. Ecology and Evolution 4: 397–407.

Urban, M. C. & L. De Meester, 2009. Community monopolization: local adaptation enhances priority effects in an evolving metacommunity. Proceedings of the Royal Society B: Biological Sciences 276: 4129–4138.

Valls, L., J. Rueda & F. Mesquita-Joanes, 2013. Dynamics of Ostracoda (Crustacea) assemblages in a Mediterranean pond system (Racó de l'Olla, Albufera Nat. Park) with focus on the exotic species *Candonocypris novaezelandiae* (Baird, 1843). International Journal of Limnology-Annales de Limnologie 49: 237–247.

Valls, L., A. Castillo-Escrivà, F. Mesquita-Joanes & X. Armengol, 2016a. Human-mediated dispersal of aquatic invertebrates with waterproof footwear. Ambio 45: 99–109.

Valls, L., L. Zamora, J. Rueda & F. Mesquita-Joanes, 2016b. Living and dead ostracod assemblages in a coastal mediterranean wetland. Wetlands 36: 1–9.

Vanschoenwinkel, B., S. Gielen, M. Seaman & L. Brendonck, 2008. Any way the wind blows - frequent wind dispersal drives species sorting in ephemeral aquatic communities. Oikos 117: 125–134.

Verleyen, E., W. Vyverman, M. Sterken, D. A. Hodgson, A. De Wever, S. Juggins, B. Van de Vijver, V. J. Jones, P. Vanormelingen, D. Roberts, R. Flower, C. Kilroy, C. Souffreau & K. Sabbe, 2009. The importance of dispersal related and local factors in shaping the taxonomic structure of diatom metacommunities. Oikos 118: 1239–1249.

Williams, W. D., A. J. Boulton & R. G. Taafe, 1990. Salinity as a determinant of salt lake fauna: a question of scale. Hydrobiologia 197: 257–266.

Winegardner, A. K., B. E. Beisner, P. Legendre & I. Gregory-Eaves, 2015. Are the landscape-level drivers of water column and surface sediment diatoms different? Freshwater Biology 60: 267–281.

Supplementary material

Disentangling species sorting, dispersal and priority effects
on ostracod assemblages in shallow lakes

Appendix I

List of lakes sampled, code, coordinates, and the selected environmental variables by means forward selection (conductivity, LOI_{550}, mean annual rainfall and lake surface values).

Lake	Code	Long (º)	Lat (º)	Conductivity (mS cm^{-1})	LOI_{550} (%DW)	Mean annual rainfall (mm)	Lake surface (ha)
Alcahozo	ALC	-2.87	39.39	25.86	16.93	417	71.60
Almodóvar	ALM	-4.16	38.70	5.99	3.37	497	19.40
Altillo Chica	ATC	-3.30	39.70	29.10	6.16	426	13.79
Altillo Grande	ATR	-3.30	39.69	17.90	8.53	427	20.29
Campo de la Mula	CAM	-3.41	39.58	34.00	8.45	423	29.61
Camino de Villafranca	CAV	-3.26	39.41	23.26	18.49	412	185.00
Caracuel	CRC	-4.07	38.82	0.99	6.04	469	66.70
Camino de Turleque	CTU	-3.42	39.61	5.77	19.36	426	24.33
Grande de Villafranca	GVI	-3.34	39.45	13.76	6.20	418	59.61
Huevero	HUE	-2.73	39.44	3.39	8.00	419	16.17
Larga de Villacañas	LVC	-3.31	39.61	20.70	15.72	420	109.50
Manjavacas	MAN	-2.86	39.42	13.20	10.45	418	152.28
Miguel Esteban	MIG	-3.06	39.51	2.66	18.79	423	55.52
Nava Grande	NGR	-3.94	39.18	1.39	17.70	421	130.05
Pozuelo	POZ	-3.83	38.92	10.02	19.85	430	47.65
Pueblo (Pedro Muñoz)	PUE	-2.95	39.41	5.20	8.15	416	29.63
Retamar	RET	-2.97	39.42	3.62	9.48	417	51.26
Sánchez Gómez	SGO	-2.84	39.43	10.37	10.33	419	58.46
Salicor	SLC	-3.18	39.46	77.65	2.77	425	60.65
Taray	TAR	-2.72	39.41	1.08	7.37	419	25.21
Tírez	TRZ	-3.36	39.54	37.00	7.18	419	105.89
La Veguilla	VGU	-3.24	39.40	2.63	9.87	412	136.40

Appendix II

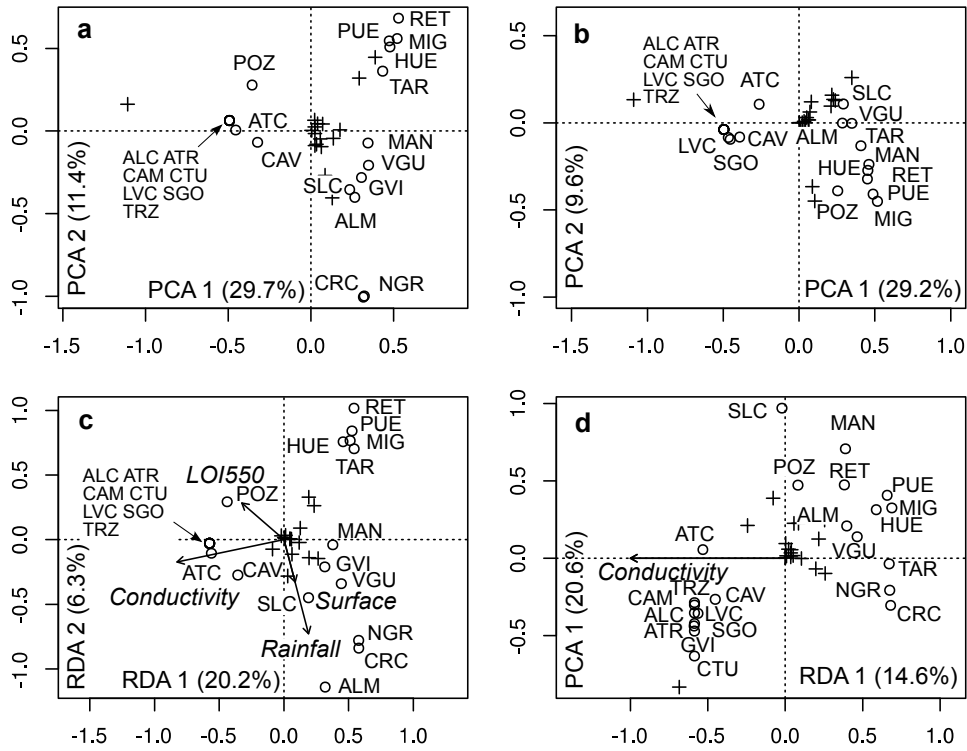Figures A1 and A2, which correspond to figures 2 and 3 with the lake labels, respectively.

Fig. A1 Ordination plots for the first two axes of biocoenoses PCA (a), taphocoenoses PCA (b), biocoenoses RDA (c), and taphocoenoses RDA (d) constrained by selected environmental variables. Circles and crosses represent lakes and species, respectively. Lake codes as in Appendix I.
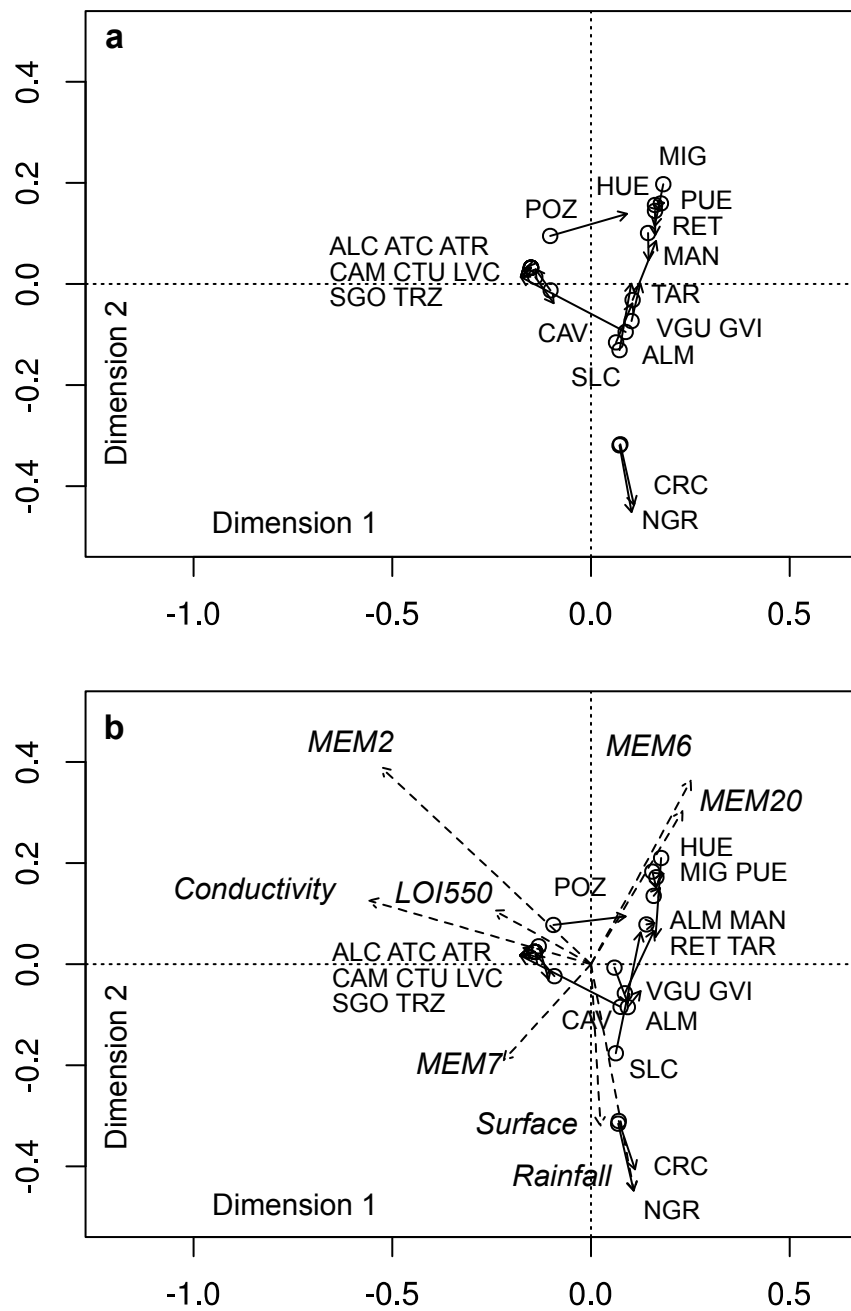
Fig. A2 Procrustean plots comparing the PCAs (a) and RDAs constrained by environmental and spatial variables selected (b). Circles represent the rotated matrix (taphocoenoses), and the heads of the arrows represent the target matrix (biocoenoses). The lengths of the arrows are proportional to the procrustean residuals (long arrow-high residual-low concordance). We also represent the biocoenoses species PCA scores (a) and the selected environmental and spatial variables of the biocoenoses RDA (b). Lake codes as in Appendix I. Circles and crosses represent lakes and species, respectively.

Resum ampliat

Llacuna de Manjavacas

Resum ampliat

El concepte de metacomunitat ha promogut una nova visió teòrica de les comunitats, emfatitzant la seua interdependència en una naturalesa multi-escalar. No obstant, els estudis empírics que tracten els mecanismes estructuradors de les comunitats encara són escassos. En el **Capítol 1**, presentem una anàlisi espacial multi-escalar en una metacomunitat d'ostracodes de llacs endorreics en el centre de la Península Ibèrica. Amb aquest propòsit, utilitzàrem mètodes d'anàlisi d'ordenació multivariant, escalogrames i partició de la variància per identificar els efectes ambientals (*i.e.* ordenació d'espècies) i espacials (*i.e.* limitació dispersiva, efectes de massa) sobre les metacomunitats. Els resultat indiquen que tant l'ordenació d'espècies com els processos dispersius estructuren les metacomunitats. Els principals factors ambientals foren la salinitat i la temporalitat. Per altra banda, alguns components espacials d'escala ampla també estructuraren les comunitats de forma significativa, suggerint que els ostracodes tenen limitacions dispersives dins l'extensió espacial considerada. El nostre estudi confirma la importància de l'ordenació d'espècies, però també revela el paper que juguen els processos dispersius en l'estructura de les metacomunitats d'ostracodes.

Els estudis empírics sobre mecanismes estructuradors de les metacomunitats s'han centrat sovint en la importància relativa del filtratge ambiental i la dispersió. Alguns estudis recents suggerixen que aquesta importància relativa diferix entre organismes amb diferent grandària corporal, afiliació taxonòmica i habilitats dispersives, i també depèn de l'extensió regional i l'heterogeneïtat ambiental. Tot i això, els efectes de la connectivitat entre localitats i el mode de dispersió *per se* han sigut poc considerats explícitament als estudis sobre metacomunitats. En el **Capítol 2**, analitzem metacomunitats d'invertebrats aquàtics en basses de roca, comparant els efectes ambientals i espacials entre basses situades en dos escenaris del paisatge amb característiques diferents: un conjunt localitzat a la zona de barranc, amb un flux d'aigua efímer entre elles, i un altre conjunt en zones elevades sense aquesta connexió. També analitzem el paper dels mecanismes estructuradors comparant entre les metacomunitats d'organismes amb dispersió activa i

passiva. Utilitzàrem l'anàlisi multivariant permutacional de la variància (NPMANOVA) i l'anàlisi de l'homogeneïtat multivariant de dispersió de grups (PERMDISP) per a comparar la variació ambiental i la composició d'espècies entre els dos tipus d'escenaris. Es va emprar l'anàlisi de la partició de la variància per a determinar el percentatge de la variació de les espècies que era explicada per les variables ambientals i espacials. Com a resultat, l'efecte dels mecanismes estructuradors depengué de la connectivitat del paisatge i del mode de dispersió de les espècies. L'ordenació d'espècies estructurava la metacomunitat d'organismes amb dispersió activa en ambdós escenaris, ja que aquestos organismes poden arribar a totes les localitats dins l'extensió espacial considerada. A més, la diversitat beta dels organismes amb dispersió activa i els efectes de l'ordenació d'espècies foren majors en les basses connectades pel barranc. En els organismes amb dispersió passiva, l'ordenació d'espècies sols tingué efectes sobre la metacomunitat més connectada del barranc, mentre què les basses sense aquesta connectivitat foren més afectades per l'espai. Aquest estudi mostra la importància de les característiques del paisatge i del mode de dispersió en metacomunitats de basses de roca en una extensió espacial reduïda.

Com hem dit, la distribució heterogènia de les espècies és el resultat d'una combinació d'efectes ambientals i espacials. En el context espacial, les xarxes de rius constituïxen sistemes apropiats per a comparar la importància relativa de dos modes de dispersió en organismes aquàtics: a favor del corrent d'aigua, front a la dispersió a través de l'aire i el terra. En el **Capítol 3**, analitzem la distribució d'espècies d'ostracodes en una xarxa de rius de l'est de la Península Ibèrica, mitjançant l'anàlisi de la partició de la variància entre factors ambientals i espacials, utilitzant mapes de vectors propis de Moran i asimètrics (MEMs, AEMs) com a variables espacials. L'objectiu era determinar la importància relativa de l'ambient i l'espai i comparar el paper de la dispersió terrestre-aèria front a la dispersió a favor del corrent d'aigua, en la distribució d'ostracodes. Els nostres resultats suggerixen que la dispersió a favor del corrent d'aigua podria ser el tipus de dispersió més important, afavorint els efectes de massa. El paper de l'ordenació d'espècies també fou significatiu i estigué relacionat amb la temperatura, l'amplada del riu i la qualitat de l'aigua, mesurada com un índex biòtic (IBMWP). Aquestos resultats mostren que la connectivitat pot tindre una major importància que l'ordenació d'espècies en l'estructuració de comunitats d'organismes aquàtics amb dispersió passiva.

Els estudis sobre metacomunitats solen estar centrats en els patrons estructurals de les metacomunitats i en els mecanismes que les estructuren. Però, les dinàmiques de les metacomunitats i la variació temporal del paper dels mecanismes estructuradors han sigut rarament estudiats. En el **Capítol 4** hem analitzat la variació temporal en una metacomunitat d'ostracodes de llacunes somes temporals de la Península Ibèrica. El nostre objectiu fou determinar la variabilitat de les comunitats d'ostracodes estudiades periòdicament al llarg d'un cicle hidrològic, mitjançant anàlisis triàdiques parcials (PTA), tot i avaluant així mateix els efectes ambientals i espacials sobre la metacomunitat al llarg del temps. La metacomunitat fou moderadament estable al llarg del període de temps de l'estudi, amb una major variabilitat entre localitats que entre mesos. Tot i això, l'estructura de les metacomunitats a l'inici de l'hiperíode fou notablement diferent de la resta de mesos. L'ordenació d'espècies fou el mecanisme estructurador predominant de la metacomunitat al llarg del mesos mostrejats, establint una conspícua separació entre espècies que habiten llacunes molt salades i aquelles que preferixen llacunes poc salades. En canvi, els processos espacials foren menys importants. Els nostres resultats mostren el potencial d'una aproximació temporal en l'estudi de les metacomunitats, front a una única instantània temporal, on veiem diferències al principi de l'hiperíode en cosos d'aigua temporals, però dominat majoritàriament per l'ordenació d'espècies sota un gradient ambiental estepari.

L'estructura de les comunitats està determinada per una varietat de mecanismes ecològics, incloent no només control ambiental i processos de dispersió, sinó també la contingència històrica. Recentment, molts estudis s'han centrat en la influència de l'ambient i la dispersió en l'estructura de les metacomunitats, però les contingències històriques (*i.e.* efectes prioritaris) han sigut rarament considerades, encara que podrien tindre un paper clau. En aquest context, l'ús dels mètodes paleoecològics, podria ajudar a avaluar la influència dels esdeveniments passats en les comunitats presents. En el **Capítol 5**, comparem les comunitats vives (*i.e.* biocenosis) d'ostracodes i les comunitats de subfòssils (*i.e.* tafocenosis) de 22 llacunes somes estepàries, i determinem la contribució relativa dels factors ambientals i espacials en ambdós assemblatges. A més, estimem el paper dels efectes prioritaris en les comunitats presents, utilitzant els dos primer eixos del PCA de les tafocenosis, com a variables històriques. Els nostres resultats indiquen una alta

concordança entre ambdós assemblatges. A més, l'ambient dominava sobre l'espai explicant les biocenosis, mentre què en les tafocenosis l'espai dominava sobre l'ambient. Finalment, es mostrà com l'estructura de la metacomunitat actual estava relacionada amb l'ordenació d'espècies, la dispersió i els efectes històrics purs, suggerint la importància d'una ocupació primerenca en aquests ecosistemes.

Discussió general

Riu Palància (Bejís)

Discussió general

Aquesta discussió general està estructurada en tres parts, en les quals revisarem i compararem els resultats dels estudis d'aquesta tesi en conjunt. En la primera part, analitzarem com el context regional pot explicar la variació de la importància relativa dels mecanismes estructuradors comparant entre distints estudis. En segon lloc, compararem els resultats obtinguts amb ostracodes amb els d'altres organismes que han sigut objecte d'estudi des del punt de vista de les seues metacomunitats (*e.g.*, bacteris, diatomees, macroinvertebrats). En la tercera part, discutirem el paper dels efectes prioritaris com a mecanisme estructurador de les comunitats, i d'altres que possiblement també siguen importants, sobre les metacomunitats d'ostracodes. Per concloure, exposarem una sèrie de possibles investigacions futures en el camp de les metacomunitats utilitzant els ostracodes com organismes model.

El context regional com a font de variació

En aquesta tesi hem observat que la importància relativa de l'ambient i l'espai sobre les metacomunitats diferix entre estudis (Taula 1; Fig. 1a). Els efectes ambientals dominaren o mostraren un efecte semblant a l'espacial en les llacunes i en les basses amb flux d'aigua. Zhai *et al.* (2015), en fonts, i Escrivà *et al.*, (2015), en capçaleres de rius, també observaren un paper similar entre l'ambient i l'espai. En canvi, en els rius, en les basses sense flux d'aigua i en la tafocenosi de les llacunes, els efectes espacials foren més importants que els ambientals. Aquestos resultats revelen que tant l'ordenació d'espècies com els processos dispersius estructuren les comunitats d'ostracodes, i que els efectes espacials s'haurien de tindre en compte en estudis futurs.

La variació existent en els efectes ambientals i espacials entre les metacomunitats estudiades, podria ser explicada pel context regional on estan situades (Heino *et al.*, 2012, 2015a; Grönroos *et al.*, 2013). Especialment per la combinació de tres característiques regionals: l'heterogeneïtat ambiental (Heino, 2013), l'extensió espacial de cada regió

Taula 1. Percentatge pur explicat per l'ambient i l'espai a partir de l'anàlisi de la partició de la variància en cada metacomunitat analitzada en els capítols anteriors i en altres estudis previs publicats. També es mostren les característiques regionals de cada metacomunitat.

Metacomunitat	Ambient (%)	Espai (%) [2]	Número localitats	Heterogeneïtat ambiental [3]	Major distància (km) [4]	Connexió aquàtica
Llacunes biocenosi	17.5	17.3	22	0.616	148	No
Llacunes desembre	-	-	8	0.516	138	No
Llacunes gener	58.8	-	9	0.665	138	No
Llacunes febrer	35.6	17.2	8	0.624	138	No
Llacunes març	22.2	12.6	9	0.619	138	No
Llacunes abril	37.4	12.4	9	0.690	138	No
Llacunes maig	24.0	-	9	0.656	138	No
Llacunes tafocenosi	7.6	27.9	22	0.616	148	No
Rius	5.3	21.3	39	0.777	93	Si
Basses amb flux d'aigua [1]	9.5	-	25	0.261	1.4	Si
Basses sense flux d'aigua [1]	-	21.7	28	0.220	1.4	No
Fonts (Zhai *et al.*, 2015)	6.4	4.3	74	-	~250	No
Capçaleres de rius (Escrivà *et al.*, 2015)	4.1	6.7	147	-	~700	Si

[1] En les basses hem tingut en compte els resultats referents a les espècies passives, de les quals la meitat són ostracodes (5 de les 9 espècies).
[2] Els efectes purs de l'espai han sigut re-calculats de nou, si calia, amb totes les variables espacials seleccionades (MEMs d'escala ampla i fina), encara què podria ser que en alguns casos no estigueren relacionades amb variables ambientals no mesurades. En el cas dels rius hem agrupat els MEMs i AEMs seleccionats com efectes espacials.
[3] L'heterogeneïtat ha sigut calculada com en el capítols 2 i 4 (Anderson *et al.*, 2006). Per evitar descompensacions entre estudis, hem utilitzat únicament conductivitat, temperatura mitjana anual i grandària del cos d'aigua. La grandària ha sigut mesurada en les llacunes i les basses considerant la màxima longitud entre dues vores, i en els rius com l'amplada del riu.
[4] L'extensió espacial de cada regió ha sigut mesurada com la màxima distància entre localitats (Heino *et al.*, 2015a).

(Soininen *et al.*, 2011) i el grau de connexió aquàtica de cada sistema (Vanschoenwinkel *et al.*, 2007; Fernandes *et al.*, 2014). El conjunt de mostres dels rius fou el que més heterogeneïtat ambiental tenia, seguit de les llacunes i de les basses, les últimes amb molt poca heterogeneïtat ambiental (Taula 1; Fig. 1b). No obstant, la regió de les llacunes fou la regió amb major extensió espacial, seguida pels rius. L'extensió espacial de les basses era molt reduïda, amb la qual cosa les variacions ambientals, pel que fa a factors com ara el clima, no poden ser grans. La regió amb major heterogeneïtat ambiental no concorda amb
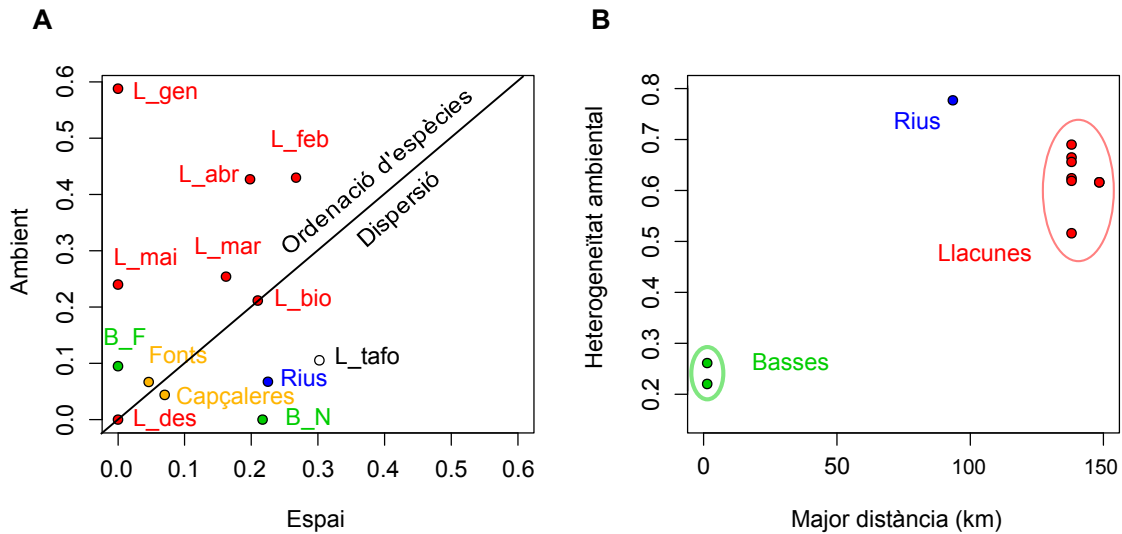
Figura 1. Relació entre els efectes purs de l'ambient i l'espai (A) en les metacomunitats d'ostracodes estudiades en aquesta tesi i en un estudi sobre fonts (Zhai *et al.*, 2015) i sobre capçaleres de rius (Escrivà *et al.*, 2015), després de corregir per mútua interdependència els efectes ambientals (Ambient|Espai / [100% - E|A]) i els espacials (E|A / [100% - A|E]). A la dreta (B), es mostra la relació entre l'heterogeneïtat ambiental i l'extensió espacial (major distància entre localitats). L = llacunes; B = basses; F = amb flux d'aigua; N = sense flux d'aigua; bio = biocenosi; tafo = tafocenosi; des = desembre; gen = gen; feb = febrer; mar =març; abr =abril; mai = maig.

la de major extensió espacial com podria esperar-se (veure Jackson *et al.*, 2001), perquè la regió dels rius tenia major diversitat d'ambients que les llacunes en una extensió menor, probablement conseqüència d'un major gradient altitudinal.

Els efectes ambientals explicaren un major percentatge de l'estructura de les comunitats que l'espai en les llacunes i en les basses amb flux d'aigua. La taxa de dispersió entre les llacunes i aquestes basses permetria l'ordenació d'espècies, gràcies a vectors com el vent o altres animals (Green *et al.*, 2008; Vanschoenwinkel *et al.*, 2008a) en el cas de les llacunes, i afegit a aquestos vectors, una connexió efímera d'aigua en les basses (Vanschoenwinkel *et al.*, 2008b). Aquest flux d'aigua podria ser la causa per la qual en aquestes basses no vam detectar cap efecte espacial, a més d'una reduïda extensió espacial que afavorix la dispersió entre localitats. En canvi, en les llacunes observàrem efectes espacials relacionats amb la limitació dispersiva, perquè tenen major extensió espacial (Taula 1; Fig. 1b) i no tenen cap flux d'aigua que les connecte. Per altra banda, el percentatge explicat per l'ambient en les llacunes fou generalment major que en les basses,

el que podria ser explicat per una major heterogeneïtat ambiental en les llacunes, en part a causa d'una major extensió espacial (Fig. 1b), però també pel gradient abiòtic de salinitats i hidroperíode.

En els rius i en les basses sense flux d'aigua, els efectes espacials dominaren sobre els ambientals. No obstant, hem suggerit que els efectes dispersius eren diferents en els dos casos. La taxa de dispersió en els rius podria ser més alta que en els altres sistemes degut a la corrent del riu (Grant *et al.*, 2007), afavorint els efectes de massa i disminuint l'ordenació d'espècies. Aquesta hipòtesi concordaria amb què els rius, malgrat tindre una major heterogeneïtat ambiental que les llacunes, no tenen major efecte de l'ordenació d'espècies, degut a un emmascarament per la dispersió (Fig. 1a; Heino *et al.*, 2015a).

En el cas de les basses sense flux d'aigua, vam suposar que la manca de connexió aquàtica provocaria una menor taxa dispersiva que en les basses connectades (*i.e.* limitació dispersiva). No obstant, les distàncies entre les basses són molt menudes i no deurien ser un problema per als ostracodes (Vanschoenwinkel *et al.*, 2008b) –sobretot per a especialistes de basses temporals com *Heterocypris bosniaca* (Aguilar-Alberola & Mesquita-Joanes, 2011)– i més, comparant aquestes distàncies amb les llacunes, les quals semblen tindre major taxa de dispersió. De totes maneres, per fer aquesta comparació seria necessari calcular directament les taxes de dispersió entre localitats. Una altra causa de què no es detectara cap efecte ambiental podria ser que les basses tenien molt poca heterogeneïtat ambiental (Fig. 1b), reduint el filtratge ambiental i afavorint fenòmens espacials o estocàstics (Chase, 2007).

En resum (Fig. 2), una major heterogeneïtat ambiental propicia l'ordenació d'espècies en les metacomunitat d'ostracodes (llacunes i basses amb flux d'aigua), sempre que hi haja una taxa de dispersió relativament moderada. Però si la taxa de dispersió és relativament alta, els efectes de massa anul·len aquesta relació (rius), sent més importants els efectes espacials. En cas contrari, si la taxa de dispersió és relativament baixa, la limitació dispersiva també provoca que els efectes espacials siguen més importants (basses sense flux d'aigua). Aquesta taxa de dispersió, sembla majoritàriament estar relacionada amb la connexió aquàtica entre les localitats dels diferents sistemes estudiats, encara què també podria deure's a diferències en els vectors animals de cada regió, del vent o de la
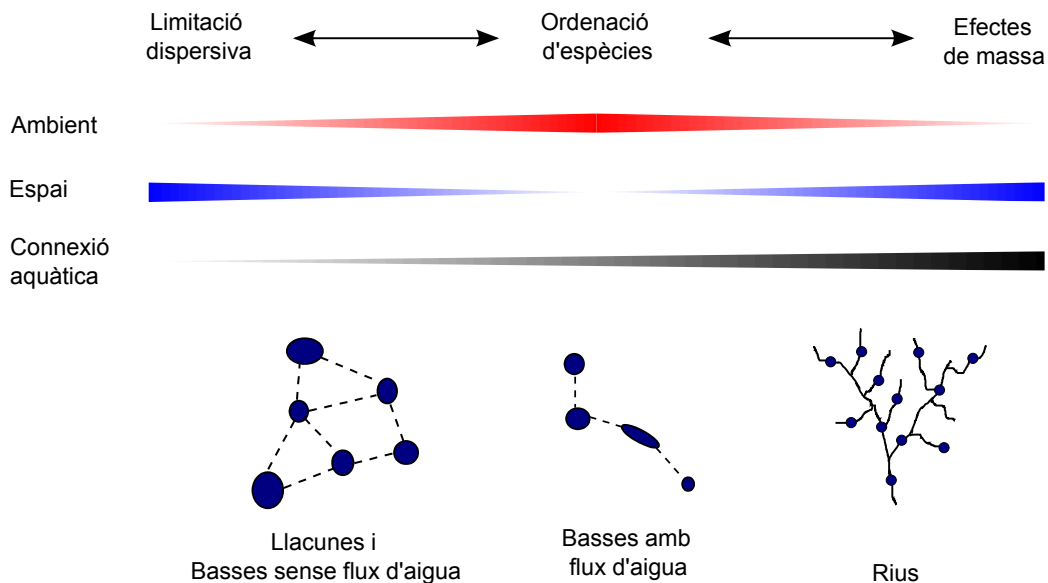
Figura 2. Una possible ordenació de les metacomunitats estudiades en uns gradients de percentatge explicat per l'ambient i l'espai en la composició d'espècies i el grau de connectivitat aquàtica de cada sistema aquàtic, relacionat amb els mecanismes que estructuren cada metacomunitat.

grandària i hidroperíode de les localitats. Malgrat tot, hem de tindre present que aquesta comparació té certes limitacions per extrapolar els resultats entre sistemes aquàtics molt diferents en grandària (des de basses de roca a llacunes), composició d'espècies o número de localitats.

Diferències entre grups d'organismes

En el Capítol 2, podem observar que el percentatge explicat per l'ambient i l'espai de la composició d'espècies varia entre organismes amb dispersió activa i passiva. L'ambient explicava un percentatge major de la composició dels organismes actius que dels passius, perquè els organismes actius poden arribar i escollir millor les localitats favorables (Resetarits, 2001). En els organismes passius, inclús els efectes espacials foren més forts que els ambientals en un context sense flux d'aigua entre basses. Aquestes diferències també han estat assenyalades en altres estudis comparatius entre grups d'organismes amb estratègies dispersives diferents (Astorga *et al.*, 2012; Heino *et al.*, 2012; Grönroos *et al.*, 2013). No obstant, no hem trobat cap altre estudi que compare els ostracodes en solitari

amb altres grups.

De Bie *et al.* (2012) van suggerir que el tipus de dispersió i la grandària de l'organisme eren característiques clau que determinaven l'estructura de les metacomunitats. Entre els organismes d'aigua dolça amb dispersió passiva, els ostracodes presenten una grandària relativament mitjana (0.3 a 5 mm; Baltanás & Danielopol, 2013), entre organismes molt menuts (*e.g.*, bacteris, ciliats, diatomees) i organismes grans (*e.g.*, gasteròpodes, amfípodes, macròfits). Els organismes amb dispersió passiva menuts, són dispersats fàcilment (Finlay, 2002), perquè presenten grans poblacions i produïxen gran quantitat de propàguls (Brown *et al.*, 2004; Fenchel & Finlay, 2004). No tenen limitacions, espacials, fins a certes distàncies enormes (veure Verleyen *et al.*, 2009) i l'ordenació d'espècies és el mecanisme estructurador dominant (Van der Gucht *et al.*, 2007; Lindström & Langenheder, 2012; Souffreau *et al.*, 2015). En les comunitats d'organismes amb dispersió passiva grans, a banda de l'ordenació d'espècies, els processos dispersius també són importants. (Hájek *et al.*, 2011; Alahuhta & Heino, 2013; Rádková *et al.*, 2014). Els ostracodes ocupen un rang de grandària en el qual es donaria una transició entre metacomunitats estructurades principalment per l'ordenació d'espècies i en les que també són importants els processos dispersius (Fig. 3; veure Finlay, 2002). Aquest rang seria compartit amb altres organismes semblants en grandària i amb dispersió passiva, com els

Figura 3. Model hipotètic de la transició d'organismes amb metacomunitats estructurades únicament per l'ordenació d'espècies i les que els processos dispersius també tenen un paper estructurador, depenent de la grandària de l'organisme (modificat a partir de Finlay, 2002). En gris representem el rang en què es trobarien els ostracodes.
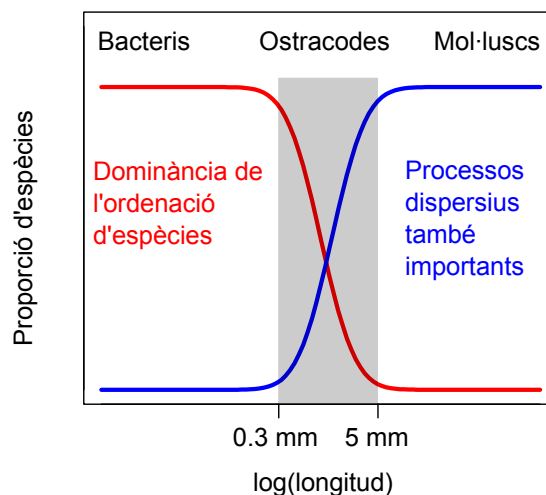
cladòcers i els copèpodes (Cottenie *et al.*, 2003; Ng *et al.*, 2009; Çakıroğlu *et al.*, 2014).

Altres mecanismes estructuradors

Els estudis sobre els mecanismes estructuradors de les metacomunitats solen tractar únicament l'ordenació d'espècies i la dispersió. No obstant, altres mecanismes podrien actuar com a mecanismes estructuradors, com ara els efectes prioritaris, els fenòmens estocàstics i les dinàmiques interespecífiques. En el Capítol 5, vam suggerir que els efectes prioritaris juguen un paper en l'estructuració de les metacomunitats d'ostracodes de llacunes temporals, analitzant la similitud entre les comunitats vives i les restes d'ostracodes, com s'ha realitzat en altres organismes (Levi *et al.*, 2014; Çakıroğlu *et al.*, 2014; Winegardner *et al.*, 2015). Aquest estudi revela la importància del banc d'ous en els sistemes aquàtics temporals (De Meester *et al.*, 2002; Chase, 2007; Urban & De Meester, 2009), que permet que les comunitats siguen semblants en diferents períodes d'inundació, independentment dels efectes ambientals i espacials (Mergeay *et al.*, 2011).

En el Capítol 4, també degut al banc d'ous, observàrem com al principi de la inundació de les llacunes temporals els fenòmens estocàstics podrien ser els causants de que no detectàrem ni efectes ambientals ni espacials. Nosaltres vam suggerir que aquest resultat podria ser degut a que després de la inundació els ous de moltes espècies oportunistes eclosionen ràpidament, sense cap filtre ambiental. Per altra banda, en el rius mediterranis estudiats els fenòmens estocàstics també podrien ser els causants d'un reduït percentatge explicat per l'ambient i l'espai (Capítol 3; veure també Datry *et al.*, 2015), el què també és freqüent en altres estudis sobre metacomunitats de rius (Landeiro *et al.*, 2011; Heino *et al.*, 2012; Grönroos *et al.*, 2013).

En les basses de roca, degut a la seua grandària reduïda, també poden jugar els efectes prioritaris i els fenòmens estocàstics un paper més important que les condicions abiòtiques i l'espai (Chase, 2007). A més, les interaccions interespecífiques com la depredació i la competència (les condicions biòtiques) podrien ser molt importants en les basses de roca (Jocque *et al.*, 2010). Per exemple, en altres estudis s'ha observat com l'arribada de depredadors a una bassa suposa la desaparició de la seua presa (Vanschoenwinkel *et al.*, 2010). També s'ha observat com les espècies amb dispersió activa

eviten les localitats on habiten potencials depredadors (Resetarits, 2001).

Metacomunitats d'ostracodes i perspectives de futur

Probablement, una de les conclusions més importants d'aquesta tesi és que les comunitats d'ostracodes no solament estan determinades per les variables ambientals. Els efectes espacials i altres factors expliquen un percentatge de la variació en les comunitats. Això significa que deuríem tindre en compte aquest fet per fer un ús més precís dels ostracodes com paleoindicadors, com s'han utilitzat sovint. Per altra banda, els ostracodes oferixen un gran potencial com a organismes model en l'estudi de les metacomunitats. En aquest últim apartat dibuixarem quatre possibles línies futures d'investigació en les quals els ostracodes podrien contribuir en el camp de les metacomunitats.

En primer lloc, els estudis paleolimnològics amb ostracodes podrien servir de gran ajuda en l'estudi de les metacomunitats (Gregory-Eaves & Beisner, 2011). El Capítol 5 representa una primera aproximació al que aquest tipus d'estudis poden ensenyar-nos sobre metacomunitats d'ostracodes, com ja s'ha fet amb diatomees (Winegardner *et al.*, 2015), cladòcers (Çakıroğlu *et al.*, 2014) i macròfits (Levi *et al.*, 2014). Per una banda, aquestos estudis ens permeten observar altres mecanismes diferents a l'ordenació d'espècies i la dispersió, com són els efectes prioritaris (Mergeay *et al.*, 2011). Per altra banda, seria molt interessant estudiar els canvis en la importància relativa dels mecanismes estructuradors al llarg de sèries de temps extenses amb diversos registres sedimentaris (com per exemple en els últims 100, 500 o 1000 anys), per observar com afecten els canvis de les condicions climàtiques a la dinàmica de les metacomunitats. Els ostracodes (com les diatomees) han sigut més utilitzats com a paleoindicadors que altres organismes utilitzats normalment en estudis de metacomunitats (*e.g.*, insectes i peixos), i gran part dels estudis sobre metacomunitats realitzats solament amb ostracodes serien d'interès general amb aquest enfocament paleolimnològic.

En segon lloc, en el Capítol 3 vam predir que depenent del mode de vida de cada espècie d'ostracode (*e.g.*, ostracodes que s'arrosseguen *vs.* ostracodes nadadors), les seues poblacions podrien estar més afectades per les condicions locals o per la dispersió, perquè uns són més fàcilment arrastrats pel corrent d'aigua que els altres. No obstant, això hauria

d'ésser comprovat en futurs estudis comparant grups d'espècies amb diferents comportaments, o bé generalistes *vs.* especialistes (Pandit *et al.*, 2009). Aquesta dependència del mode de vida o comportament de les espècies fou exposada per Heino i Peckarsky (2014) en insectes, ja que aquestos autors suposen que depenent d'on dipositen la posta les distintes espècies d'insectes aquàtics (per exemple, flotant o enterrades en el substrat) són més propenses a ser dispersades corrent avall que altres. De tota manera, és un tema que ocuparà segurament futures investigacions, com ja s'ha vist entre diatomees amb mobilitat alta i baixa (Göthe *et al.*, 2013).

En tercer lloc, l'estudi de l'efecte d'altres mecanismes estructuradors (a banda dels efectes ambientals i espacials) també és important per entendre millor el funcionament de les comunitats. Ja hem comentat que la paleolimnologia podria ajudar a estudiar els efectes prioritaris (Mergeay *et al.*, 2011). A més, la utilització de variables explicatives que incorporen la presència de potencials predadors podrien indicar-nos l'efecte d'aquestos sobre l'estructura de les comunitats de preses (Göthe *et al.*, 2013).

En quart lloc, les metacomunitats poden ser estudiades des d'altres perspectives diferents a la utilitzada en aquesta tesi (Heino *et al.*, 2015b). Nosaltres hem estudiat les metacomunitats d'ostracodes des d'una perspectiva mecànica, determinant el paper dels mecanismes estructuradors sobre les metacomunitats. No obstant, podríem haver estudiat el patró estructural de la metacomunitat, sense tindre en compte cap variable explicativa, aplicant el que s'anomena anàlisi dels elements de l'estructura de la metacomunitat (EMS de l'anglès *Elements of Metacommunity Structure*; Leibold & Mikkelson, 2002; Presley *et al.*, 2010; Henriques-Silva *et al.*, 2012). Un bon enfocament per a futures investigacions seria una integració d'ambdues perspectives, dels efectes dels mecanismes estructuradors i dels patrons estructurals de les metacomunitats, com ja s'ha realitzat recentment (Fernandes *et al.*, 2014; Gascón *et al.*, 2016).

L'estudi de l'estructura de les metacomunitats és important perquè significa la connexió entre els patrons de diversitat de les espècies i les característiques del paisatge, i per aquesta raó és una eina bàsica en els plans de conservació de la biodiversitat (Economo, 2010). Des d'un punt de vista mecànic de les metacomunitats, en un escenari en què aquestes estan determinades per l'ordenació d'espècies, l'atenció en la gestió del

paisatge deuria estar enfocada a mantindre la diversitat dels hàbitats locals. Però si els processos dispersius són importants, la planificació del territori hauria de tindre en compte també la connectivitat entre les localitats i promoure localitats favorables a certes espècies per a que funcionen com una font d'aquestes (Bengtsson, 2011). Per tant, és necessari un esforç per a comunicar aquestes idees als gestors del medi ambient, de la mateixa manera que és necessari que ens continuem preguntant: Per què uns organismes habiten uns llocs i no uns altres?

Referències

Aguilar-Alberola, J. A., & F. Mesquita-Joanes, 2011. Population dynamics and tolerance to desiccation in a crustacean ostracod adapted to life in small ephemeral water bodies. *Limnologica* 41: 348–355.

Alahuhta, J., & J. Heino, 2013. Spatial extent, regional specificity and metacommunity structuring in lake macrophytes. *Journal of Biogeography* 40: 1572–1582.

Anderson, M. J., K. E. Ellingsen, & B. H. McArdle, 2006. Multivariate dispersion as a measure of beta diversity. *Ecology Letters* 9: 683–693.

Astorga, A., J. Oksanen, M. Luoto, J. Soininen, R. Virtanen, & T. Muotka, 2012. Distance decay of similarity in freshwater communities: do macro- and microorganisms follow the same rules? *Global Ecology and Biogeography* 21: 365–375.

Baltanás, A., & D. L. Danielopol, 2013. Body-size distribution and biogeographical patterns in non-marine ostracods (Crustacea: Ostracoda). *Biological Journal of the Linnean Society* 109: 409–423.

Bengtsson, J., 2011. Applied (meta)community ecology: diversity and ecosystem services at the intersection of local and regional processes. In: Verhoef, H. A., & P. L. Morin (eds), *Community Ecology: Processes, Models and Applications*. Oxford University Press, Oxford: 115–130.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, & G. B. West, 2004. Toward a metabolic theory of ecology. *Ecology* 85: 1771–1789.

Çakıroğlu, A. İ., Ü. N. Tavşanoğlu, E. E. Levi, T. A. Davidson, T. Bucak, A. Özen, G. K. Akyıldız, E. Jeppesen, & M. Beklİoğlu, 2014. Relatedness between contemporary and subfossil cladoceran assemblages in Turkish lakes. *Journal of Paleolimnology* 52: 367–383.

Chase, J. M., 2007. Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences* 104: 17430–17434.

Cottenie, K., E. Michels, N. Nuytten, & L. De Meester, 2003. Zooplankton metacommunity structure: regional *vs.* local processes in highly interconnected ponds. *Ecology* 84: 991–1000.

Datry, T., N. Bonada, & J. Heino, 2015. Towards understanding the organisation of metacommunities in highly dynamic ecological systems. *Oikos* 125: 149–159.

De Bie, T., L. De Meester, L. Brendonck, K. Martens, B. Goddeeris, D. Ercken, H. Hampel, L. Denys,

L. Vanhecke, K. Van der Gucht, J. Van Wichelen, W. Vyverman, & S. Declerck, 2012. Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. *Ecology Letters* 15: 740–747.

De Meester, L., A. Gómez, B. Okamura, & K. Schwenk, 2002. The Monopolization Hypothesis and the dispersal–gene flow paradox in aquatic organisms. *Acta Oecologica* 23: 121–135.

Economo, E. P., 2010. Biodiversity conservation in metacommunity networks: linking pattern and persistence. *American Naturalist* 177: 167–180.

Escrivà, A., J. M. Poquet, & F. Mesquita-Joanes, 2015. Effects of environmental and spatial variables on lotic ostracod metacommunity structure in the Iberian Peninsula. *Inland Waters* 5: 283–294.

Fenchel, T., & B. J. Finlay, 2004. The ubiquity of small species: patterns of local and global diversity. *BioScience* 54: 777–784.

Fernandes, I. M., R. Henriques-Silva, J. Penha, J. Zuanon, & P. R. Peres-Neto, 2014. Spatiotemporal dynamics in a seasonal metacommunity structure is predictable: the case of floodplain-fish communities. *Ecography* 37: 464–475.

Finlay, B. J., 2002. Global dispersal of free-living microbial eukaryote species. *Science* 296: 1061–1063.

Gascón, S., I. Arranz, M. Cañedo-Argüelles, A. Nebra, A. Ruhí, M. Rieradevall, N. Caiola, J. Sala, C. Ibàñez, X. D. Quintana, & D. Boix, 2016. Environmental filtering determines metacommunity structure in wetland microcrustaceans. *Oecologia* 181: 193–205.

Göthe, E., D. G. Angeler, S. Gottschalk, S. Löfgren, & L. Sandin, 2013. The influence of environmental, biotic and spatial factors on diatom metacommunity structure in swedish headwater streams. *PLoS ONE* 8: e72237.

Grant, E. H. C., W. H. Lowe, & W. F. Fagan, 2007. Living in the branches: population dynamics and ecological processes in dendritic networks. *Ecology Letters* 10: 165–175.

Green, A. J., K. M. Jenkins, D. Bell, P. J. Morris, & R. T. Kingsford, 2008. The potential role of waterbirds in dispersing invertebrates and plants in arid Australia. *Freshwater Biology* 53: 380–392.

Gregory-Eaves, I., & B. E. Beisner, 2011. Palaeolimnological insights for biodiversity science: an emerging field. *Freshwater Biology* 56: 2653–2661.

Grönroos, M., J. Heino, T. Siqueira, V. L. Landeiro, J. Kotanen, & L. M. Bini, 2013. Metacommunity structuring in stream networks: roles of dispersal mode, distance type, and regional environmental context. *Ecology and Evolution* 3: 4473–4487.

Hájek, M., J. Roleček, K. Cottenie, K. Kintrová, M. Horsák, A. Poulíčková, P. Hájková, M. Fránková, & D. Dítě, 2011. Environmental and spatial controls of biotic assemblages in a discrete semi-terrestrial habitat: comparison of organisms with different dispersal abilities sampled in the same plots. *Journal of Biogeography* 38: 1683–1693.

Heino, J., 2013. Environmental heterogeneity, dispersal mode, and co-occurrence in stream macroinvertebrates. *Ecology and Evolution* 3: 344–355.

Heino, J., M. Grönroos, J. Soininen, R. Virtanen, & T. Muotka, 2012. Context dependency and metacommunity structuring in boreal headwater streams. *Oikos* 121: 537–544.

Heino, J., A. S. Melo, & L. M. Bini, 2015a. Reconceptualising the beta diversity-environmental

heterogeneity relationship in running water systems. *Freshwater Biology* 60: 223–235.

Heino, J., T. Nokela, J. Soininen, M. Tolkkinen, L. Virtanen, & R. Virtanen, 2015b. Elements of metacommunity structure and community-environment relationships in stream organisms. *Freshwater Biology* 60: 973–988.

Heino, J., & B. L. Peckarsky, 2014. Integrating behavioral, population and large-scale approaches for understanding stream insect communities. *Current Opinion in Insect Science* 2: 7–13.

Henriques-Silva, R., Z. Lindo, & P. R. Peres-Neto, 2012. A community of metacommunities: exploring patterns in species distributions across large geographical areas. *Ecology* 94: 627–639.

Jackson, D. A., P. R. Peres-Neto, & J. D. Olden, 2001. What controls who is where in freshwater fish communities the roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 157–170.

Jocque, M., B. Vanschoenwinkel, & L. Brendonck, 2010. Freshwater rock pools: a review of habitat characteristics, faunal diversity and conservation value. *Freshwater Biology* 55: 1587–1602.

Landeiro, V. L., W. E. Magnusson, A. S. Melo, H. M. V. Espírito-Santo, & L. M. Bini, 2011. Spatial eigenfunction analyses in stream networks: do watercourse and overland distances produce different results? *Freshwater Biology* 56: 1184–1192.

Leibold, M. A., & G. M. Mikkelson, 2002. Coherence, species turnover, and boundary clumping: elements of meta-community structure. *Oikos* 97: 237–250.

Levi, E. E., A. İ. Çakıroğlu, T. Bucak, B. V. Odgaard, T. A. Davidson, E. Jeppesen, & M. Beklİoğlu, 2014. Similarity between contemporary vegetation and plant remains in the surface sediment in Mediterranean lakes. *Freshwater Biology* 59: 724–736.

Lindström, E. S., & S. Langenheder, 2012. Local and regional factors influencing bacterial community assembly. *Environmental Microbiology Reports* 4: 1–9.

Mergeay, J., L. De Meester, H. Eggermont, & D. Verschuren, 2011. Priority effects and species sorting in a long paleoecological record of repeated community assembly through time. *Ecology* 92: 2267–2275.

Ng, I. S. Y., C. M. Carr, & K. Cottenie, 2009. Hierarchical zooplankton metacommunities: distinguishing between high and limiting dispersal mechanisms. *Hydrobiologia* 619: 133–143.

Pandit, S. N., J. Kolasa, & K. Cottenie, 2009. Contrasts between habitat generalists and specialists: an empirical extension to the basic metacommunity framework. *Ecology* 90: 2253–2262.

Presley, S. J., C. L. Higgins, & M. R. Willig, 2010. A comprehensive framework for the evaluation of metacommunity structure. *Oikos* 119: 908–917.

Rádková, V., J. Bojková, V. Křoupalová, J. Schenková, V. Syrovátka, & M. Horsák, 2014. The role of dispersal mode and habitat specialisation in metacommunity structuring of aquatic macroinvertebrates in isolated spring fens. *Freshwater Biology* 59: 2256–2267.

Resetarits, W. J., 2001. Colonization under threat of predation: avoidance of fish by an aquatic beetle, *Tropisternus lateralis* (Coleoptera: Hydrophilidae). *Oecologia* 129: 155–160.

Soininen, J., J. J. Korhonen, J. Karhu, & A. Vetterli, 2011. Disentangling the spatial patterns in community composition of prokaryotic and eukaryotic lake plankton. *Limnology and Oceanography* 56: 508–520.

Souffreau, C., K. Van der Gucht, I. van Gremberghe, S. Kosten, G. Lacerot, L. M. Lobão, V. L. Moraes

Huszar, F. Roland, E. Jeppesen, W. Vyverman, & L. De Meester, 2015. Environmental rather than spatial factors structure bacterioplankton communities in shallow lakes along a > 6000 km latitudinal gradient in South America. *Environmental Microbiology* 17: 2336–2351.

Urban, M. C., & L. De Meester, 2009. Community monopolization: local adaptation enhances priority effects in an evolving metacommunity. *Proceedings of the Royal Society B: Biological Sciences* 276: 4129–4138.

Van der Gucht, K., K. Cottenie, K. Muylaert, N. Vloemans, S. Cousin, S. Declerck, E. Jeppesen, J. M. Conde-Porcuna, K. Schwenk, G. Zwart, H. Degans, W. Vyverman, & L. D. Meester, 2007. The power of species sorting: Local factors drive bacterial community composition over a wide range of spatial scales. *Proceedings of the National Academy of Sciences* 104: 20404–20409.

Vanschoenwinkel, B., C. De Vries, M. Seaman, & L. Brendonck, 2007. The role of metacommunity processes in shaping invertebrate rock pool communities along a dispersal gradient. *Oikos* 116: 1255–1266.

Vanschoenwinkel, B., S. Gielen, M. Seaman, & L. Brendonck, 2008a. Any way the wind blows - frequent wind dispersal drives species sorting in ephemeral aquatic communities. *Oikos* 117: 125–134.

Vanschoenwinkel, B., S. Gielen, H. Vandewaerde, M. Seaman, & L. Brendonck, 2008b. Relative importance of different dispersal vectors for small aquatic invertebrates in a rock pool metacommunity. *Ecography* 31: 567–577.

Vanschoenwinkel, B., A. Waterkeyn, M. Jocqué, L. Boven, M. Seaman, & L. Brendonck, 2010. Species sorting in space and time—the impact of disturbance regime on community assembly in a temporary pool metacommunity. *Journal of the North American Benthological Society* 29: 1267–1278.

Verleyen, E., W. Vyverman, M. Sterken, D. A. Hodgson, A. De Wever, S. Juggins, B. Van de Vijver, V. J. Jones, P. Vanormelingen, D. Roberts, R. Flower, C. Kilroy, C. Souffreau, & K. Sabbe, 2009. The importance of dispersal related and local factors in shaping the taxonomic structure of diatom metacommunities. *Oikos* 118: 1239–1249.

Winegardner, A. K., B. E. Beisner, P. Legendre, & I. Gregory-Eaves, 2015. Are the landscape-level drivers of water column and surface sediment diatoms different? *Freshwater Biology* 60: 267–281.

Zhai, M., O. Nováček, D. Výravský, V. Syrovátka, J. Bojková, & J. Helešic, 2015. Environmental and spatial control of ostracod assemblages in the Western Carpathian spring fens. *Hydrobiologia* 745: 225–239.

Conclusions

La Veguilla

Conclusions

1. En les 22 llacunes temporals de La Mancha estudiades en maig de 2013 vam registrar 18 espècies d'ostracodes, la distribució de les quals estava afectada pels efectes ambientals (17.5%) i pels efectes espacials (17.3%).

2. La conductivitat –com a indicador de la salinitat– fou el principal factor ambiental que afectava de forma significativa la composició d'ostracodes de les llacunes temporals estudiades, trobant generalment *Heterocypris barbara* en les llacunes amb major conductivitat.

3. Els efectes espacials d'escala ampla els relacionàrem amb la limitació dispersiva per l'aïllament de les llacunes temporals (però també podrien estar relacionats amb els efectes de massa o els efectes prioritaris), i els efectes espacials d'escala fina no tenien una relació ecològica clara.

4. En les basses de roca de Rafelguaraf, l'ordenació d'espècies fou el principal mecanisme estructurador en les metacomunitats faunístiques amb dispersió activa (amb 10 taxons), tant en les basses connectades per un flux d'aigua efímer com les que no el tenien, i sent els organismes més representatius els culícids i els ceratopogònids.

5. En les espècies de dispersió passiva de les basses de roca (10 taxons dels quals 5 eren espècies d'ostracodes), el mecanisme estructurador dominant depenia de la presència d'una connexió efímera d'aigua entre les basses: l'ordenació d'espècies era més important que els processos dispersius en les basses amb flux d'aigua, i els processos dispersius eren més importants que l'ordenació d'espècies en les basses sense aquesta connexió.

6. En els rius Millars, Palància i la Rambla de Veo, els efectes espacials eren més importants que l'ordenació d'espècies en l'estructuració de les comunitats d'ostracodes (31 espècies), probablement degut als efectes de massa.

7. En aquestos rius la dispersió dels ostracodes pel corrent d'aigua fou la ruta de dispersió més rellevant, per damunt d'altres mecanismes de dispersió relacionats amb rutes

terrestres o aèries, que també podrien ser importants.

8. La temperatura anual fou un dels principals factors ambientals que afectaven la composició d'espècies en els rius, trobant generalment les espècies més comunes en el nord d'Europa (per exemple, *Candona neglecta*) en els trams amb temperatures més baixes, i les espècies circum-Mediterrànies en els més càlids (com *Herpetocypris brevicaudata*).

9. L'amplitud del rius també fou un factor significatiu en les comunitats d'ostracodes dels rius, trobant els ostracodes nadadors (com *Potamocypris villosa*) en les parts amples i els que s'arrosseguen (com *Herpetocypris brevicaudata*) en les estretes.

10. Les comunitats no van variar massa dins d'una mateixa llacuna al llarg del temps estudiat, mantenint les diferències degudes a la salinitat en les 10 llacunes temporals de La Mancha seguides mensualment al llarg d'un hidroperíode.

11. En general, l'ordenació d'espècies fou el mecanisme estructurador més important al llarg d'un hidroperíode en les llacunes temporals estudiades, encara què al principi de l'hidroperíode no vam detectar cap efecte (ni ambiental ni espacial), el que ens suggerix importants fenòmens estocàstics relacionats amb l'eclosió d'ous d'espècies oportunistes.

12. Existix una gran concordança entre la biocenosi i la tafocenosi en les 22 llacunes temporals de La Mancha estudiades en maig de 2013, encara què es trobaren més registres d'espècies no compartides entres els dos assemblatges en la tafocenosi (24 registres) que en la biocenosi (6 registres).

13. Els efectes espacials explicaven un percentatge major que els ambientals en la tafocenosi, probablement degut a què el que trobem en la tafocenosi mostra la distribució potencial dels ostracodes o fins a quines localitats són capaços de dispersar-se, tot i què no els trobàrem vius en les condicions ambientals d'eixe moment.

14. Els efectes ambientals (10.1%), espacials (7.6%) i històrics (10.3%) explicaren la variació d'un percentatge significatiu de la composició d'espècies en la biocenosi de les llacunes, indicant que els efectes prioritaris també podrien ser un important mecanisme estructurador de la metacomunitat.