



Original article

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



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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.

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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).

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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

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