Environmental and spatial patterns as drivers of littoral macroinvertebrate assemblages in patchily distributed mountain lakes: Contribution to typology design

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ABSTRACT

Biological assemblages are affected by both environmental and spatial processes. Spatial autocorrelation can be specially marked in discrete ecosystems patchily distributed over a large region (e.g., lakes arranged in districts). Lake typologies are exclusively based on environmental features, but we hardly know to what extent spatial patterns can hinder their implementation. We analysed the role of environmental factors and spatial autocorrelation in shaping littoral macroinvertebrate communities of 51 mountain lakes from a large Spanish region in order to test: 1) the suitability of the variables currently used to construct typologies; 2) the influence of spatial patterns on typology implementation. Biologically meaningful types of lakes were created and described by means of cluster analysis (Jaccard index) and multiple discriminant analysis. Water permanence, substrate type and vegetation were the main drivers of the assemblage composition. The cluster analysis and Mantel tests showed that spatial patterns did not generally hamper recognizing lake types. Only in the district with lakes closest to each other (Sanabria Natural Park), spatial autocorrelation was strong enough to overcome the effects of some factors (substrate type), but not others (water permanence).

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1. Introduction

Most organisms are non-randomly distributed. Communities have a spatial structure resulting from a large number of processes acting at different spatial scales. Local conditions are essential drivers of community composition, as shown for lakes by a number of studies conducted on macroinvertebrates (Free et al., 2009; Hinden et al., 2005; Johnson and Goedkoop, 2002). However, the composition of a local community is not only the result of environmental factors. Metapopulation dynamics and large-scale biogeographical and historical constrictions may play a role as well. Following the principles of metacommunities (Leibold et al., 2004), in small-scale studies, among-site differences in community structure can be attributed to environmental conditions of each particular site (including species interactions and environmental pressures), and to the importance of dispersal. With increasing geographic distance, dispersal limitation is likely to increase. This can cause spatial autocorrelation in the assemblages, that is, a tendency of neighbouring sites to harbour similar biotic assemblages (Legendre and Legendre, 1998). Therefore, in broad-scale studies, we might expect closely connected sites to harbour more similar assemblages than sites further apart although the intensity of the effect depends on the characteristics (e.g., dispersal ability) of the organisms (Beisner et al., 2006; Borthagaray et al., 2015; Rádková et al., 2014; Razeng et al., 2016; Shurin et al., 2009). Statistical models of species distribution neglecting this aspect of ecology can lead to mis-estimations (Dormann, 2007). Since the 80’s, a growing concern about the spatial structure of communities has arisen in the scientific community. This concern has resulted in a number of studies aimed at disentangling the effects of spatial processes and environmental conditions (see a meta-analysis in Cottenie, 2005), some of them dealing with aquatic invertebrate communities (Briers and Biggs, 2005; Rádková et al., 2014). This issue can be particularly relevant in discrete ecosystems such as lakes, even more if sites have a patchy distribution, with lakes clustered in lake districts as is usual in mountain lakes of glacial origin (Catalan et al., 2009a).

Monitoring of freshwater is usually undertaken at large spatial scales. The Water Framework Directive (WFD, Directive 2000/60/EC, 2000) established the catchment as the management unit, although monitoring programmes (e.g., typologies) are often designed for larger areas (national scale). At this scale, assemblage structure may be influenced by broad-scale spatial patterns

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Fig. 1. Map of Castilla y León with the situation of the lakes included in the study. Lakes are named after the district (when assigned to one) or after the province they belong to.

resulting from dispersal limitation and historical effects, as well as by environmental differences. Most monitoring programmes are based on typologies aimed at reducing variability. For that purpose, they use a number of variables to account for both environmental features and geographical position (ecoregions). The need of differentiating ecoregions is widely accepted. In this respect, Kernan et al. (2009) found a strong geographical influence on the composition of several assemblages from mountain lakes at a pan-European scale and recommended dividing Europe into three regions. However, spatial patterns might arise at smaller spatial scales (Briers and Biggs, 2005; Mykrä et al., 2007), especially if patchiness of waterbodies is high. A crucial point is checking to which extent spatial patterns caused by the proximity of waterbodies (and not by differences in local, environmental conditions) may hamper the use of a typology and if this effect is noticed at the level of taxonomic resolution used in bioassessment, usually genus or family in the case of macroinvertebrates. Studies of this type must be undertaken at the catchment rather than pan-European scale (Catalan et al., 2009a).

It is also necessary to clarify which environmental variables are to be selected to create ecotypes. Several attempts have been made to create typologies for management of European lakes (Kagalou and Leonards, 2009; Kolada et al., 2005; Moss et al., 2003; Little et al., 2006). These typological schemes are often based on general limnological knowledge, usually skewed toward pelagic environment and biological groups (phytoplankton and zooplankton). It is hardly known to which extent they have a biological meaning for littoral macroinvertebrates, which might strongly depend on factors currently overlooked such as substrate type (Zenker and Baier, 2009). We need to gain knowledge on the factors shaping these assemblages at the spatial scale and taxonomical level used in management. A great deal of work has been done in mountain lakes since the approval of the WFD (for example, Kernan et al., 2009). The distribution of the studied areas, however, is uneven. There are many contributions for central Europe (e.g., Free et al., 2009; Fürer et al., 2006; Hinden et al., 2005; Oertli et al., 2008) but not so for Spain, where research has mainly focused on the Pyrenees (e.g., De Mendoza and Catalan, 2010) and, to a lesser extent, the Central Range (Toro et al., 2006).

Castilla y León is an extensive region largely coincident with one of the water management units in Spain: the Spanish part of the Duero River Basin. Its area is larger than several EU countries and comparable to many other river basins in Europe. The findings of this research, therefore, might be useful for management in other river catchments across Europe. A peculiar feature of the study area, common to many other mountain regions, is the presence of a number of patchily distributed mountain ponds and small lakes. Applying current typologies to littoral macroinvertebrate assemblages in these waterbodies poses several potential difficulties. Firstly, it is not known whether the variables used in these typological schemes are relevant for macroinvertebrates. Secondly, the patchy distribution of mountain lakes (in groups or districts) might create spatial patterns capable of blurring among-ecotype differences in the assemblages. The aim of this study was to determine which environmental factors influenced the composition of littoral macroinvertebrate assemblages in the mountain lakes of the region as a means to check whether the typological schemes commonly proposed for European lakes are appropriate for this assemblage. In particular, certain habitat variables usually overlooked, such as substrate type, might be relevant for littoral macroinvertebrates. We also aimed to check the role of spatial autocorrelation (community similarity among lakes of the same district) on the assemblage composition. We hypothesized that lakes in the same district would tend to show similar taxonomic compositions regardless of the type they belong to.

2. Material and methods

2.1. Study area

Castilla y León (94,223 km²) is dominated by a vast, flat, central area (around 700 to 800 ma.s.l. on average) surrounded by moun-
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