



Bioassessment in a metacommunity context: Are diatom communities structured solely by species sorting?



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ABSTRACT

Aquatic ecosystems face a variety of anthropogenic pressures, urging the development of efficient biological indicators. In addition to local environmental conditions, the community structure of indicator organisms is affected by spatial processes, such as high and limited dispersal rates. Understanding the relative roles of environmental factors and spatial processes for ecological communities should thus be associated with bioassessment practices. We examined the main drivers, both environmental and spatial, influencing community structure and several indices derived from diatom communities. We sampled 81 stony littoral sites in a large boreal lake system (305 km²), where relatively large gradients in water chemistry (35 variables measured) exist, but no dispersal limitation can be expected. Instead, high dispersal rates should interfere with species sorting. Our response variables, including commonly-used diatom indices, diversity indices and taxonomic distinctness indices, were better explained by pure effects of spatial variables and shared effects of spatial and environmental variables than by pure effects of environmental variables. Thus, high dispersal rates between sites are likely to interfere with environmental filtering and can result in clear spatial structures in index values used in bioassessment. Bioassessment should thus acknowledge the importance of spatial processes and not take it for granted that only local environmental conditions determine index values. Failure to consider high dispersal rates may lead to biased information about the state of freshwater ecosystems. The same idea should also be considered in systems with similarly highly-connected sets of bioassessment sites, such as marine coastal systems and stream networks.

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1. Introduction

Biological diversity in freshwater ecosystems is threatened by various anthropogenic stressors, including agriculture, forestry and urbanisation (Dudgeon et al., 2006; Friberg, 2014). Protecting, managing and restoring freshwater biodiversity and associated natural resources is urgent, and development and testing of different bioassessment approaches are thus necessary to provide information about the current state of freshwater ecosystems (Vörösmarty et al., 2010). Effective bioassessment should be question-driven and include a conceptual model of an ecosystem (Lindenmayer and Likens, 2010). Such conceptual models should also be used to guide freshwater bioassessment (Angeler et al., 2014).

A key idea underlying all bioassessment is that differences in biological communities reflect environmental variation between locations (Friberg et al., 2011; Siqueira et al., 2014). The biological community occupying a site thus forms the basis from which various biological indices are constructed (Heino, 2013; Rapport and Hildén, 2013). The purpose of the use of indicators is to provide information about the state of the environment, and, consequently, to help detect targets for environmental management and associated policy (Friberg, 2010; Rapport and Hildén, 2013). However, many commonly used indicators are generally based on traditional assessment ideas which ignore many natural processes other than those related to local environmental factors (for recent examples, see Gray and Arnott, 2011; Siqueira et al., 2014). Hence, it is challenging to identify the various causes of environmental degradation (Friberg et al., 2011; Hering et al., 2015), because environmental factors are not necessarily the sole drivers of change of community structure (e.g. Heino, 2013).

The majority of studies linking biological indicators to environmental gradients also show a large degree of unexplained variation

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in the responses of various indices to those gradients (Friberg, 2010). A possible reason for such low degrees of explained variation may be that the existing assessment approaches largely ignore potentially important factors, such as stochasticity (e.g. Vellend et al., 2014), biotic interactions and dispersal-related phenomena (see reviews by Heino, 2013; Friberg, 2014). It is also important to acknowledge the connectivity of ecological systems (Mouquet and Loreau, 2003; Heino et al., 2015). High levels of connectivity appear, for example, as natural interactions related to the movements of organisms and materials among sites (Massol et al., 2011; Gray and Arnott, 2012).

Recent advances in theoretical ecology have shown that species diversity in biological communities has a complex relationship with dispersal (Mouquet and Loreau, 2003; Cadotte, 2006). In general, dispersal typically increases local diversity and decreases regional diversity (Cadotte, 2006), local diversity reaches its maximum at an intermediate level of dispersal, and between-community and regional diversities decline as dispersal increases. Local communities are thus shaped by both local ecological factors and exchange of species between neighbouring sites or from more distant sites through dispersal (Mouquet and Loreau, 2003). The idea of high dispersal rates has been rarely incorporated in applied ecology, including the development of bioassessment approaches (Siqueira et al., 2014).

Dispersal-related effects are typically studied in the context of metacommunity theory (Leibold et al., 2004; Logue et al., 2011). There are four traditional perspectives which have been widely used when considering metacommunities: the neutral, the mass effects, the species sorting and the patch dynamics perspectives (Leibold et al., 2004). Winegardner et al. (2012) proposed that metacommunities are either neutral or structured by species sorting. The latter perspective can hence be divided into three types depending on the nature of dispersal: (1) species sorting with limited dispersal rates, (2) “pure” species sorting and (3) species sorting with high dispersal rates. High dispersal rates tend to homogenise community structure regardless of local environmental conditions (Leibold et al., 2004; Gonzalez, 2009). Hence, high dispersal rates from “source” sites may allow species to occur in “sink” sites that cannot support population without a high flux of individuals (Pulliam, 1988). The “pure” species sorting perspective assumes that species have preferences for different environmental conditions owing to niche differences (Chase and Leibold, 2003), and that organisms can also freely track variation in suitable habitat conditions through intermediate dispersal rates (Leibold et al., 2004).

Despite the recognition of the importance of dispersal in metacommunity ecology, most bioassessment programmes rely solely on the assumptions of the “pure” species sorting perspective (see reviews by Heino, 2013; Friberg, 2014). However, both species sorting- and dispersal-related processes should be taken into account in bioassessment (Siqueira et al., 2014). This goal could be at least partly achieved by including information about spatial location as a proxy for dispersal effects. The importance of spatial effects may, however, be contingent on spatial scale (Heino et al., 2015). If bioassessment is conducted over too large spatial extent, signals related to anthropogenic environmental changes can be partly masked by dispersal limitation (Heino, 2013). Conversely, bioassessment conducted over small spatial extents where distances between sites are negligible may give equivocal information if high dispersal rates interfere with the effects of environmental factors on biological communities (Hitt and Angermeier, 2011; Siqueira et al., 2014). Both limited and high dispersal rates may emerge as spatial structure in index values (Ng et al., 2009), but their effects cannot be separated without consideration of the spatial scale, nature of spatial variables and connectivity between sites (Heino et al., 2015). These ideas thus relate directly to limited versus high dispersal rates between sites, but are different from

large-scale regionalisation approaches which only consider differences in species pools caused by limited dispersal.

Here, we aimed to reveal the effects of water chemistry and spatial relations among sites on community structure and various biological indices which are commonly used in bioassessment of aquatic systems. First, we present a schematic overview of two extreme cases where a hypothetical environmental variable varies randomly or is spatially structured (Fig. 1). In the first scenario (a), variation in the environmental variable is random across the study area. Hence, we can draw two opposing inferences: (1) if the biological communities are controlled entirely by the environment, then species sorting should be perfect. Therefore, our index values should vary similarly as the environmental variable, providing “correct” indicator value in relation to environmental variation. Alternatively, (2) if the sites are controlled purely by spatial relations among sites, the biological communities and index values should not vary the same way as the environmental variable. This would suggest that other processes, such as high dispersal between sites, determine variation in the community structure and index values. In the second scenario (b), we illustrate the opposite extreme situation where the values of the environmental variable are spatially structured, which is a common situation in nature (Heino et al., 2015). We can thus draw a third inference: (3) if the community structure and index values perfectly follow variation in the environmental variable, the effect of environmental and spatial variables cannot be separated. This scenario thus illustrates spatially-structured environmental effect on our response variables.

Our model organismal group to examine the above ideas was littoral diatoms. Diatoms are widely used as environmental indicators due to their supposed quick response to environmental changes (Dixit et al., 1992; Round et al., 2007), thus reflecting the state of the freshwater environment (De Bie et al., 2012; Gottschalk and Kahlert, 2012; Schneider et al., 2012). Several studies however suggest that the effect of local environmental variables and spatial processes to diatom assemblages are largely scale-dependent (Potapova and Charles, 2002; Soininen, 2007; Vyverman et al., 2007; Verleyen et al., 2009). As diatoms are considered efficient passive dispersers (Kristiansen, 1996) and are known to have huge population sizes (Finlay, 2002), we expected that diatoms in our highly-connected lake system would not be limited by dispersal. Instead, high dispersal rates could lead to spatial structure in bioassessment index values. We modelled the responses of community structure and several biological indices to environmental and spatial variables. We hypothesised that (1) variation in community structure and diversity indices are related to both environmental and spatial variables, whereas (2) variation in taxon-specific diatom indices and taxonomic distinctness indices are related to local environmental variables only. This is because community structure should portray the effects of both environmental and dispersal processes (e.g. Heino et al., 2015), whereas more complex indices should be immune to factors other than those they are targeted to indicate (e.g. Clarke and Warwick, 1998).

2. Materials and methods

2.1. Study area and field sampling

In September 2013, we sampled the littoral zone of a large (305 km²), highly-connected lake system for diatoms and water. The Kitkajärvi lake system (centred at N 66°8', E 28°43') is originally oligotrophic, but some signs of eutrophication have appeared in recent years (e.g. Vilmi et al., 2015). The ongoing eutrophication process is mainly of anthropogenic origin, caused by various kinds of loading from the catchment area (forestry, agriculture and

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