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Taxonomic surrogacy, numerical resolution and responses of stream macroinvertebrate communities to ecological gradients: Are the inferences transferable among regions?

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ABSTRACT

It is typically at the species level where the responses of organisms to natural environmental gradients are the most clearly visible. However, due to the fact that many organismal groups are poorly resolved at the species level in various geographical regions, many studies have to still rely on supra-specific taxa when analyzing community-environment relationships. This study examined the community-environment and richness-environment relationships of stream macroinvertebrates at three taxonomic levels (i.e., species, genus, family) in three high-latitude drainage basins. Despite the fact that species-to-genus and species-to-family ratios were low and of similar magnitude in all drainage basins, each region showed different rankings in terms of the species-, genus- and family-level data being best explained by environmental variables. Furthermore, within each region the three taxonomic levels did not respond similarly to the underlying environmental gradients, which was evident with taxonomic richness and taxonomic composition based on both quantitative and qualitative data (adjusted R^2 of models varied from 0 to 0.604 for taxonomic richness and from 0.068 to 0.307 for taxonomic composition). The present findings thus do not support the views: (i) taxonomic surrogacy in stream macroinvertebrate communities is transferable among regions and (ii) that higher taxon taxonomic surrogates can be used without restraints to infer species-level community-environment and richness-environment relationships in studies of community ecology, conservation biology and environmental assessment.

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1. Introduction

Studying the responses of biodiversity to environmental gradients is a key topic in community ecology, conservation biology and environmental assessment. These research fields typically utilize data at the species level due to the notion that species are the generally accepted units of ecological analyses (Gaston, 2000; Lenat and Resh, 2001; Bertrand et al., 2006). Species are undoubtedly suitable units of study in the context of community–environment relationships, as it is typically at the species level where the responses of organisms to natural environmental gradients are the most clearly visible (Warwick, 1993; Bevilacqua et al., 2012). However, due to the fact that many organismal groups are poorly resolved at the species level in various geographical regions, many studies have to still rely on supra-specific taxa when analyzing

* Correspondence to: Finnish Environment Institute, Natural Environment Centre, Ecosystem Change Unit, P.O. Box 413, FI-90014 University of Oulu, Finland. Tel.: +358 505845977. community–environment relationships. Evidence to date suggests that species richness varies quite predictably with richness at higher taxonomic levels, suggesting that taxonomic surrogates may perform well in regions where little or no species level data exist (Gaston and Williams, 1993; Williams and Gaston, 1994). While early studies focused on congruence in richness patterns among different taxonomic levels, more recent studies have also addressed variation in community composition and community–environment relationships in the same context (Heino and Soininen, 2007; Terlizzi et al., 2009).

Taxonomic surrogacy (i.e., the degree to which higher taxonomic levels portray species-level patterns; Bertrand et al., 2006) and taxonomic sufficiency (i.e., identifying organisms to the taxonomic level needed to satisfy the objectives of a study; Ellis, 1985) have been under considerable study in terrestrial, marine and freshwater environments, although no consensus surrounding the two concepts exists (Ferraro and Cole, 1990; Pik et al., 1999; Lovell et al., 2007; Bevilacqua et al., 2012). The idea behind both concepts is that higher taxonomic levels could be used to reproduce patterns at the species level, which would also entail that communities described at different taxonomic levels show similar responses to environmental variation. Despite the fact that many







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studies have found higher taxa to portray community responses to ecological gradients similarly to species-level data (Dethier and Schoch, 2006; Heino and Soininen, 2007; Terlizzi et al., 2009), there is currently no consensus whether species or higher taxa should be used in the examination of community-environment relationships. Some researchers stress that we should attempt to identify most organisms to the lowest possible taxonomic level, because species should carry most information about the responses of organisms to environmental variation (Lenat and Resh. 2001: Marshall et al., 2006; Melo, 2005; Verdonschot, 2006). By contrast, other researchers doubt that species-level identifications are worth the effort, because they provide little extra information over higher taxonomic levels about community responses to environmental conditions (Warwick, 1993; Bowman and Bailey, 1997; Bailey et al., 2001). The latter group of researchers often argues that there is not enough money, time and taxonomic expertise to devote to species-level identifications of most organisms groups (Marshall et al., 2006; Jones, 2008). They also raise concerns about possible risks of misidentifications when species-level data is the goal. It is the objective of the study, however, which dictates which level of identification should be used (Ellis, 1985; Jones, 2008). For example, conservation-oriented studies should preferably concentrate on species-level data, whereas rapid bioassessment studies might utilize higher taxa if they portray well enough the ecological state of a stressed ecosystem (Lenat and Resh, 2001; Jones, 2008).

The degree to which taxonomic surrogacy applies in a certain situation is likely to vary considerably among regions. Hawkins and Norris (2000) suggested that higher taxa could be used to reproduce patterns of species-level data in regions where species-to-higher taxon ratios are low, implying that higher taxa have not radiated considerably. By contrast, in regions where species-to-higher taxon ratios are high, implying high degrees of adaptive radiation, higher taxa may perform poorly in portraying patterns of species level data. This is because each species belonging to a higher taxon may possess different ecological niches and respond differently to environmental variation across a set of sites (Lenat and Resh, 2001), although some researchers have suggested that species within a higher taxon show some ecological coherence (Warwick, 1993). The suggestion of ecological coherence also pertains to the idea that taxonomic surrogates might perform well even in regions with high species-to-higher taxon ratios. This reasoning is also supported by empirical evidence that community-environment relationships are largely invariant at different taxonomic levels (at least up to the family level), suggesting that higher taxa could be used as shortcuts for portraying responses of biodiversity to ecological gradients (Dethier and Schoch, 2006; Heino and Soininen, 2007; Terlizzi et al., 2009).

Another topic about community-environment relationships pertains to the use of quantitative versus qualitative taxonomic data. Typically, quantitative abundance data should be preferred over qualitative presence-absence data, as the former contains more information about the responses of organisms to ecological gradients. In general, the lows and highs in the abundances of organisms across a set of sites could inform us greatly about community-environment relationships, which presence-absence data may not necessarily do as clearly. However, few such tests are available which have compared quantitative versus qualitative data in the context of community-environment relationships. These studies have typically reported equally strong community-environment relationships between quantitative and qualitative data, although the details of these relationships may differ to some degree between the data types (Cushman and McGarigal, 2004; Heino et al., 2010a,b; De Bie et al., 2012). However, it would be interesting to examine quantitative and qualitative data in the context of taxonomic surrogacy, as the resolution of data in both numerical (abundance, presence–absence) and taxonomic (species, genus, family and others) terms may affect our conclusions about community–environment relationships (Anderson et al., 2005; Heino, 2008; Landeiro et al., 2012).

Most studies on taxonomic surrogacy in the freshwater realm have dealt with the bioassessment of anthropogenic environmental changes (Bailey et al., 2001; Waite et al., 2004; see also a review by Jones, 2008). Fewer studies have been conducted across sets of streams that are near-pristine and considered to be in "reference condition" (Heino and Soininen, 2007; Heino, 2008). Studying if taxonomic surrogates can be applied in near-pristine stream ecosystems is important, given that if we can reproduce species-level patterns using higher taxa across natural environmental gradients, we are also likely to do so across anthropogenic gradients. This is because species are likely to respond to subtle environmental variation, while higher taxa are mostly responsive to more drastic anthropogenic effects (Ferraro and Cole, 1990; Warwick, 1993). However, very few stream studies have taken a multi-region approach on taxonomic surrogacy by examining if the responses to environmental gradients differ among species, genus and family levels. Furthermore, among-region differences and within-region heterogeneity in community composition have not been associated with taxonomic surrogacy in the freshwater realm, although such a study provided evidence of the similarity of patterns at the species, genus and family levels in the marine realm (Terlizzi et al., 2009).

The aims of the present study were to examine if among-region differences in "average community composition" and "heterogeneity in community composition" were similar at the species-, genusand family levels in stream macroinvertebrate data sets. Furthermore, the community-environment and richness-environment relationships at each of the three taxonomic levels were examined within each region and across the regions. Building on previous findings in the research on taxonomic surrogates, I assumed that community composition at each taxonomic level would vary significantly among the regions and be related to different environmental gradients within each of the three study areas. Furthermore, if taxonomic surrogacy is directly supported, (i) species-, genusand family-level data sets should all vary significantly among the regions (both with regard to average community composition and heterogeneity in community composition), (ii) taxonomic composition at each taxonomic level should show similar relationships to environmental gradients in each region and (iii) taxonomic richness at each taxonomic level should vary similarly along environmental gradients in each region. Finally, (iv) ecological inferences about taxonomic surrogates could be transferable among regions if variation in taxonomic composition and/or taxonomic richness at different taxonomic levels was similarly related to environmental variation in different regions (i.e., the same predictor variables entering the models and similar amount of variation in composition and/or richness explained at each taxonomic level in all regions). If strong support for these four assumptions was obtained, then higher taxonomic levels could be used as surrogates for species level patterns in terms of community-environment and richness-environment relationships.

2. Materials and methods

The test data set comprised three northern drainage basins, where detailed surveys of stream macroinvertebrates have been conducted. Partly the same data set as used in the present study has been formerly utilized in assessing community traits–environment relationships (Schmera et al., 2013) and metacommunity patterns at the species level (Heino et al., 2012). These studies found clear differences in assemblage traits among the regions, clearly discernible variation in traits along environmental gradients and

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