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Original Research Article

Decreased habitat specialization in macroinvertebrate assemblages in anthropogenically disturbed streams

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ABSTRACT

Habitat specialists are considered to be more sensitive to anthropogenic disturbance than habitat generalists. However, a number of studies have shown that habitat specialists can be tolerant to or even benefit from environmental degradation, suggesting that the effect of disturbance on distributions and abundances of habitat generalists and specialists can be unpredictable. In this study, we assessed the effects of anthropogenic disturbance on the degree of specialization of stream macroinvertebrates in boreal streams. We first measured the niche width for each macroinvertebrate species using the Outlying Mean Index (OMI) analysis and then, using independent data sets of near-pristine and anthropogenically altered streams, we examined the effects of human disturbances on stream macroinvertebrates with different tolerances to environmental conditions. As expected, human disturbance significantly decreased the level of the specialization in stream macroinvertebrate assemblages, and taxa with narrow environmental tolerances were more sensitive to disturbance than taxa with wide tolerances. Despite being more sensitive to disturbance, taxa with narrow environmental tolerances were locally more abundant than tolerant taxa in near-pristine streams, indicating their better performance in their optimal environments. However, many tolerant taxa decreased in their occurrence in disturbed streams, suggesting that habitat generalists also tend to negatively respond to disturbance. Species-rich assemblages harboured more taxa with narrow tolerances compared with species poor assemblages, suggesting a high conservation value of streams with diverse macroinvertebrate assemblages. Consistent with findings for many biological groups, our results indicate that macroinvertebrate species specialised in certain habitats are more sensitive to environmental degradation than habitat generalists. However, contrary to many previous studies, our results suggest that only a few species are likely to benefit from anthropogenic disturbance and, therefore, environmental degradation does not necessary result in macroinvertebrate assemblages composed of a few tolerant taxa.

1. Introduction

Increasing evidence shows that environmental disturbances can disproportionately affect environmentally specialized species, resulting in spatially homogenized communities composed of tolerant habitat generalists (Warren et al., 2001; Munday, 2004; Devictor et al., 2008; Filippi-Codaccioni et al., 2010; Davey et al., 2012). However, it has also been shown that habitat specialist species can be tolerant to (Vázquez and Simberloff, 2002; Mayor et al., 2015) or even benefit from environmental degradation (Clavero and Brotons, 2010; Suhonen et al., 2014; Tolkkinen et al., 2015), suggesting that specialists may not always be more prone to local extinction than generalists. Hence, more comprehensive understanding of the influences of environmental degradation on distributions of habitat specialists and generalists is needed. Besides being of basic ecological interest, understanding the mechanisms changing biological assemblages in response to anthropogenic disturbance is a prerequisite for effective conservation planning and environmental management.

Habitat specialists are typically defined as species that occupy a restricted range of habitats or utilize resources with restricted availability (McKinney and Lockwood, 1999; Clavel et al., 2011). While specialist species are likely to have a high abundance in only highly suitable habitats, generalist species can be both locally abundant and widespread in many different environments (Brown 1984; Brown et al., 1995; Gaston et al., 1997). Specialists are generally expected to benefit from stable environments, whereas

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unstable environmental conditions should favour generalists (Büchi and Vuilleumier, 2014). Environmental degradation may thus not only affect specialists negatively, but it could even benefit generalists that may increase in their prevalence in disturbed environments due to a competitive release (Tabarelli et al., 2012). However, habitat specialist can also be adapted to rather extreme environments and show increased occurrence in disturbed environmental conditions. Tolkkinen et al. (2015), for example, showed that naturally acidic streams that were altered by forestry practices supported acid-tolerant fungi that were very abundant in, or even unique to, these streams. The effects of environmental changes could also be most negative on species with intermediate specialization because of their weak competitive ability compared to more specialized species but restricted demand of resources and weak ability of dispersal compared to generalist species (Dapporto and Dennis, 2013).

A positive relationship between local abundance and regional occupancy is among the most common macroecological patterns (Hanski, 1982; Brown, 1984). The relationship has also been documented for various groups of stream organisms, including periphytic diatoms (Soininen and Heino, 2005), bryophytes (Heino and Virtanen, 2006), macroinvertebrates (Heino, 2005), and fish (Tales et al., 2004). This relationship reflects species' responses to environmental conditions, and deviations from the relationship reflect the importance of niche versus neutral processes in shaping interspecific differences in abundance and occupancy of species (Verberk et al., 2010). Because of their wide tolerance to environmental variation and a high ability of dispersal, habitat generalists should be less affected by the spatial distribution of environmental conditions compared with habitat specialist (Pandit et al., 2009). However, although generalist species are able to persist in various habitats, specialist species could be expected to perform better than generalist in their optimal habitats (Jasmin and Kassen, 2007; Büchi and Vuilleumier, 2014). Specialist species could hence be expected to be the locally best adapted species and, therefore, to be locally more abundant than generalist species in undisturbed environments. In contrast, environmental changes should more readily affect local abundances of specialists than those of generalists. Few studies have, however, studied this topic which we call "macroecology of anthropogenic disturbance effects on specialists and generalists".

In this study, we assessed the effects of human disturbance (i.e., environmental alteration resulting from land use) on distributions and abundances of stream macroinvertebrates with different tolerances to environmental conditions. We expected that anthropogenically altered streams harbour less specialized species and biological assemblages. We further tested the influences of anthropogenic disturbance on the abundance-occupancy relationships of taxa with different tolerances to environmental conditions. We expected that taxa with narrow environmental tolerances are abundant in suitable environments but highly sensitive to environmental change and, therefore, for a given occupancy, they should be locally more abundant in pristine streams but less abundant in disturbed streams than taxa with wide tolerances.

2. Methods

2.1. Study streams

This study was based on macroinvertebrate data compiled from the data base of the Finnish Environment Institute (SYKE) and research projects conducted at the University of Oulu. The data set was collected from streams encompassing Finland (60°N–70°N, 20°E–32°E, Appendix A in Supplementary material). The data set includes near pristine reference sites (less than 5% agriculture in the catchment area, no point source pollution and only minor human influence on channel morphology or riparian zone) and sites that have been altered by anthropogenic activities, mainly by agriculture and forestry. Altogether 262 reference sites and 196 anthropogenically disturbed sites were included in the data set. All streams had data on water chemistry (i.e., pH, conductivity, total phosphorus) and instream characteristics (i.e., moss cover and particle size) measured simultaneously with benthic sampling (for field survey methods, see Mykrä et al., 2007). Mean air temperature, mean precipitation and percentages of lakes and peatlands in catchments were also available for each site.

2.2. Biological data

Each macroinvertebrate sample consisted of four replicate 30-s kick-samples (net mesh size 0.5 mm) taken in autumn from swiftly flowing riffles. Riffle sites are the foci of most stream environmental monitoring schemes in Finland (e.g., Mykrä et al., 2009) and elsewhere (e.g. Hawkins, 2006). All macroinvertebrates were sorted from the samples and identified mainly to species or genus level, with the exception of a few dipteran and caddisfly families. In case of taxonomic inconsistency, identifications were harmonized to a consistent higher taxonomic level. Non-biting midges (Diptera: Chironomidae) were not identified beyond family level and were omitted from all statistical analyses, as they occurred at all sites.

2.3. General approach

Our main aim was to compared distributions and abundances of specialist and generalist species of stream macroinvertebrates between reference-quality and human-disturbed sites. Variation in distributions of habitat specialists and generalists among near-pristine (i.e., reference) and anthropogenically altered environments likely reflect both environmental degradation and possible differences in natural environmental gradients. To isolate the effects of environmental degradation from natural environmental variation, we first selected sets of reference and disturbed sites with the same number of sites, similar gradients in natural background environmental variables and similar geographical distribution of sites. Niche width for each taxon was next determined using OMI (outlying mean index) analysis (Dolédec et al., 2000). Niche width is thus based on the occurrence of a species along environmental gradient, and it is therefore a proxy of the ecological traits responsible for environmental tolerance of species (Violle et al., 2007). Because using the same sites to measure species niches and to assess environmental influence on the distributions of species with differing niches is circular (Heino, 2005), we conducted the OMI analysis based on the remaining sites that were not selected into the set of reference and disturbed sites. We then tested the influences of anthropogenic disturbance on the specialization of macroinvertebrate assemblages. In order to further evaluate the potential causes of observed patterns, we conducted analysis to examine (1) differences in abundance-occupancy relationships of taxa with narrow or wide environmental tolerances and (2) differences in niche widths of taxa that were either decreasing or increasing in their occurrence at disturbed sites.

2.4. Site selection

To ensure that reference and disturbed sites equally represented the major environmental gradients and had similar geographical distributions, we used non-metric multidimensional scaling (NMDS) based on Euclidean distances of standardized environmental variables to view all our study sites in two-