



Research paper

Taxonomic and functional diversity of stream invertebrates along an environmental stress gradient

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ABSTRACT

Anthropogenic stress has been identified as main driver of freshwater biodiversity loss. Adverse effects on the biodiversity of freshwater organisms, such as macroinvertebrates, may propagate to associated ecosystem functions, such as organic matter breakdown (OMB). In this context, the functional diversity (FD) of communities has been suggested to be a more suitable predictor of changes in ecosystem functions than taxonomic diversity (TD). We investigated the response of TD and FD of invertebrate communities to an environmental stress gradient and the relation of both metrics to the rate of organic matter breakdown. For this, we sampled macroinvertebrates and determined OMB using leaf bags along an environmental stress gradient (i.e. changes in physicochemical and hydromorphological conditions) in 29 low-order streams. Taxonomic richness decreased with increasing environmental stress ($r = -0.55$) but was not related to OMB. Conversely, the Simpson diversity of communities was not associated with the gradient but correlated moderately ($r = 0.41$) with OMB. Of three functional diversity indices (functional richness, evenness and divergence), only functional richness correlated moderately with the stress gradient ($r = -0.41$) and any of the indices correlated with OMB. Nevertheless, functional metrics such as specific trait modalities and the total abundance of the dominant shredders correlated higher ($r = 0.46$ and 0.48) with OMB than the TD indices. Given a relatively small species pool in our study and methodical constraints such as the limited resolution of autecological information, the FD might perform better in other contexts and if focusing on response and effect traits for the stressor and ecosystem function under scrutiny, respectively.

1. Introduction

Freshwater ecosystems provide ecosystem services on which human societies depend, such as the regulation of water quality, recreation and aquatic organisms as food (Maltby, 2013). These services rely on ecosystem functions provided by a range of freshwater organisms that are adversely affected by multiple stressors, many of which are anthropogenic. Overexploitation, water pollution, habitat loss, flow modification and species invasion have been identified as main stressors for freshwater ecosystems (Dudgeon et al., 2006). Effects of stressors such as the loss of taxa can translate to changes in the taxonomic diversity (TD). For example, water pollution in the form of elevated salinity or inputs of pesticides has been shown to reduce the TD in terms of species richness of lotic communities (Cañedo-Argüelles et al., 2013; Beketov et al., 2013). Changes in the TD can propagate to ecosystem functioning as both are linked (Naeem and Wright, 2003) through mechanisms such as complementarity, niche partitioning or functional redundancy (Cardinale, 2011; Cardinale et al., 2011; Ebeling et al., 2014), where

functional redundancy means that other species can functionally compensate for the loss of a species (Fetzer et al., 2015). Although the loss in TD has been associated with impairment of ecosystem functions such as nutrient cycling (McIntyre et al., 2007) or organic matter breakdown (McKie et al., 2008), the direction and magnitude of changes in ecosystem functions depends rather on functional traits, defined as components of an organism's phenotype that influence ecosystem functioning (Petchev and Gaston, 2006), of individuals, populations and communities (Cadotte et al., 2011; Tolkkinen et al., 2013). For instance, species loss can be indifferent for ecosystem functions in the case of functional redundancy (Fetzer et al., 2015). However, the loss of species with key functional roles most likely results in a reduction in ecosystem functions (Cardinale et al., 2006). Stressors affect the functional composition of communities through the loss of functional traits associated with species loss (Chapin et al., 2000) or through environmental filtering for specific traits (e.g. stressor-tolerance), which can control species colonization (Weiher et al., 2011). Such stress-related changes in the functional composition can be measured with functional diversity

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(FD) indices (Gutiérrez-Cánovas et al., 2015; functional diversity (FD) is defined following Mason et al. (2005) as the distribution of species and their abundance within the functional space, including functional richness, – divergence and – evenness. See methods for details). For example, elevated nutrients and pollution with metals and PAHs (Polycyclic Aromatic Hydrocarbons) from sediments as well as alternating flow conditions in urban streams caused shifts in the functional composition of invertebrate communities, resulting in reduced FD (Fanny et al., 2013; Feio et al., 2015; Konrad and Booth, 2005). The variety of environmental stressors, both natural and anthropogenic, that may affect the FD in streams and rivers has been reviewed by Schmera et al. (2017).

Although several studies described effects of changes in the FD on ecosystem functions (e.g. Díaz and Cabido, 2001; Flynn et al., 2009; Fraïner and McKie, 2015) and suggested the incorporation of functional indicators in environmental assessment (Bruno et al., 2016; Dolédec and Statzner, 2008; Young et al., 2008), freshwater ecosystems are still largely assessed using taxonomic indicators (e.g. EPT richness – i.e. richness in *Ephemeroptera*, *Plecoptera* and *Trichoptera* taxa, saprobic index or RIVPACS). These do not allow for a direct evaluation of the status of ecosystem functions. However, organism traits, which form the basis of FD, allow for the connection to ecosystem functions (Cadotte et al., 2011) and often respond rapidly and predictably to multiple stressors (Dolédec et al., 2006; Dolédec and Statzner, 2010; Mouillot et al., 2013). Thus, FD-indices may be better indicators of changes in ecosystem functions than TD-indices (Cadotte et al., 2011). Yet, few studies have compared TD- and FD-indices of freshwater organisms in the context of stressor effects on ecosystem functions, such as organic matter breakdown (OMB) or related FD to freshwater ecosystem functions (Schmera et al., 2017; but see Fraïner and McKie, 2015; Tolkkinen et al., 2015). OMB represents the most important energy source in forested headwaters and subsequent food webs (Wallace et al., 1997; Webster, 2007). Leaf material from the riparian vegetation is decomposed by microbial decomposers and invertebrate detritivores (Graça et al., 2001; Hieber and Gessner, 2002). Accrued fine particular organic material and gained biomass also subsidizes downstream sections, which emphasizes the importance of OMB (Webster, 2007).

The main aim of this study was to investigate the response of TD- and FD-indices of invertebrate communities to an environmental stress gradient representing changing physicochemical and hydro-morphological conditions. Furthermore, we examined whether the indices would be related to the rate of organic matter breakdown. We hypothesized (i) changes in the taxonomic and functional (trait) structure of communities along the environmental stress gradient. The assumed changes in the taxonomic and functional structure could be due to the selection of species by the environmental conditions (Jackson and Sax, 2010) and to environmental filtering for specific traits or trait combinations (Cadotte, 2009; Verberk et al., 2008), respectively. In addition, we hypothesized (ii) a reduction in the total taxonomic and functional diversity indices with increasing environmental stress. These assumptions are based on the inherent linkage between TD and FD, although this can be non-linear (Cadotte et al., 2011; Woodward et al., 2015; Schriever et al., 2015). Moreover, as a consequence of the reduction in TD and FD, we assumed that (iii) OMB would decrease because of the loss of taxa with OMB-relevant trait modalities. Finally, we expected (iv) FD-indices to be better predictors of OMB than TD-indices (Wooster et al., 2012; Cadotte et al., 2011).

2. Methods

2.1. Study area and environmental variables

The sampling sites were located in the south-west of Germany between the Palatinate Forest Nature Park in the North and West, the River Rhine in the East and the Vosges in the South (Table A1). We sampled 29 sites in low-order streams over different land use categories

assuming that they would be characterised by changing environmental conditions and associated species turnover or loss. Streams were selected based on the dominant land-use (> 50% areal cover, i.e. forest, agriculture, viniculture or urban areas, respectively, cf. Table. A1) within a 100-wide riparian buffer zone of 3 km length upstream, which was considered the local scale for the sampling reaches (for more details refer to Voß et al., 2015). All streams originate in the Palatinate Forest or in Northern Vosges and sampling sites were located outside of the nature park, but within 1–5 km from the border of the nature park (except for the forested sites that were located inside the park). Given that the larger scale catchment land use was dominated by forest, we focused on land use in the immediate riparian upstream zone (i.e. local scale)(cf. Feld, 2013). The following physicochemical variables were measured during September and October 2012: flow velocity, oxygen, pH, electrical conductivity (EC), water temperature and four nutrients (nitrate, nitrite, ammonium, phosphate) by on-site analysis with Macherey-Nagel visicolor® (Düren, Germany) kits. Moreover, we recorded habitat-structural variables, i.e. stream substrates and microhabitats at each sampling site within a 50-m stream section, as described in the AQEM/STAR protocol (AQEM, 2002) as well as the percentage of shading, total riparian zone and percentage of tree cover within the riparian zone (left bank and right bank maximum), as described by a protocol of the EPA (EPA, 2003). All streams were regulated (i.e. straightened), except those of forested sampling sites. See supplementary information for the complete list of measured environmental variables (Table A2). In a previous study, we found that OMB was much stronger associated with specific environmental variables than with the land-use categories (Voß et al., 2015). Thus, building on these results, we focused on the gradient of environmental conditions in this study rather than on land-use categories (for details refer to 2.6 Statistical Analysis).

2.2. Invertebrate sampling

Invertebrate sampling was conducted in concert with the measurement of environmental variables in autumn 2012. At each sampling site, invertebrates were sampled within a 50-m stream section following the standardized AQEM multi-habitat sampling method (Barbour et al., 1999; AQEM, 2002). According to the method, 20 sub-samples were taken in the major habitats proportionally to their presence within a sampled reach. Each sub-sample represents a kick sample (mesh size 50 µm) of invertebrates. Additionally, invertebrates were collected manually from stones, dead wood or plants. They were identified to species or genus level (exception: e.g. larvae of Chironomidae) using a microscope (Olympus SZX9, Tokio, Japan) and identification keys (Brohmer et al., 2000; Bährmann, 2011). In total 66 invertebrate taxa were identified (Table A3).

2.3. Taxonomic diversity

To quantify effects by changing environmental variables on the invertebrate community we calculated two TD indices: i) total taxonomic richness (TTR, i.e. number of different taxa found) and ii) the Simpson diversity (SD) of invertebrate taxa. Simpson diversity for each site k was calculated as:

$$D_k = \sum_{i=1}^{S_k} p_{ik}^2$$

with S_k , the taxonomic richness of site k and p_{ik} the relative abundance of the i^{th} taxa in site k . We selected SD because we expected that dominant species could be more important (Morris et al., 2014). Furthermore, we used $1/D_k$ instead of $1-D_k$ to correct for bias encountered for high richness (Peru and Dolédec, 2010). Additionally, we used the reciprocal index as its rise indicates an increase in diversity and consequently simplifies interpretation (Magurran, 1988).

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