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Quantitative hydrological preferences of benthic stream invertebrates in Germany

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ABSTRACT

Current knowledge regarding the flow preferences of benthic stream invertebrates is mostly based on qualitative data or expert knowledge and literature analysis. These established flow preferences are difficult to use in predictions of the effects of global change on aquatic biota. To complement the existing categories, we performed a large-scale analysis on the distribution of stream invertebrates at stream monitoring sites in order to determine their responses to various hydrological conditions.

We used 325 invertebrate surveys from environmental agencies at 238 sites paired to 217 gauges across Germany covering a broad range of hydrological conditions. Based on these data, we modelled the respective probabilities of occurrences for 120 benthic invertebrate taxa within this hydrological range using hierarchical logistic regression models.

Our analyses revealed that more than one-third of the taxa (18–40%) can be considered as ubiquitous and having a broad hydrological tolerance. Furthermore, 22–41% of the taxa responded to specific ranges of flow conditions with detectable optima. "Duration high flow event" represented the flow parameter that correlated best with the abundance of individual taxa, followed by "rate of change average event", with 41 and 38% of the taxa showing a peak in their probability of occurrence at specific ranges of these metrics, respectively. The habitat suitability for these taxa may be potentially affected by global change-induced hydrological changes.

Quantified hydrological traits of individual taxa might therefore support stream management and enable the prediction of taxa responses to flow alteration. The hydrological traits of stream benthic invertebrates may be used in forecasting studies in central Europe, and the methods used in this study are suitable for application in other regions with different flow regimes.

1. Introduction

Hydraulic conditions are key habitat variables for all biota living in running waters and result from the interaction between river morphology and discharge or flow. Benthic invertebrates show high biodiversity in streams and rivers, have been shown to include indicator species sensitive to flow conditions, occupy a central position in the functioning of river ecosystems, and display some fascinating adaptations to flowing waters, *e.g.*, in terms of life history, nutrition, respiration, or behavioral and morphological characteristics (Bellard et al., 2012; Lytle and Poff, 2004; Poff et al., 2007; Statzner et al., 1988). However, quantitative empirical knowledge on the flow requirements or preferences of lotic benthic invertebrates is limited but is essential (i) to assess the effects of hydrological alterations, *e.g.*, due to global change or water uses, and (ii) to identify environmental flow regimes that aim to preserve the ecological integrity of river ecosystems (Bunn and Arthington, 2002; Poff and Julie Zimmerman, 2010). There are three main approaches to assessing flow preferences. First, they are usually assessed based on literature reviews and/or expert knowledge and described at nominal (*e.g.*, "generalist", "lentic" or "lotic") or ordinal scales (*e.g.*, "limnobiont" to "rheobiont") (Schmidt-Kloiber and Hering, 2015) and have already been collated for many taxa and compiled in databases such as the *freshwaterecoloy.info*-database (Schmidt-Kloiber and Hering, 2015). Such descriptive classifications of invertebrate flow preferences are suitable and widely used to compare the flow trait composition of different sampling sites (Armanini et al., 2011). However, due to their qualitative nature, they are less suited to assess, model and predict the effects of flow changes that are described in quantitative terms (*e.g.*, discharge changes due to global change). Second, the hydraulic preferences of invertebrates have already been described in semi-quantitative terms in several studies by recording species' probability of occurrence and relating it to near-bed shear

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stress measured using FST-hemispheres (Schmedtje, 1995; Statzner et al., 1988). However, data requirements and computational time make it infeasible to map or model the hydraulic conditions at larger than reach scales (*e.g.*, for whole river networks) to apply such hydraulic preferences, *e.g.*, for their application in catchment or larger scale species distribution models. Moreover, the hydraulic shear stress recorded for a specific discharge only partly reflects the complex relationship between changing flow conditions over time, since it effects species throughout different life stages and finally determines reproductive success and hence, the presence or absence of individual invertebrate species. Third, flow preferences can be based on qualitative discharge measurements, which can be summarized into typical flow or hydrological regimes when analyzed over time. It has been shown that the flow regime strongly influences ecological processes and that changes in the abundance and distribution of aquatic invertebrates are caused, in part, by flow alterations (Brooks et al., 2011; Poff and Julie Zimmerman, 2010). In contrast to shear-stress data, long-term discharge time series (gauging data) are readily available at large spatial scales. Additionally, these data are useful for statistical modelling and for its large-scale upscaling, *e.g.*, to predict the effects of discharge changes due to global change. Despite this clear relationship between the hydrological conditions and biota, few studies have used hydrological data to quantify the flow preferences of benthic invertebrates in rivers. Among these, most studies represent specific case studies and reviews on flow alteration and associated ecological processes (Dunbar et al., 2010a; Monk et al., 2007; Monk et al., 2006; Poff and Julie Zimmerman, 2010), with a prevailing focus on the community structure (Brooks et al., 2011; Death, 2008; Konrad et al., 2008; Principe et al., 2007) preferentially on individual taxa (Armanini et al., 2011).

We aimed to quantitatively determine the flow preferences of lotic invertebrates—thereby defining “hydrological traits” for central European rivers by analyzing existing hydrological and biomonitoring data. More specifically, we (i) investigated whether invertebrates show a clear response and have an optimum along the gradient of different hydrological variables and hence have specific hydrological traits at all and (ii) aimed to quantify the hydrological thresholds at which species abundance and presence sharply change.

2. Methods

2.1. Datasets and pairing biomonitoring sites with gauging stations on the river network

We gathered and analyzed two independent, already existing long-term datasets from Germany: (i) daily hydrological data (gauging data) and (ii) results from benthic invertebrate surveys conducted by regional water managers in German rivers. Our dataset covers a wide range of hydrological conditions in Germany, including streams and rivers in the northern lowlands, central lower-mountain areas, and Alpine region of southern Germany.

Using the German national flow gauge network and the geographical coordinates of the benthic invertebrate sampling sites, we searched for gauging stations located in the same river reach as at least one biomonitoring site. As the locations of biomonitoring sites did not usually match those of the gauging stations, they were assigned to the nearest station (DeWeber and Wagner, 2014) when the following criteria were met: (i) having no tributaries in between and (ii) located within a maximum distance of 12 km from the paired gauging station. This pairing resulted in 371 invertebrate surveys from 238 sites paired to 217 gauging stations (Fig. 1). To consider the effect of distance on discharge, the discharge data from the gauging station was recalculated for the sampling sites according to the ratio between the catchment size at the biomonitoring site and at the paired gauge.

The biological dataset included abundance data for benthic invertebrate taxa that had been sampled in either spring or summer between 2004 and 2013 according to the currently used standard biomonitoring protocols. All sites were in a good or high ecological status according to the EU Water Framework Directive. We analyzed the hydrological preferences of 120 taxa that occurred in at least eight sites for each season (spring and summer). Rare taxa with an abundance of fewer than three occurring in fewer than eight sampling sites were excluded from the dataset because such sparse data do not allow statistical analysis (Heino and Soininen, 2010; Leigh and Datry, 2016). The taxonomic resolution was the species level (111 taxa), while nine taxa were only identified to the genus level (Supplementary Table ST1). The most frequent orders were Trichoptera (43 taxa), Ephemeroptera (25), Coleoptera (12) and Diptera (12) (Table 1). Prior to all analyses, the abundance data were log (x + 1)-transformed.

Since the addition of pseudo-absences is strongly recommended when modelling species preferences and distributions (Vaughan and Ormerod, 2005; Lobo and Tognelli, 2011) we added absence data for species at specific sites. Instead of randomly generated absence data (Lobo and Tognelli, 2011; VanDerWal et al., 2009), we preferentially generated absence data using a semi-random stratified approach, considering the stream type (Schmedtje et al., 2000) of the sampling sites according to their common environmental and hydromorphological characteristics. Sites with absences were selected based on two criteria: (i) having the same stream type as sites where the taxa were already recorded and (ii) being located in the same region/federal state as the present sites. These two criteria ensured the exclusion of sites representing inappropriate habitat conditions for the occurrence of taxa. All sites meeting these criteria were added as pseudo-absences to the analysis.

2.2. Computation and pre-selection of hydrological metrics

There are 171 hydrological metrics known as Indicators of Hydrologic Alteration (IHA) that are ecologically relevant and can be calculated based on daily discharge data, describing the duration, frequency, timing, magnitude, and rate of flow events (Olden and Poff, 2003). These metrics were calculated using discharge data from the 12-month period prior to the date of the biological sampling (*e.g.*, for a macroinvertebrate sample from 12.06.2012, flow data between 13.06.2011 and 12.06.2012 were considered). This period has been shown to best describe the effects of hydrological conditions on benthic invertebrates (Leigh and Datry, 2016). Twenty metrics were excluded due to the need for longer periods of discharge data, resulting in 151 metrics for further analysis. There was no significant gap (*i.e.*, missing values for more than 5 days) in the discharge data for any of the sampling sites. Missing discharge data were filled in for individual gaps according to the trends before and after failures and by comparing trends with the data from nearby gauge(s) for which pairwise correlations exceeded the reliable threshold of $|r| > 0.5$ (Kennard et al., 2010; Leigh and Datry, 2016). All flow metrics were computed using the R package EflowStats (Archfield et al., 2014; Henriksen et al., 2006).

We aimed to select at least one metric from each of the five flow regime categories (duration, frequency, timing, magnitude and rate) to minimize redundancies prior to the development of the hierarchical logistic regression models (see below). A pairwise collinearity test and a principal component analysis facilitated the selection among the 151 hydrological metrics using data from the 217 paired gauges. When pairwise correlations exceeded the sensitive threshold of $|r| > 0.7$ (Dormann et al., 2013), and hence redundancy occurred, the metric with the lower loading on the most significant principal component axis was removed from the list.

2.3. Temporal and spatial pseudo-replication

It was necessary to analyze temporal and spatial pseudo-replication because some sampling sites were paired with the same gauging station