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The added value of geodiversity indices in explaining variation of stream macroinvertebrate diversity

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ABSTRACT

Geodiversity, i.e. the variety of the abiotic environment, is considered to be positively correlated to biodiversity. In streams, the importance of physical heterogeneity for biodiversity variation is well known, but the usefulness of explicitly measured geodiversity indices to account for biodiversity has not been tested. We developed a technique to measure in-stream geodiversity, based on different types of stream flow, geomorphological processes and landforms observed from photographs taken during the field work, and substrates based on traditional field observations. We further tested the utility of these geodiversity measures in explaining variation in the biodiversity of macroinvertebrates in near-pristine streams. Our specific objective was to examine the explanatory power of geodiversity compared to traditional environmental variables, such as water chemistry, depth and current velocity. While most biodiversity indices correlated more strongly with traditional environmental variables, the influence of geodiversity on biodiversity was also evident. Unique effect of flow richness on species richness and that of total geodiversity on functional richness were higher than those of the traditional environmental variables. Our findings suggested that in-stream geodiversity offers a valuable concept for characterizing stream habitats. If further developed and tested, in-stream geodiversity can be used as a cost-efficient proxy to explain variation in biodiversity in stream environments.

1. Introduction

Geographical variation in biodiversity is dependent on environmental factors prevailing at different spatial levels (Ricklefs, 1987; Whittaker et al., 2001). This also holds true for stream systems where the determinants of fluvial habitats can be arranged to different spatial scales, ranging from the whole drainage system through the reach scale to the smallest microhabitats (Frissel et al., 1986). Across these spatial scales, physical habitat heterogeneity is one of the main characteristics controlling the distribution of organisms in stream ecosystems (Cooper et al., 1997; Allan and Castillo, 2007). Physical habitat heterogeneity is formed by in-stream physical factors, such as stream geomorphology, hydraulic features, and also by biological factors such as large woody debris and other non-living organic materials. For example, in headwater streams, the physical characteristics of habitats are often changing constantly at relatively small scales, and changes in these factors are also affecting organisms' oviposition choices, feeding preference and refugia from predation (Lancaster and Downes, 2013; Heino and Peckarsky, 2014). Hence, through affecting various ecological processes, these habitat factors are responsible for spatial variation in biodiversity among streams (Ward, 1992; Tickner et al., 2000; Schmera et al., 2007).

Information on in-stream habitat features is important for understanding the influences of physical changes on the biota (Armitage et al., 1997). Traditional habitat evaluation is based on direct measures of physical and chemical variables at stream sites. For example, the use of local in-stream measures, such as current velocity, stream width, water depth, substratum composition and water chemistry, has proved to be a suitable approach in stream ecology (Malmqvist and Mäki, 1994; Heino and Mykrä, 2008). A complementary approach is to evaluate stream habitats at a mesoscale. Mesoscale habitats of streams can be considered to be formed by the relations between hydrological and geomorphological forces. For instance, in headwater streams, visually determined discrete areas of macrophyte stands or patches of gravel are considered as mesoscale habitats (Tickner et al., 2000). Another approach is to consider streams at the reach scale by focusing on channel types within geomorphological typologies. This approach can be used to examine how different channel types affect biodiversity

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(Brown and Brussock, 1991; Milner et al., 2015), and how biodiversity varies between specific habitat types (e.g. waterfalls vs riffles; Rackermann et al., 2012) or between different microhabitats in the same reach (e.g. substratum types; Robson and Chester, 1999). However, little is known how such mesoscale variation of habitats correlates with stream biodiversity.

Geodiversity is the variety of the earth's surface materials, processes and forms. It includes materials such as soils, processes like erosion, and forms such as river meanders (Gray, 2013). The physical variability of the abiotic environment can be considered as a measure of geodiversity, and this has been recognized for its effect on biodiversity in many ecosystems (Andersson and Ferree, 2010; Parks and Mulligan, 2010; Stein et al., 2014; Hjort et al., 2015). In terrestrial ecosystems, geodiversity is thought to increase species richness through three mechanisms (Stein et al., 2014). First, the number of habitat types, amount of resources and structural complexity should increase at the same time as environmental gradient length increases (e.g. Tews et al., 2004). Second, for at least plant species, more heterogeneous environment should provide shelter and refuges from unfavorable abiotic and biotic conditions, thus promoting the co-occurrence and persistence of more species (e.g. Seto et al., 2004). Third, with higher spatial environmental heterogeneity there is also increased probability of speciation events through isolation or adaption to various conditions (e.g. Rosenzweig, 1995). In general, the exploration of biodiversity-geodiversity relationships has gained increasing attention recently (Beier et al., 2015; Lawler et al., 2015; Theobald et al., 2015; Tukiainen et al., 2017; Kaskela et al., 2017). However, most of these studies have considered scales > 1 km^2 (Räsänen et al., 2016) and, according to our best knowledge, there are no studies focusing on fine-scale (e.g. < 100 m^2) connections between biodiversity and geodiversity. While we are aware of the vast number of studies focusing on the relationship between abiotic and biotic elements of riverine landscapes (e.g. Robson and Chester, 1999; Lepori et al., 2005; Milner et al., 2015), there are no studies where the influence of geodiversity indices on biodiversity has

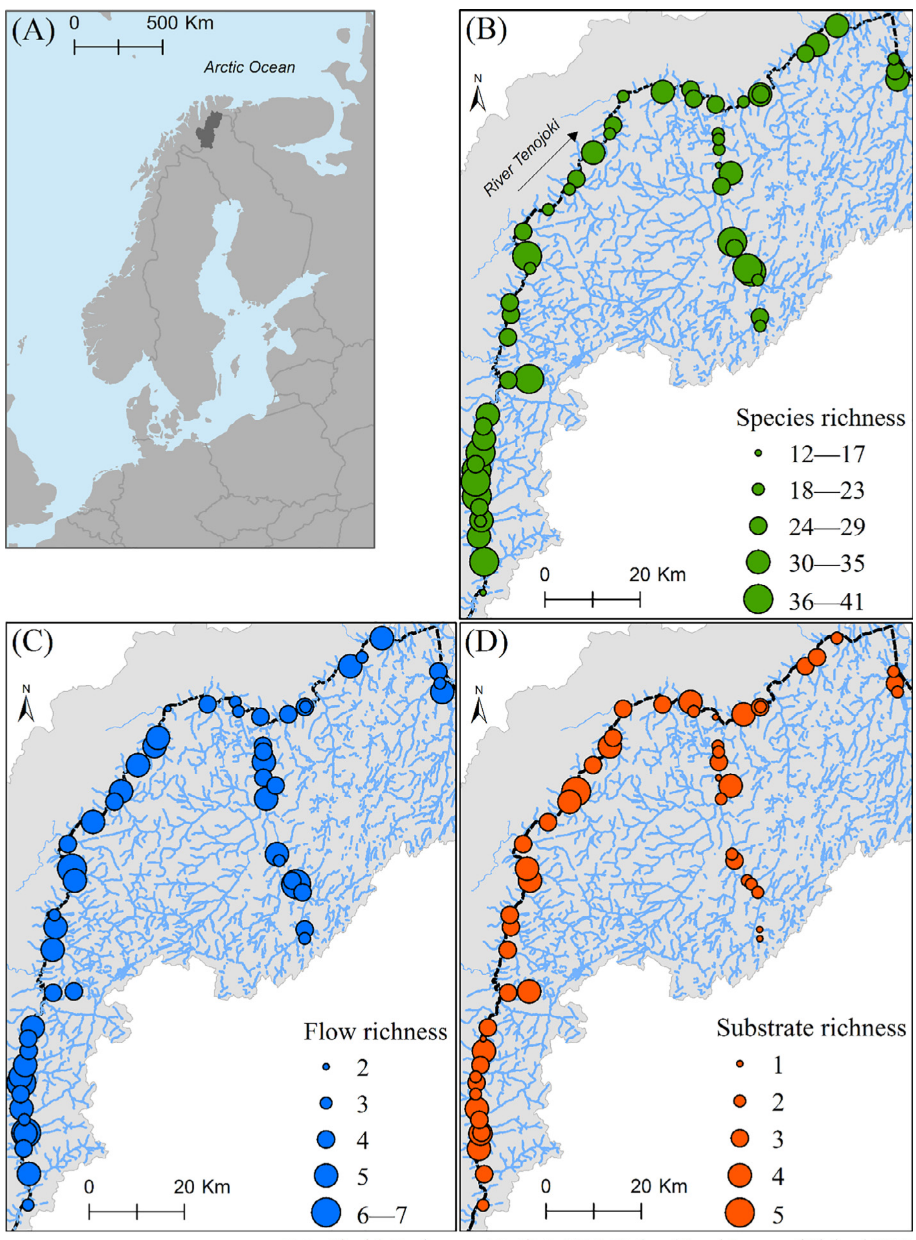

Fig. 1. Map showing the location of the Tenojoki drainage basin (A), and the study sites in the basin. Also, shown are species richness (B), flow richness (C) and substrate richness (D) variations among study sites. Note that all sites are tributary streams and no site is located in the main stem of the River Tenojoki.