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

Running head: Biodiversity-geodiversity relationships in stream environments

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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 (Frissell 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 (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 larger than 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 been tested in lotic environments.

The aims of this study were (i) to develop simple in-stream measures of geodiversity, and (ii) to test their utility in explaining variation in biodiversity in stream ecosystems. We specifically measured the variability of stream surface flow, geomorphology and substratum features to characterize geodiversity in streams. We addressed the following questions: 1) How well can macroinvertebrate biodiversity be accounted for by simple geodiversity measures? 2) Which are the most useful geodiversity indices in accounting for variation in macroinvertebrate biodiversity? 3) Are there substantial differences in the abilities of the novel geodiversity and traditional local-scale environmental variables to explain variation in macroinvertebrate biodiversity?

2. Materials and methods

2.1. STUDY AREA

The study area is located in the Tenojoki drainage basin (centred on 70 °N, 26 °E; total basin area: 16 386 km^2; Fig. 1). The River Tenojoki basin drains large areas in the northernmost Finland and Norway, ending up in the Arctic Ocean. In the study area, human activities, such as forestry and agriculture, are scarce and situated close to scattered population centers. Therefore, streams in our study area are in a pristine or near-pristine condition.

The topography of the study area is dominated by rounded mountains (i.e., fells), and elevation varies between 10 and 640 m above sea level. However, relative elevational variations in the river valleys are slightly smaller, mainly varying from 200 to 360 m. The bedrock comprises mainly of Precambrian bedrock, including igneous rock types, such as granites, gneisses, diorites and gabbros. Peatlands are quite rare, and they are located in valleys between fells. The study area mainly belongs to the subarctic deciduous birch zone (Hustich, 1961), where mountain birch (*Betula* *pubescens* ssp.*czerepanovii*) woodland is the main vegetation type. The tops of the highest fells are covered by barren tundra, with very sparse vegetation mostly consisting of low-statured shrubs, lichens and mosses. Scattered Scotch pine (*Pinus sylvestris*) woodlands occur in the southernmost part of the study area, which denotes a strong boundary for terrestrial vegetation (Mansikkaniemi, 1970).

A total of 55 streams were surveyed in the first half of June in 2012. We selected streams with following criteria: (1) the length of stream should be at least one kilometer, (2) the minimum distance from the study site to lake or pond upstream had to be at least 0.5 km, (3) the streams should have permanent flow, and (4) large rivers (width > 25 m, water depth > 50 cm) were excluded owing to difficulties of obtaining representative samples.

2.2. LOCAL STREAM VARIABLES

We measured several in-stream variables at each site. These variables included both physical habitat and water chemistry variables that have previously been found important in studies of stream macroinvertebrate communities in northern areas (Malmqvist and Mäki, 1994; Heino et al., 2014). Depth (cm) and current velocity (m s^{-1}) were measured at 30 random spots in a riffle site, and mean width (m) of the stream site was determined based on five cross-channel measurements. In analysis, instead of using standard deviations of stream depth, current velocity and width we utilized mean values, because of weak and non-significant correlations between the standard deviations of explanatory variables and the biodiversity indices (see Table S1). We measured pH and conductivity (μS cm^{-1}) at each riffle site in the field using YSI device model 556 MPS (YSI Inc., Yellow Springs, OH, USA). Additional water samples taken in field were frozen at the Kevo Field Station in Utsjoki and were subsequently analyzed for total nitrogen (μg L^{-1}), colour (mg Pt L^{-1}), iron (μg L^{-1}) and manganese (μg L^{-1}) in the laboratory of the Finnish Environment Institute in Oulu following Finnish national standards (National Board of Waters and the Environment, 1981). While the physical habitat variables showed wide variations typical of pristine running waters, water chemistry varied relatively little within the study area (Table 1).

2.3. STREAM GEODIVERSITY

To systematically map stream flow and geomorphological richness for each 50 m^2 study site, we used photographs taken simultaneously during the field surveys in 2012. Representative photographs were carefully examined visually, and from each photograph we determined how many different stream flow types (Wadeson and Rowntree, 1998) and geomorphological landforms and processes (Hjort and Luoto, 2010) were present at a site (Table 2; Fig 2). Using these photographs, it was possible to classify the different forms and processes afterwards, guaranteeing that the geodiversity measures were independent of the choices made during the field surveys (see below). Moreover, the use of photographs improved the consistency of the classification because special attention could be given to targets difficult to map and classify in the field. Surface flow type (i.e. 'flow richness') describes the number of different feature types of the water surface (Wadeson and Rowntree, 1998). We focused on surface flow types owing to the difficulties to visually map near-bed flow types. Despite the semi-quantitative nature of the classification system, the approach is included in the river habitat surveying methods in the United Kingdom (Environment Agency, 2003). Different erosion and deposition features represent mapped geomorphological landforms and processes (Charlton, 2007). Moreover, we used field observations of sediment granulometry to determine the number of different substrate types. More precisely, substrate material was classified according to a slightly modified Wentworth scale (1922). In addition to the different measures of geodiversity, a measure of total geodiversity (i.e. 'georichness') was computed by summing stream flow, geomorphological and substrate richness values (see Hjort and Luoto, 2010; Hjort et al., 2012). Although this is a simple way to quantify geodiversity, it follows the current standard in the geodiversity literature (see review in Pellitero et al., 2015). For example, there are no explicit means to weight different features of geodiversity at present.

2.4. STREAM MACROINVERTEBRATE DATA

At each stream site, we took a pooled 3-min kick-net sample (net mesh size 0.3 mm, net width 30 cm). Each pooled sample consisted of six 30-s subsamples covering environmental variation at a 50 m^2 total riffle area. Because one subsample consisted of 1-meter kicking (in the upstream direction) the total sampling effort per site comprised 1.8 m^2 of stream bed distributed across different microhabitats. Different microhabitats were sampled based on visual observations of water depth, flow conditions, moss cover and particle size. We chose to focus the sampling on different microhabitats rather than use a fully randomized sampling scheme because our approach provides samples with a larger share of the species present at a site than fully random samples. According to previous research (Mykrä et al., 2006), this kind of a sampling method and even a lower effort (i.e. four 30-s subsamples) has proved to be highly effective in northern streams, capturing most riffle-dwelling macroinvertebrate species at a site in a given season and revealing main spatial patterns in macroinvertebrate community structure (Heino et al., 2014). A larger sampling effort per site was logistically impossible because of high amounts of moss and organic material at some sites. The six subsamples of each sample were immediately pooled and preserved in ethanol in the field for further processing and identification in the laboratory. Most animals were identified to the lowest possible taxonomic level, i.e. mostly to species level. Also, species group and genus level identifications were used in some cases, because of the absence of the required morphological features for species-level identification or lack of identification keys for some insect larvae.

2.5. SPECIES TRAIT DATA AND BIODIVERSITY INDICES

For assigning macroinvertebrates to different trait groups, we utilized the approach that has been recently used in research on northern streams (Tolonen et al., 2016). Stream macroinvertebrates were divided to three grouping features, each containing several traits (Schmera et al., 2015). First, functional feeding group (FFG) classifications were based on the ways how macroinvertebrates obtain food. These included filterers, gatherers, shredders, scrapers and predators (Cummins and Klug, 1979; Merrit and Cummins, 1996). Assignments to different groups followed mainly Moog's (2002) 10-point system, in which each species is given 1 to 10 points for each of the possible feeding classes. In our case, if a species got ≥ 5 points for a certain FFG, it was assigned that particular FFG. If a species was missing from Moog's (2002) categorization, information from Merritt and Cummins (1996) or our expert judgment was used. Second, habit trait groups (HTGs) provide information about microhabitat use, mobility, and where food is obtained. HTGs included burrowers, climbers, clingers, sprawlers and swimmers (Merrit and Cummins, 1996). A third grouping was based on the maximum larval body length of species, where each species was classified to 1 of 6 size categories: >0-0.25, 0.25-0.5, 0.5-1, 1-2, 2-4, or 4-8 cm. The body size categorizations were based on our own information or on information from personal communication with S. Dolédec (Université Lyon 1, France), Jari Ilmonen (Metsähallitus, Finland) or Lauri Paasivirta (Salo, Finland).

Using the data described above, we calculated eight measures of biodiversity, of which four described species diversity and four portrayed functional diversity. (1) Species richness (i.e. the number of species), (2) Shannon diversity, (3) Simpson diversity, (4) Pielou evenness, (5) functional richness, (6) functional evenness, (7) functional dispersion and (8) Rao's quadratic entropy. All of the four functional diversity indices were calculated using the "FD" package for R (Laliberte et al., 2014), following the analytical approaches devised by Botta-Dukat (2005) and Villeger et al. (2008). To compute FD indices, we created a simple species-by-traits matrix based on FFGs, HTGs and size classes mentioned above (see also Table S2).

2.6. STATISTICAL ANALYSIS

First, we tested the response and explanatory variables for normality, and transformed them if necessary. Second, Pearson correlation was used to examine congruence between the biodiversity indices and to evaluate correlations between environmental variables and geodiversity indices. Third, we used multiple linear regression-based commonality analysis to explore variation in the biodiversity indices (Ray-Mukherjee et al., 2014).

In multiple linear regression, there are three main effects that can be examined: (1) total effects of all variables, (2) direct effects or independent effect of one variable, and (3) partial effects or effect of a specific subset of variables (LeBreton et al., 2004). Here, we aimed to find out how well each predictor variable alone could explain variation in the response variables. Using commonality analysis, we can separate a regression effect into unique and common effects. Unique effects provide information about observed variance unique to one predictor variable, and common effects detect how much variance is common to groups of different variables (Ray-Mukherjee et al., 2014). In this study, the final linear regression model with forward selections was run for all the environmental and geodiversity variables to obtain the lowest possible AIC value. Normality of model residuals was explored visually. All statistical analyses were run using R with the packages "stats", "BiodiversityR" (Kindt, 2017) and "yhat" (Nimon et al., 2015).

3. Results

A total of nine different flow-types were identified from the study area, with a maximum of seven being detected in a single site (Table 3). The most common flow types were the chute (44 out of 55 sites) and broken standing waves (50). Instead, free fall (8) and unbroken standing waves (8) were the rarest types. The number of geomorphological features varied from zero to five per site. The most common types were side erosion and meander, characterizing the dominance of erosional processes in the studied streams, whereas sand bar was observed only in one site. In general, there was less variation in the substrate classes between the study sites when compared to the geomorphological features. Boulders were found from all but one site, and cobbles from a total of 50 sites. Sand was the rarest substrate type, as it was observed only from two sites. Variations of flow richness and substrate richness were quite evenly present at the study sites.

We found a total of 37 035 macroinvertebrate individuals and 106 macroinvertebrate taxa across the 55 study streams. The average number of individuals per sample was 673 (SD = 591; range = 63 – 3134), and the average number of taxa per site was 28 (range = 12 – 41; Table 4). Descriptive statistics of biodiversity indices are presented in Table 4 and summary of the species trait categories is shown in Table S3. Although there were strong correlations between the individual biodiversity indices (Table 5), we did not exclude any of the indices to systematically test the relationship between different biodiversity measures and environmental variables.

Pearson correlations between geodiversity and traditional environmental variables were typically rather weak. The strongest positive correlation was noted between flow richness and current velocity, and between substrate richness and stream width (Table 6). Interestingly, geomorphological richness seemed to be negatively correlated with many traditional environmental variables. On the other hand, there were stronger correlations among the traditional environmental variables. For example, of the physical habitat variables, stream width correlated significantly with velocity and depth, and most of the chemical variables also correlated with each other (Table 6).

The biodiversity indices showed statistically significant correlations with at least one of the measures of geodiversity or traditional environmental variables (Table 7). Of the measures of geodiversity, flow richness correlated most strongly with species richness, and this correlation was stronger than with any other environmental variable ($r = 0.407$, $p < 0.01$). The georichness variable also correlated significantly with species richness and functional richness. In contrast, substratum richness was not correlated statistically significantly with any of the biodiversity measures. More importantly, the correlations between the biodiversity and geodiversity indices were dominantly positive. For example, the measure of total geodiversity was positively associated with species richness and functional richness (Fig. 3). Of the traditionally measured environmental variables, stream width and depth showed negative and significant correlation with several biodiversity indices.

The linear regression models were quite similar for the different biodiversity indices considering the explanatory power (Table 8). Adjusted (R^2_{adj}) values of the models varied between 0.010 and 0.394. The highest R^2_{adj} values were observed for the models of Rao's quadratic entropy ($R^2_{adj} = 0.394$) and functional dispersion ($R^2_{adj} = 0.352$; Table 8). The lowest R^2_{adj} values were detected for functional evenness ($R^2_{adj} = 0.010$) and Pielou evenness ($R^2_{adj} = 0.169$).

The main results of the commonality analyses are shown in Figure 4 (see Table S4 for common effects of explanatory variables). Flow richness was the best variable in accounting for variation in species richness, with a high 82 % relative independent contribution ($R^2 = 0.20$). Notable unique explanatory power of flow richness also appeared in the models of Shannon diversity, Simpson diversity, functional evenness and Rao's quadratic entropy. More precisely, the unique effect of flow richness on Shannon diversity was the third highest after stream width and conductivity. For Rao's quadratic entropy, flow richness was the third best variable after stream width and pH. For functional richness, there was a clear unique effect of total geodiversity which accounted for 42 % of the explained variation. In four cases, stream width was the most important unique variable for biodiversity. This was especially evident in the models of Simpson diversity and functional dispersion indices. For Shannon diversity and Rao's quadratic entropy, common effect of depth and width was considerable (Shannon diversity = 20.45 % of explained variation; Rao's Quadratic entropy = 40.69 %). Otherwise, common effects of explanatory variables on biodiversity were minor and, in many of cases, even negative effects appeared (Table S4).

4. Discussion

It is well understood that variation of local habitat conditions affects the biodiversity of stream macroinvertebrates (Poff, 1997; Vinson and Hawkins, 1998). However, most studies have described fluvial habitats as larger hydraulic units, i.e. as patches of relatively homogenous flow and substratum characters (e.g. Thomson et al., 2001), studied differences in species composition between different channel types (Milner et al., 2015), or examined differences between microhabitats in the same reach type (Robson and Chester, 1999), instead of focusing directly on the local diversity of combined geomorphological and surface flow types at the mesoscale. To fill this knowledge gap, we considered the variation of reach-scale conditions. More precisely, we developed a novel photograph-based system to characterize stream habitats at mesoscale by measuring different hydraulic and geomorphological features, combined with the information of stream bed material determined during the field surveys. Using this information, we could directly explore biodiversity-geodiversity relationship across streams.

Spatial environmental heterogeneity has been shown to increase species richness in many ecosystems (Stein et al., 2014). In the present study, although the biodiversity-geodiversity relationships were modest, our results highlight the value of visually determined geodiversity in the analysis of stream macroinvertebrate biodiversity. This is because commonality analysis revealed differences between the utility of geodiversity and traditional in-stream measures in accounting for variation of different biodiversity indices. For example, geodiversity measures explained functional richness better than the traditional in-stream measures. Also, flow diversity explained variation in species richness better than the commonly-used physical habitat and water quality variables. We also noted that various aspects of geodiversity appeared to be correlated relatively strongly with different measures of biodiversity. Thus, variables describing heterogeneity in flow, substrate and geomorphological conditions may complement the traditional in-stream variables in explaining stream macroinvertebrate biodiversity.

For geodiversity of the stream sites, we found a total of nine flow types, eight geomorphological features and five substrate classes. The study sites varied from those with high flow diversity and coarse substrate to those with stable flows and gravel bottoms. The rather substantial variation of flow conditions among sites was a bit surprising because the study sites were located only in riffles and in an area of quite similar topography and lithology. In high-gradient areas, the morphology of stream corridors is typically characterized by eroded channels with small cascades, boulders and other large-sized particles (Vezza et al., 2014). This also seemed to be true in the Tenojoki River basin where substrates were quite coarse-sized, such as boulders and cobbles. Coarse bed materials and high flow velocities often cause excessive variety of flow types (Zavadil et al., 2012), as was also observed in our study area. In addition, the geomorphological features of the study sites followed this characterization of high-gradient streams, as the most common features were bottom erosion and side erosion. Consequently, depositional landforms like sand bars were rare in our study sites.

Based on our analyses, we emphasize the shared variation in biodiversity explained by geodiversity variables and the typically-used stream environmental variables. However, the visual measures of habitat features explained slightly better variation in some indices of biodiversity than the traditionally used stream site variables. For example, surface flow type showed a positive correlation with species richness. This supports the findings of Reid and Thoms (2008) and Silva et al. (2014) who found that visually-estimated flow type correlate with variation in macroinvertebrate assemblages at the mesoscale. It is possible that flow richness, for example, affects species richness indirectly via its effects on food availability and shelter from harsh flow conditions. For instance, Pastuchová et al. (2008) found that taxa associated with stony substrate clearly favored habitats with flow types of unbroken standing waves and broken standing waves, indicating exposed stream bottoms due to higher velocity. It is possible that flow type richness could also reflect variability in stream depth and channel morphology (Zavadil et al., 2012). Thus, surface flow heterogeneity indirectly describes substratum diversity and hydraulic conditions of the streambed, which makes it an essential component for ecological studies (Newson and Newson, 2000). On the other hand, our results did not support a clear relationship between substrate richness and biodiversity. This is a bit surprising, because many other studies have shown the importance of substratum as a predictor of macroinvertebrate community composition in stream ecosystems (Vinson and Hawkins, 1998; Robson and Chester, 1999; Johnson et al., 2004; Mykrä et al., 2007). The weak role of substratum can reflect problems related to obtaining a comprehensive view of stream bottom conditions using a simple binary classifications (i.e. exists vs does not exist) only. For example, using percent area of different substrates types could offer more qualified image of stream substrate.

Most of the functional diversity indices were best explained by the traditionally-used environmental variables. An interesting exception was functional richness which was better accounted for by the combination of different geodiversity measures (i.e. georichness). As functional richness is used to quantify the trait space that is occupied by the species in a community (Mason et al., 2005), it may be that georichness captures better fine-scale variations in overall habitat conditions than in single environmental variables. Of the traditional environmental variables, stream width and pH were most important in explaining variation of functional diversity, as they were the most important predictors for functional dispersion and Rao's Quadratic entropy. For example, it has been noted that the responses of Rao's Quadratic entropy to natural environmental variation will usually remain stable, and this index is more sensitive to pollution sources than natural environmental variables (Péru and Dolédec, 2010). To summarize, physical and chemical variables typically affect the functional composition of macroinvertebrate communities at a local scale (Heino, 2005; Schmera et al., 2017), and our present results thus corroborated previous findings.

The use of in-stream geodiversity measures can improve our understanding of biodiversity-environment relationships. Moreover, geodiversity indices could be used in predictive models as cost-efficient surrogates of habitat heterogeneity (cf. Hjort et al., 2012; Tukiainen et al., 2017). However, we also have to consider possible weaknesses related to the determination of simple geodiversity measures. Although the visual examination of photographs was shown to be suitable approach, field-based observations of flow-patterns and geomorphology could provide more comprehensive data about geodiversity (however, note the methodological strengths in the use of field-based photographs presented in the materials and methods section). Also, it would be advisable to acquire information from more than just one site per studied stream to cover the full range of environmental conditions (Heino et al., 2013). In addition to the visual determination of geofeatures, it is possible to apply remote sensing-based techniques (e.g. unmanned aerial system and structure-from-motion photogrammetry). For example, Woodget et al. (2016) emphasized the possibility to acquire spatially continuous and high-resolution remotely sensed data of physical habitat of streams. The temporal variation of stream flow conditions should also be considered in the mapping of hydraulic diversity. Thus, a more comprehensive assessment could include data from both high (e.g. spring flood) and low (e.g. late summer) discharge periods. The approach to measure geodiversity could also be developed further. For example, more ecologically relevant measures might be developed by considering the specific habitat requirements of stream macroinvertebrates or other organisms. Further development of measures of geodiversity could include the weighting of different features according to their importance for the target species. Quinn et al. (1996) and Reid and Thoms (2008) found that turbulence of water and high velocities were important factors for macroinvertebrate distributions. High turbulence may, for example, decrease the amount of material available for filter-feeding animals (Quinn et al., 1996). Because broken standing waves are characterized by high velocities (Reid and Thoms, 2008), it could be advisable to highlight this category over other flow types. Of substratum types, one could highlight boulders because they provide suitable microhabitats for many macroinvertebrates which is seen by their higher densities around boulders than on bedrock (Robson and Chester, 1999). Also, Bouckaert and Davis (1998) showed that biodiversity was higher in the wakes of the boulders and, according to our observations, boiling surface water type characterized well such boulder areas.

To conclude, we described in-stream measures of geodiversity using photographs taken in the field and explored how well the developed geodiversity measures can be used to explain the variation in macroinvertebrate biodiversity in near-pristine streams at the mesoscale. Based on our findings, we conclude that simple measures of geodiversity may explain species diversity better than traditional environment variables alone. For example, the measures of flow and substrate richness appear to be promising surrogates complementing commonly-used physical habitat and water quality variables in stream environments. The use of photographs could offer an interesting new approach for exploring stream habitats because, as a relatively fast method, it could offer time for taking more biological samples during time-restricted field investigations. With further development, such a geodiversity-based approach, especially if conducted by unmanned aerial systems (e.g. drones), holds potential for becoming a cost-efficient tool for evaluating and defining stream habitat features.

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Tables

Table 1. Summaries of physical and chemical characteristics of the 55 stream sites studied.

Variable	Min.	Median	Mean	Max.
Depth (cm)	14.6	24.4	24	34.5
Channel width (m)	1.2	4.6	5.8	22.0
Current velocity (m s^{-1})	0.28	0.57	0.57	0.89
pH	6.58	6.85	6.86	7.51
Conductivity (μS cm^{-1})	16	26	26	36
Total nitrogen (μg L^{-1})	62	130	129	260
Colour (mg Pt L^{-1})	10	25	27	50
Iron (μg L^{-1})	8	68	67	160
Manganese (μg L^{-1})	<0.1	1.4	1.6	5.5

Table 2. Flow types (Wadeson & Rowntree, 1998; see also Environment Agency, 2003), geomorphological features (i.e. processes and landforms; Charlton, 2007) and substrate types (modified Wenthworth's (1922) scale) as used to describe geodiversity of sites.

Surface flow type	**Definition**	**Surface flow type**	**Definition**
Broken standing waves	Typical turbulent white water.	Rippled surface	The water surface with symmetrical, small, ripples.
Boil/Upwelling	Surface with a look of "boiling" water. Marks of vertically directed flow.	Scarcely perceptible flow	In wider low gradient patches, close to stream banks.
Chaotic flow	Combination of three of the four most turbulent flow-types (free fall, chute, broken standing waves and upwelling).	Smooth	Smooth water surface. Typical behind large obstacles.
		Unbroken standing waves	Waves not broken, surface like ”dragon's back”.
Chute	Fast and steeply falling water, water enfolds the substrate.		
Free fall	Vertically falling water.		
Geomorphology	**Definition**	**Geomorphology**	**Definition**
Bottom erosion	Water flowing in a relatively deep channel.	Sand/gravel bar	Sand or gravel bars above water level.
Evorsion	The formation of round erosional features or signs due to vortex of water and sediments.	Sedimentation	Deposition of fine sediments at the bottom of a stream.
Landslide scar	Small-scale landslides on the banks transporting sediments to stream.	Side channel	Side flow separated from the main channel with vegetation or soil.
Meander	Large stream: if the site is situated on curve/meander. Small stream: ≥two meanders/curves.	Side erosion	Cut bank resulted from side erosion, even the smallest signs (e.g. undercutting).
Substrate type	**Diameter (mm)**		
Sand	0.25 – 2		
Gravel	2 – 16		
Pebble	16 – 64		
Cobble	64 – 256		
Boulder	256 – 1024		

Table 3. Geodiversity characteristics of the 55 stream sites studied

Variable	Min.	Median	Mean	Max.
Flow type richness	2	4	4.3	7
Geomorphological richness	0	2	2.4	5
Substrate richness	1	3	2.8	5
Total geodiversity	5	10	9.5	14

Table 4. Descriptive statistics of biodiversity indices used in analysis.

Biodiversity index	Min.	Median	Mean	Max.
Species richness	12	27	28	41
Shannon diversity	1.18	2.03	2.07	2.87
Simpson diversity	0.42	0.78	0.75	0.91
Pielou evenness	0.40	0.63	0.62	0.88
Functional richness	9	18	18	25
Functional evenness	0.26	0.46	0.46	0.64
Functional dispersion	0.26	0.45	0.45	0.54
Rao's quadratic entropy	0.13	0.24	0.23	0.30

Table 5. Pearson correlations between the eight biodiversity indices. Statistically significant ($p<0.05$) correlations are in bold.

	Species richness	Shannon diversity	Simpson diversity	Pielou evenness	Functional richness	Functional evenness	Functional dispersion
Shannon diversity	**0.560****						
Simpson diversity	**0.474****	**0.952****					
Pielou evenness	0.165	**0.904****	**0.897****				
Functional richness	**0.869****	**0.505****	**0.423****	0.163			
Functional evenness	**–0.447****	–0.236	**–0.317***	–0.028	–0.203		
Functional dispersion	**0.453****	**0.769****	**0.832****	**0.704****	**0.498****	–0.254	
Rao's quadratic entropy	**0.444****	**0.738****	**0.775****	**0.668****	**0.510****	–0.198	**0.983****

*P < 0.05, **P < 0.01

Table 6. Pearson correlations between geodiversity (FlowRich = flow type richness; GeomRich = geomorphological richness; SubstrRich = substrate richness; GeoRich = total geodiversity) and traditional environmental variables. Statistically significant (p<0.05) correlations are in bold.

	FlowRich	GeomRich	SubstrRich	GeoRich	Velocity	Depth	Width	Total N	pH	Colour	Conductivity	Manganese
GeomRich	0.066											
SubstrRich	0.191	0.160										
GeoRich	**0.549****	**0.764****	**0.609****									
Velocity	**0.291****	–0.035	–0.022	0.091								
Depth	0.158	**-0.297***	–0.186	–0.210	**0.337***							
Width	0.232	–0.234	**0.270***	0.056	**0.469****	**0.475****						
Total N	0.026	**–0.266***	–0.142	–0.227	0.017	**0.375****	**0.061***					
pH	**0.323***	–0.031	0.132	0.172	–0.048	–0.068	–0.050	0.214				
Colour	–0.018	–0.153	0.055	0.087	–0.030	0.126	–0.053	**0.677****	–0.107			
Conductivity	–0.063	0	0.232	0.071	0.056	–0.010	0.044	0.206	0.105	**0.384****		
Manganese	0.054	**–0.268***	**–0.316***	**–0.289***	0.022	0.214	–0.076	**0.577****	–0.096	**0.489****	0.051	
Iron	0.001	–0.201	–0.118	–0.184	–0.007	0.182	0.093	**0.637****	–0.182	**0.735****	0.211	**0.794****

*P < 0.05, **P < 0.01

Table 7. Pearson correlations between the biodiversity indices, traditional environmental and geodiversity variables. Statistically significant ($p<0.05$) correlations are in bold.

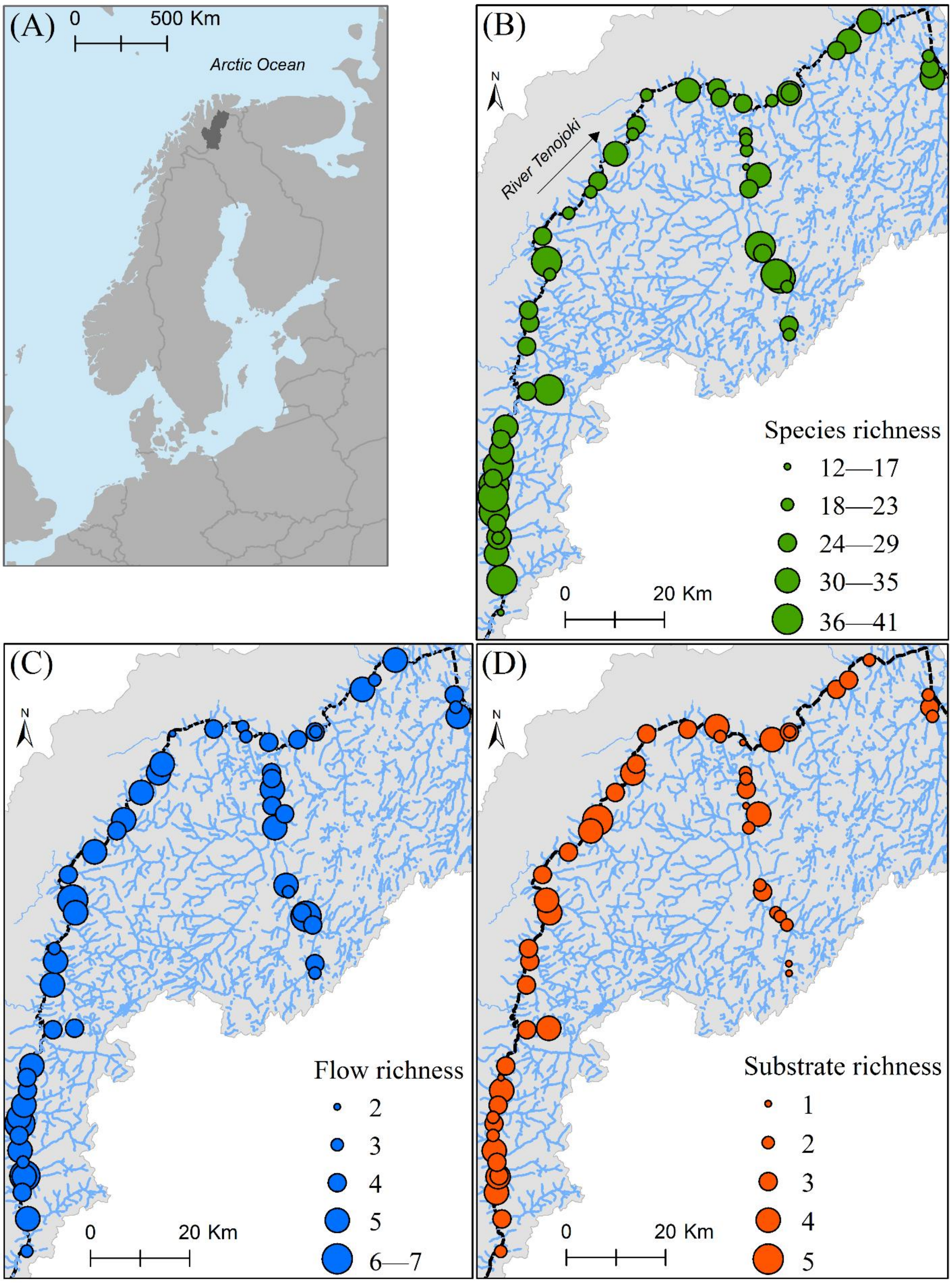
	Species richness	Shannon diversity	Simpson diversity	Pielou evenness	Functional richness	Functional evenness	Functional dispersion	Rao's quadratic entropy
Velocity	0.156	0.034	–0.026	–0.055	0.032	–0.124	–0.225	–0.217
Depth	–0.211	–0.212	–0.258	–0.153	**–0.339***	0.184	**–0.393****	**–0.406****
Width	–0.146	**–0.344***	**–0.444****	**–0.360****	–0.254	0.153	**–0.597****	**–0.576****
Total N	–0.167	–0.102	–0.045	–0.032	–0.211	0.234	–0.122	–0.162
pH	0.137	–0.074	–0.040	–0.122	–0.103	0.056	–0.142	–0.213
Colour	–0.065	0.074	0.112	0.104	–0.088	0.109	–0.033	–0.003
Conductivity	0.048	0.256	0.245	**0.267***	–0.003	0.034	0.066	0.042
Manganese	0.077	0.117	0.169	0.102	–0.020	–0.071	0.063	0.032
Iron	0.025	0.049	0.063	0.029	–0.044	–0.024	–0.036	–0.057
Flow type richness	**0.407****	0.117	0.027	–0.044	**0.270***	0.032	–0.043	–0.061
Geomorphological richness	0.091	0.024	0.057	–0.043	0.222	**–0.276***	0.192	0.189
Substrate richness	0.179	0.009	–0.073	–0.106	0.219	0.037	–0.116	–0.085
Total geodiversity	**0.309***	0.069	0.050	–0.092	**0.355****	–0.156	0.061	0.065

$P < 0.05$, $^{**}P < 0.01$

Table 8. Summaries of the results of linear regressions. The explanatory variables selected for each model are shown in Figure 4.

	Multiple R^2	R^2adj.
Species richness	0.243	0.214
Shannon diversity	0.293	0.221
Simpson diversity	0.318	0.264
Pielou evenness	0.215	0.169
Functional richness	0.199	0.168
Functional evenness	0.081	0.010
Functional dispersion	0.388	0.352
Rao’s quadratic entropy	0.450	0.394

Figures



Data: Finnish Environment Institute 2015; National Land Survey of Finland 2010

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.

Fig. 2. Examples of study sites, illustrating the range of total geodiversity (georichness): A = 5; B = 7; C = 9; D = 11; E = 13; F = 14.

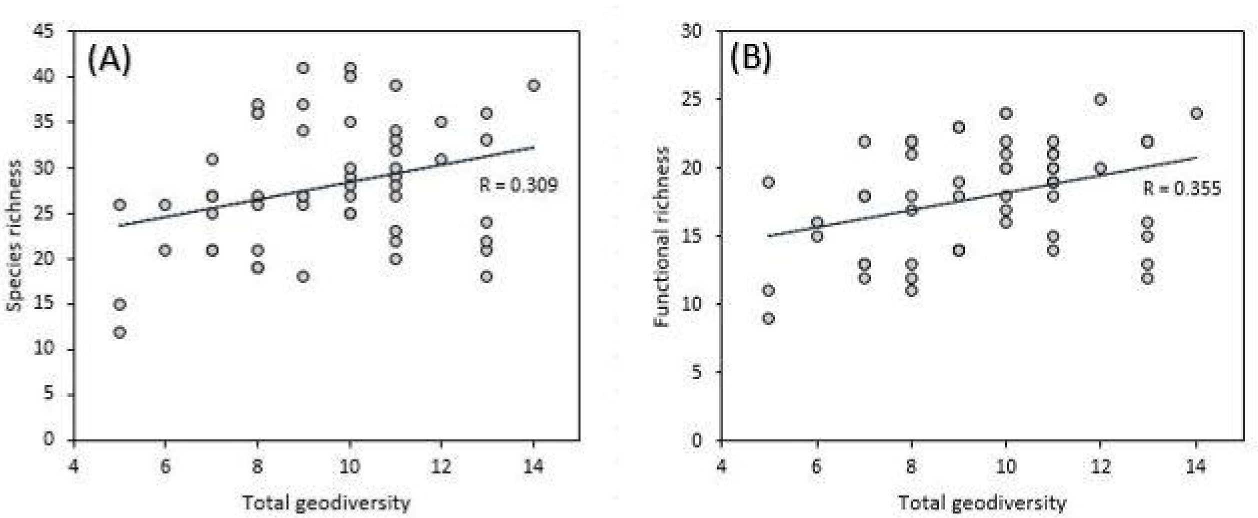


Fig. 3. The relationship between total geodiversity and species richness (A) or total geodiversity and functional richness (B).

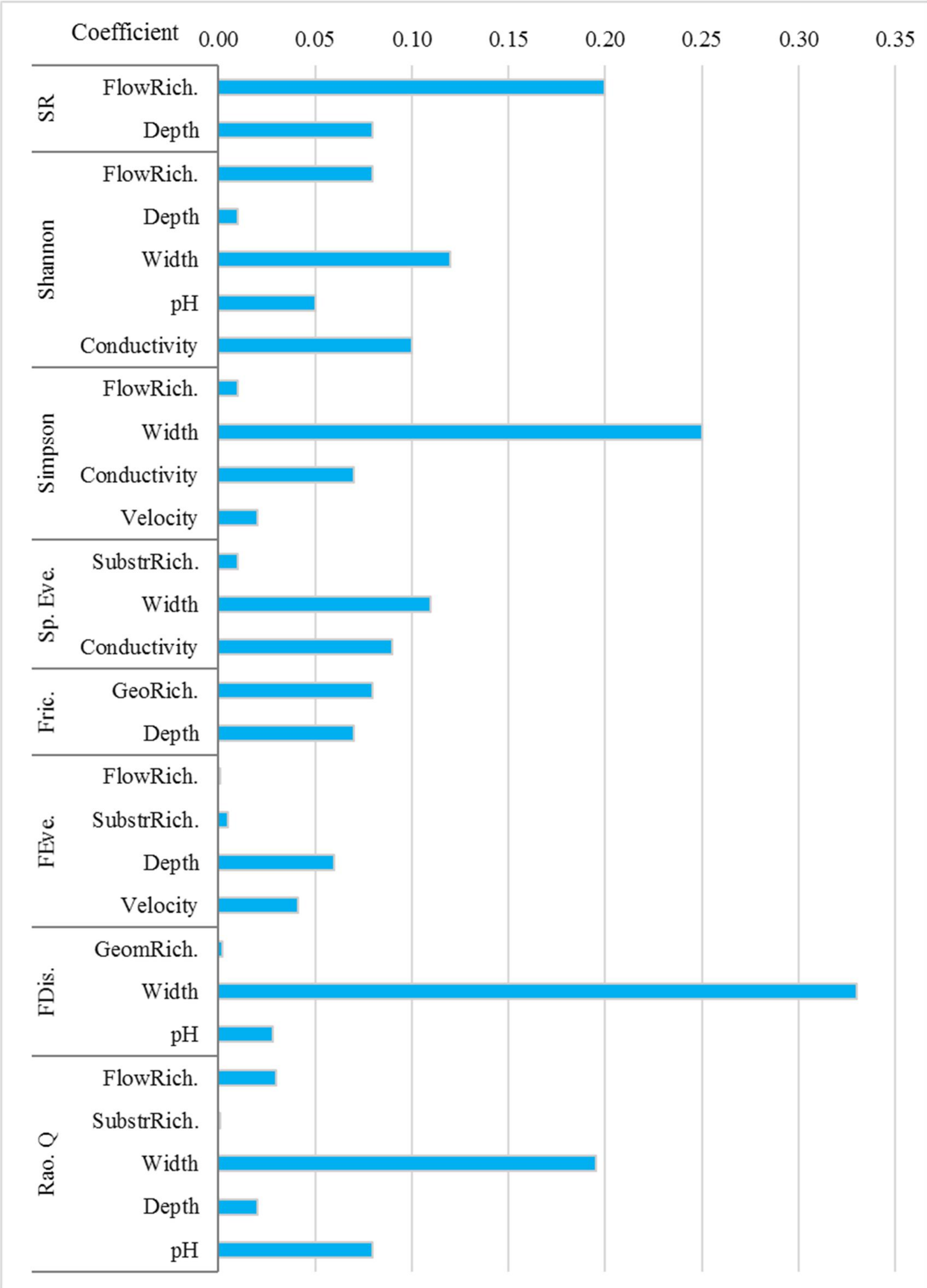


Fig. 4. Summaries of the results of the commonality analysis, showing unique regression effects of selected explanatory variables on biodiversity indices. Note that the common effects of variables have been omitted from the figure because of clarity. Abbreviations: SR = Species richness; Shannon = Shannon diversity; Simpson = Simpson diversity; Sp. Eve = Pielou evenness; Fric = functional richness; FEve = functional evenness; FDis = functional dispersion; Rao.Q = Rao's quadratic entropy; FlowRich = flow type richness; GeomRich = geomorphological richness; SubstrRich = substrate richness; GeoRich = total geodiversity.