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Local environment and space drive multiple facets of stream macroinvertebrate beta diversity

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Abstract

Aim Understanding variation in biodiversity typically requires consideration of factors operating at different spatial scales. Recently, ecologists and biogeographers have recognized the need of analyzing ecological communities in the light of multiple facets including not only species-level information, but also functional and phylogenetic approaches to improve our understanding of the relative contribution of processes shaping biodiversity. Here, our aim was to disentangle the relative importance of environmental variables measured at multiple levels (i.e. local, catchment, climate and spatial variables) influencing variation in macroinvertebrate beta diversity facets (i.e. species, traits and phylogeny) and their components (i.e. replacement and abundance difference) in boreal streams.

Taxon Aquatic macroinvertebrates

Location Western Finland

Methods A total of 105 streams were sampled in western Finland, encompassing a geographical extent over 500 km. We analyzed variation in the different beta diversity facets and components using distance-based redundancy analysis (db-RDA) and associated variation partitioning procedures. We modelled spatial structures using distance-based Moran eigenvector maps.

Results We found that the relative influence of explanatory variables on each diversity facet and component revealed relatively similar patterns. Our main finding was that local environmental and spatial variables generally contributed most to the total explained variability in all facets and components of beta diversity, whereas catchment and climate variables explained less variation in the beta diversity facets at the spatial scale considered in this study.

Main conclusions Different facets of beta diversity were mainly influenced by local environmental variables and spatial structuring, likely acting through deterministic and stochastic pathways, respectively. Identifying the ecological variables and mechanisms that drive variation in beta diversity may be used to guide the conservation and restoration efforts for biodiversity under global change.

Key words Beta diversity components, biodiversity facets, multi-level variables, species, traits, phylogeny

1 | INTRODUCTION

Understanding the relative importance of factors driving biodiversity patterns is among the key research topics in ecology and biogeography. Traditionally, variation in community composition has been studied based on species identities (Ricklefs, 1987; Leibold et al., 2004), which are blind to functional and phylogenetic differences among species. Thus, to improve our understanding of the relative contribution of factors shaping biodiversity patterns, community ecologists have recently recognized the need to analyze ecological communities in the light of multiple facets, including not only species-level information, but also functional and phylogenetic approaches (Cavender-Bares et al., 2009; Devictor et al., 2010; Gianuca et al., 2016; Heino & Tolonen, 2017). Based on the relationships among species, traits and evolutionary history, integrating measures of different facets of biodiversity provide valuable additional information of the determinants of community composition (Cavender-Bares et al., 2009; Devictor et al., 2010).

The use of functional traits in ecology and biogeography has greatly expanded over the last decades, and it has proved to be a useful approach in examining biodiversity patterns and the importance of underlying environmental factors (Meynard et al., 2011; Heino & Tolonen, 2017). Species traits may help to understand how environmental conditions filter species from the regional species pool and how species compete for resources, potentially linking ecological processes to biodiversity patterns (e.g. McGill et al., 2006). Also, because the effects of environmental variation on species compositions are mediated by traits (e.g. body size, feeding habits, habitat use), differentiating the influences of local environmental conditions, landscape features and climatic factors on traits can improve our understanding on mechanisms structuring ecological communities (McGill et al., 2006; Verberk et al., 2013).

Ecologists and biogeographers have also become interested in integrating phylogenetic information into biodiversity studies. Phylogenies play an important role in community ecology by relating ecological patterns to evolutionary processes underlying diversification and trait variation (Webb et al., 2002; Cavender-Bares et al., 2006). Assuming a strong phylogenetic signal, closely-related species tend to resemble each other in their traits more than distantly-related species; thus, they are expected to co-occur more often in the same community, reflecting their shared environmental tolerances, morphology and behavioral characteristics (e.g. Webb et al., 2002). In contrast, competitive interactions are expected to limit coexistence, selecting less related and functionally less similar species to co-occur in local communities (e.g. Gerhold et al., 2015).

Beta diversity can be measured based on species, functional, and phylogenetic data (Cardoso et al., 2014). In addition, studies have recently shown that partitioning beta diversity into species replacement and species richness-difference components (Podani & Schmera, 2011) can provide additional insights into the mechanisms that shape biodiversity patterns across large spatial scales (Baiser et al., 2012; Carvalho et al., 2012). The replacement component accounts for changes in species composition, whereas the richness-difference component derives from the loss or gain of species along environmental gradients (Carvalho et al., 2012). Here, we focus on an extension of this approach, where we can use abundance data instead of presence-absence data (Cardoso et al., 2015). Moreover, functional and phylogenetic beta diversity metrics can also be partitioned into the replacement and abundance-difference components (e.g. Cardoso et al., 2014), allowing one to make comparisons of all facets of beta diversity (i.e. species-, trait- and phylogeny-based beta diversity) and providing different information about biodiversity patterns along spatial and environmental gradients.

Stream biodiversity patterns are structured by factors prevailing at multiple spatial scales (Townsend et al., 2003; Johnson et al. 2004; Heino et al., 2007), but surprisingly few studies have concurrently studied the importance of local environmental, catchment and climatic factors in shaping biodiversity patterns (Sandin & Johnson, 2004; Jyrkänkallio-Mikkola et al., 2017). To the best of our knowledge, no study has focused on biodiversity patterns considering species, traits and phylogenetic facets in this multi-scale environmental context. Previous studies have shown that stream biodiversity patterns were related to local-scale variables, such as current velocity, water chemistry, substratum, and more (Sandin 2003; Heino et al., 2007). Also, various catchment properties (e.g. land cover, slope, and area) have been shown to be correlated with the biodiversity patterns of stream macroinvertebrates (Townsend et al., 2003; Allan, 2004; Johnson et al. 2004), and catchment features have been demonstrated to be as important or even more important than local stream characteristics (Corkum, 1989; Richards et al., 1996; Lammert & Allan 1999). In addition, climate may have a strong influence on stream biodiversity (e.g. Pajunen et al., 2016), and can even exceed the importance of catchment characteristics (e.g. Kampichler et al., 2012). However, these previous studies did not consider all three facets of beta diversity

In this study, we used a large-scale dataset on benthic macroinvertebrates aiming to disentangle the effects of environmental variables measured at multiple levels on species-, traits-, and phylogeny-based beta diversity. We examined the relative roles of environmental variables at local (including physical-chemical environmental variables), at the catchment (comprising land cover and land use characteristics) and at regional-levels (comprising climate variables). We also accounted for spatial structure in the species-, traits- and phylogeny-based beta diversity while analyzing variation related to local, catchment and climate variables. Traditionally, local environmental factors have been considered as a key to understand variation in stream macroinvertebrates communities (Sandin 2003, Mykrä et al., 2007, Heino et al., 2007). However, because of the growing body of evidence on the role catchment and climate variables contributing to variation in stream macroinvertebrates communities (Sandin & Johnson, 2004; Heino et al., 2007; Mustonen et al., 2018), we also expected that these large-scale variables would correlate to different facets of beta diversity.

2 | MATERIALS AND METHODS

2.1 | Study area and biological sampling

This study was based on a dataset collected from 105 stream sites located in western Finland, reaching a spatial extent of 520 km in the north-south and 330 km in the east-west direction (Figure 1). These streams belonged to 21 major river basins draining into the Baltic Sea, mainly into the Gulf of Bothnia, and covered a wide variation in land use, ranging from almost pristine to agricultural landscapes (Jyrkänkallio-Mikkola et al., 2017). These streams are located within three climatic-vegetation zones (i.e. hemiboreal, south boreal and middle boreal) in Finland (Ahti et al., 1968, Tapio & Heikkilä 2010). Hemiboreal vegetation zone is located in the southern and southwestern coastal areas in Finland. The forests there are mainly mixed, but deciduous forests more typical of central Europe also occur. Elevation varies from sea level to 150 m above sea level (a.s.l.). South boreal vegetation zone covers mostly southern and southeastern Finland. This zone is featured by mixed and coniferous forests, although pure deciduous woodlands often occur near water bodies. Elevation ranges from 80 to 360 m (a.s.l.). Middle boreal vegetation zone covers the central parts of Finland. Vegetation is mainly a mixture of coniferous forests and peatlands. Elevation ranges from sea level to 230 m (a.s.l.) (Heino et al. 2002).

Macroinvertebrate samples were taken in each of the 105 sites surveyed in this study. Our biological, physical and chemical data were measured over the span of a few weeks at all sites in September 2014. Sampling consisted of a 2-min kick-net sampling, which incorporated four 30-s one-meter subsamples that covered most of the gradients of depth, moss cover, particle size and current velocity found within ca. 50 m^2. In the field, these four subsamples were pooled into a composite sample for each stream and preserved in 70% alcohol. This type of sampling provides the best possible coverage of species occurring at a stream site, bearing in mind cost-effective sampling and sample processing time (Mykrä et al., 2004). Most macroinvertebrates were identified to the species level (c. 88 %), but early larval stages were identified to genus level (c. 12 %), resulting in a list of 133 taxa. The taxonomic data at site-level will be published under the public repository PANGAEA (https://www.pangaea.de/).

2.2 | Macroinvertebrate trait and taxonomic information

Functional feeding groups (FFGs), habit trait groups (HTGs) and body mass measures (BM) were used as macroinvertebrates trait information, following previous studies in northern streams (Tolonen et al. 2016, 2017). Macroinvertebrates were assigned into FFGs according to Moog (2002), Merritt & Cummins (1996), and Tachet et al., (2010) based on the mode of feeding (filterers, gatherers, shredders, scrapers, piercers, and predators). In addition, macroinvertebrates were assigned into HTGs using information from Merritt & Cummins (1996), Merritt et al. (2008), and Tachet et al. (2010) providing details about mobility and microhabitat use (burrowers, climbers, crawlers, sprawlers, semi-sessile and swimmers-divers). The BM measurements were based on the length-weight relationships calculated as potential maximum size (as dry mass, mg) of the aquatic stages of species. This information was obtained from the literature (Supporting Information Table S1). Although information for some other macroinvertebrate traits are available, we focused on these 13 traits because they are fundamental characteristics of these freshwater organisms (Merritt & Cummins, 1996; Tolonen et al., 2003), which affect how they use the habitat (i.e. locomotion–substrate relation), their food and feeding behavior (i.e. feeding habits), and their life histories and vulnerability to fish predators (i.e. body mass).

In the absence of true phylogenetic information for all the macroinvertebrate species, we used taxonomic distance based on the path lengths in the Linnean taxonomic trees as a proxy for phylogeny (Clarke & Warwick, 1998; Winter et al., 2013). Six taxonomic levels (i.e., species, genus, family, order, class, and phylum) were included in this taxonomic tree. Species taxonomic levels were verified against the Fauna Europaea online database (http://www.fauna-eu.org) (Supporting Information Table S2).

2.3 | Local environmental variables

Local variables comprised chemical and physical habitat variables measured immediately after taking the biological samples. Water samples were taken a few meters upstream from the macroinvertebrate sampling sites and further analyzed in the laboratory for total phosphorus, total nitrogen and water color following standard methods (EN1189 1996; EN ISO11905-1 1998; EN ISO7997, respectively). In a riffle site, 30 random spots were selected to obtain measures of current velocity (m/s) and depth (cm) using a Schiltknecht MiniAir 2 flow meter (Schiltknecht, Gossau, Switzerland) and a yardstick, respectively. Conductivity (µS/cm) and pH were measured using an YSI-Professional Plus field meter (YSI Incorporated, Yellow Springs, USA), and stream width, from 10 locations covering the stream site, was taken using a tape. Substrate particle size and moss cover were visually estimated from 10 locations using a 50 × 50 cm quadrat randomly placed in each stream site (e.g. Mykrä et al., 2007). The classification of particle size was assessed using a modified Wentworth scale (Wentworth, 1922): sand (0.25-2 mm), gravel (2-19 mm), pebble (16-64 mm), cobble (64-256 mm) and boulder (256-1024 mm). Substratum diversity was calculated using Shannon diversity index (Shannon, 1948). Shading (%) was visually estimated at 20 different locations along both sides of the river banks (Supporting Information Table S3).

2.4. | Catchment variables

We calculated catchment variables by first delineating the upstream catchment of each sampling site based on GTOPO 30 digital elevation model (www.worldcliml.org) in GRASS-GIS (“*r.stream.watersheds*” add-on, Domisch et al., 2015, Neteler et al., 2012). We then used the “*r.stream.variables*” function to extract catchment-scale variables. For more details about the extraction of catchment-scale variables, see http://www.earthenv.org/streams. Land cover variables (Tuanmu & Jetz, 2014) consisted of eight variables of upstream tree percent coverage, and the evergreen needleleaf trees, broadleaf trees and other trees were summarized into one “forest” variable to reduce dimensionality in the data. The variable ‘Human Footprint’ was calculated based on Sanderson et al. (2002) and the data were accessed from Global Human Footprint (http://sedac.ciesin.columbia.edu). In summary, the following catchment variables were obtained: forest, cultivated and managed vegetation, regularly flooded vegetation, urban/built-up, ice cover, sparse vegetation, open water (all in %), and human footprint. Topographic catchment variables comprised elevation (m), slope (° * 100), and flow accumulation (number of upstream cells). Stream slope and elevation were measured as the average upstream slope (or elevation) in the catchment of each sampling point. We extracted these data for each sampling site using the R package *raster* (Hijmans & van Etten, 2014). See Supporting Information Table S8 for additional information on catchment variables.

2.5 | Climate variables

Climate variables were processed by the same procedure as described for the catchment variables. Long-term temperature and precipitation data were derived from the worldclim database and subsequently processed into 19 hydroclimatic variables following the bioclim framework (Hijmans et al., 2005), with the addition that the temperature and precipitation was aggregated across the catchment (see www.earthenv.org/streams and Domisch et al., 2015 for details). In addition, we obtained daily trends of snow-cover (2000-2015) from the Global

Snowpack dataset (Dietz et al., 2015). See Supporting Information (Table S5) for additional information on climate variables.

2.6 | Spatial variables

We used distance-based Moran's eigenvector maps (db-MEM) analysis to provide spatial variables for our constrained ordination models (Dray et al., 2006). These spatial variables are typically efficient in modelling spatial structures of community structure at multiple scales (Legendre & Legendre, 2012) covered by the geographical sampling area. Altogether, using this method we produced 25 spatial variables which had positive eigenvalues and displayed significant spatial autocorrelation. The first spatial vectors show broad-scale variation and subsequent spatial vectors show smaller scale variation (Borcard & Legendre, 2002). The db-MEM spatial variables were obtained using the function 'PCNM' in the R package PCNM (Legendre et al., 2012).

2.7 | Statistical analyses

We analyzed variation in three facets of beta diversity (i.e. species, traits and phylogeny) using distance-based redundancy analysis (db-RDA, Legendre & Anderson, 1999) and associated variation partitioning procedures (Legendre et al., 2005). Before running the analyses described below we checked the sets of predictor variables used in the models (i.e. local, catchment, and climate) for multicollinearity utilizing Variance Inflation Factors (VIF). If variables showed VIF < 10, they were retained in the sets of predictor variables used in the statistical analyses (Oksanen et al., 2017). All analyses were based on abundance data and were conducted in the R environment (R Core Team, 2017). In the following, we will detail the three phases of the analyses conducted (see also Figures S1, S2, and S3 in Supporting Information).

Firstly, we generated three dissimilarity matrices: species beta diversity (B-total), replacement (B-repl), and abundance difference (Ab-Diff)) based on macroinvertebrate species abundance using the function “beta” in the package *BAT* (Cardoso et al., 2015). Subsequently, each of these three pairwise matrices was used in distance-based redundancy analysis (db-RDA) and variation partitioning. Before running these analyses, we selected the final sets of local environmental variables (LE), catchment variables (CA), climatic variables (CC), and spatial variables (SP) using the function “ordistep” (1000 permutations) in the R package *vegan* (Oksanen et al., 2017). We used only those variables which did not show strong collinearity. Variation partitioning was used to assess beta diversity components-environment relationships in detail through the pure and shared effects of LE, CA, CC and SP (Legendre & Anderson 1999). Distance based redundancy analysis (db-RDA) was run using the function “capscale” in the R package *vegan* (Oksanen et al., 2017). Finally, we also tested for the significance of the pure fractions using the function “anova” in the R package *vegan*. Results from variation partitioning were represented by Venn diagrams, which is a standard way to show the fractions explained uniquely by our sets of predictor variables (LE, CA, CC and SP) as well as by their intersections (see Legendre 2008). In all db-RDA analyses, the “sqrt.dist” correction for negative eigenvalues was added in the R script (Legendre, 2014).

Secondly, three dissimilarity matrices were produced as described above utilizing this time macroinvertebrate trait data (i.e. total functional beta diversity (fun.B-total), replacement (fun.B-repl), and abundance difference (fun.Ab-Diff)). Before acquiring these matrices, we used the Gower distance (Gower 1971) to calculate between-species distances based on the trait data using the function “gowdis” in the R package FD (Laliberté et al., 2014). Gower distance was used because it can handle different types of variables. Subsequently, this species-by-species matrix was subjected to a hierarchical clustering (UPGMA agglomeration method) procedure using the function “hclust” from the package *stats*. Clustering was needed because the *BAT* package requires a “hclust” object to calculate beta diversity metrics. Using the same steps as used for species-based beta diversity, we used the functions “ordirstep” and “capscale” in the R package *vegan* (Oksanen et al., 2017) for the variable selection, proceeded with distance-based redundancy analysis (db-RDA), and partitioning the variation in the three dissimilarity matrices (i.e. fun.B-total, fun.B-repl, and fun.Ab-Diff) using local environmental LE, CA, CC, and SP as predictors.

Thirdly, three dissimilarity matrices were produced as described above but utilizing this time macroinvertebrate taxonomic information as a proxy for phylogeny [i.e. total phylogenetic beta diversity (phylo.B-total), replacement (phylo.B-repl), and abundance difference (phylo.Ab-Diff)]. Before this step, we used the function “taxa2dist” from the R package *vegan* to calculate taxonomic distance between species (Oksanen et al., 2017). Further, this species-by-species matrix was subjected to a hierarchical clustering procedure (UPGMA agglomeration method) using the function “hclust” from the package *stats*. The calculation of taxonomic distances and the clustering procedure were applied to produce our phylogenetic tree for these species (as required by *BAT*). The steps for this third phase were based on the same procedure as used for species and trait-based beta diversity and included: variable selection, db-RDA, and partitioning variation for the three matrices (i.e. phylo.B-total, phylo.B-repl, phylo.Ab-Diff) using LE, CA, CC, and SP as predictor variables.

Finally, average species-, trait- and phylogeny-based beta diversity indices were calculated using the function “beta.multi” in the R package *BAT* (Cardoso et al., 2015).

3 | RESULTS

We found 133 macroinvertebrate taxa exhibiting a wide variation in functional traits and taxonomic relationships (see Supporting Information for details on species, traits, and taxonomic information, Tables S1 and S2). Species-based beta diversity (0.83) was driven by a slight difference between B-repl and Ab-Diff components (0.40 and 0.42, respectively), whereas trait-based beta diversity (0.22) was driven by Ab-Diff (0.12) and phylogeny-based beta diversity (0.48) mainly by B-repl (0.30) (for beta diversity indices, see Table S3 in Supporting Information).

Different sets of variables were selected in the db-RDA models for each component of beta diversity (i.e. B-total, B-repl, Ab-Diff), including variables at different scales (i.e. local, catchment, climate and spatial variables). Among local environment factors, the selected variables mostly denoted variation in water chemistry (e.g. pH, color and nutrient concentrations) and substratum diversity. At the catchment level, variation in forest cover, cultivated/managed areas and stream slope were typically included in the set of significant variables. Among climatic variables, those related to variation in temperature and snow cover were typically included in the models. Spatial variables accounting for spatial structure in species-, trait- and phylogeny-based beta diversity were usually the first 10 variables generated by the db-MEM, thus denoting relatively broad-scale spatial variation (Dray et al., 2012). For a detailed view of variable selection and adjusted R^2 values in the forward selection, see Supporting Information Tables S4, S5, and S6.

Local environmental, catchment and climate variables showed considerable variation across the study area (Supporting Information Tables S7, S8 and S9). Local environmental and spatial variables accounted for the largest fractions of variation explained in all facets (i.e. species, traits and phylogeny) of beta diversity and their components (Figure 2). Variation partitioning analyses demonstrated that unique and shared contributions of predictor variables differed slightly. In general, the unique contributions of local environmental factors (ranging from 4 to 7%) were slightly more important than or as important as the contributions of spatial variables (ranging from 3 to 8%) in explaining variation in the facets of beta diversity and their components (Figure 2). Although usually less important than local environmental and spatial variables, climate variables also accounted for statistically significant fractions of variation in B-total and Ab-diff components of all facets. Catchment variables explained minor, but statistically significant fractions of variation in two cases of Ab-diff component. For all models, the fractions representing shared effects were generally small, except for the shared fraction representing all predictors simultaneously for fun.B-repl and phylo.B-repl cases, explaining 8 and 6% of variation, respectively (Figure 2E and 2F). For species-based beta diversity, the total variation explained by the models that included all predictors (i.e. local environmental, catchment, climate and spatial variables) was 17% for B-total, 21% for B-repl, and 20% for Ab-Diff component

(Figure 2 A, D, H, respectively). In contrast, for trait-based beta diversity, the total variation explained including all predictors was 19% for fun.B-total, 33% for fun.B-repl, and 20% for fun.Ab-Diff component (Figure 2 B, F, I, respectively). Models including all predictor variables explained 19%, 29% and 21% of variation in phylo.B-total, phylo.B-repl and phylo.Ab-Diff, respectively.

4 | DISCUSSION

Biodiversity patterns in stream ecosystems are known to be affected by factors ranging from local to regional (Poff ,1997; Heino et al., 2007; Mykrä et al., 2007), and the importance of these factors may depend on the spatial extent of a study area (e.g. Heino, 2011) and the biodiversity facet considered (e.g. Heino et al., 2007). Here, our aim was to disentangle the influence of environmental variables measured at multiple levels on variation in macroinvertebrate beta diversity facets (i.e. species, traits and phylogeny) in boreal streams. We found that the influence of environmental variables on each beta diversity component separately (i.e. B-total, B-repl, Ab-Diff) and on each facet revealed relatively similar patterns. One of our main findings was that local and spatial variables generally contributed most to the total explained variability in all facets of beta diversity and their components, whereas catchment and climate variables were less important in explaining variation in beta diversity at the spatial extent of our study. This is a surprising result because a growing body of evidence suggests that correlates of biodiversity patterns require the consideration of factors and mechanisms operating at multiple spatial (and temporal) scales(Mittelbach, 2012; Soininen et al., 2015).

The similar results found for the different beta diversity facets could be due to the spatial extent of our study, influencing the relative roles of environmental and spatial variables for beta diversity (Heino & Tolonen, 2017). In general, species-based beta diversity should be strongly affected by local and regional processes (e.g. dispersal, drift), whereas trait- and phylogeny-based beta diversity should be mostly shaped by local-scale characteristics because they portray the interactions with the organisms and their environments (Poff 1997; Verberk et al., 2013, Soininen et al., 2016). Local environmental factors in our study area reflected strong gradients in water chemistry (e.g. nutrients, pH and color) and physical habitat characteristics (e.g. moss cover and substratum diversity). Broadly, the same local-scale variables were influential in accounting for variation in different beta diversity facets, and these variables have been found to be important in structuring macroinvertebrates community in previous species-based studies (Heino et al., 2003; Sandin 2003; Mykrä et al., 2007).

Our data encompassed a relatively broad spatial extent, yet local environmental conditions were more important than large-scale environmental factors in structuring macroinvertebrate beta diversity facets. Hence, environmental filtering seems to be the determining process shaping not only species compositions, but also trait pools and phylogenetic structure at different scales. Thus, changes in species identities, traits and evolutionary histories of species should exhibit similar patterns along major environmental gradients (e.g. Weinstein et al., 2014). In other words, species occurring locally are derived from regional species pools with similar evolutionary histories and combinations of traits (Webb et al., 2002; Devictor et al., 2010).

At relatively broad spatial scales, as in this study, species may also be affected by dispersal dynamics (Leibold et al., 2004). Our results showed that spatial variables were generally influential in explaining variation in all facets of beta diversity and their components. According to previous studies, spatial factors, possibly related to dispersal limitation, play an important role in determining macroinvertebrates community patterns across broad spatial scales (Sandin, 2003; Mykrä et al., 2007). Thus, considering the spatial extent of our study area, dispersal limitation may also drive the variation in macroinvertebrate beta diversity facets to some extent. However, environmental variables are often spatially structured, and species distributions reflect this structure through induced spatial dependence (e.g. Tuomisto et al., 2003). This can be an alternative explanation for the relationships between beta diversity facets and spatial variables (e.g. Dray et al., 2012). This scenario is unlikely, however, as we used a large number of influential ecological variables influencing stream macroinvertebrate community composition in boreal streams (Sandin, 2003; Heino et al., 2007; Mykrä et al., 2007). We hence believe that the spatial signals in beta diversity facets are more likely to be related with dispersal limitation in our study area.

Biodiversity patterns depend strongly on scale (e.g. Lennon et al., 2001). The relationships among different facets of beta diversity and among their respective components (i.e. B-total, B-repl, Ab-Diff) are thus also likely to be scale dependent. However, very little is known about the relative importance of ecological variables influencing beta diversity facets and their components, as partitioning facets of beta diversity appeared only recently (Podani & Schmera, 2011; Carvalho et al., 2014). To date, most of the studies have focused on species-based beta diversity patterns (Carvalho et al., 2012; Dobrovolski et al., 2012; Tonial et al., 2012), while few studies have focused on a multi-faceted beta diversity approach and their respective components in aquatic macroinvertebrates (but see Heino & Tolonen 2017). Our study emphasized the relative importance of local environmental conditions, followed by spatial variables, in explaining variation in all facets of beta diversity and their components (Figure 2). The finding that local-scale variables (i.e. chemical and physical variables) were important descriptors of variation in different facets of beta diversity showed the strong linkage between local habitat features and changes in benthic macroinvertebrate communities, agreeing with a number of previous species-based studies (Johnson et al., 2004; Sandin & Johnson, 2004). Apart from local chemical and physical factors, substratum diversity was among the most important local environmental variables driving variation in all facets of beta diversity. Substrate diversity may affect macroinvertebrate community composition by allowing more species to coexist locally (e.g. Milesi et al., 2016), and it has indeed been found to be a key structuring factor in macroinvertebrate communities (Boyero, 2003; Brown, 2003).

Catchment-scale variables may affect macroinvertebrate community composition, both directly and indirectly. This typically happens through anthropogenic land-use altering hydrological regimes and modifying stream physical habitat, and through changes in nutrient concentrations (e.g. Poff, 1997). Even though catchment variables were not strong correlates of the different facets of beta diversity in our study, we should not ignore them because of their well-known effects on local stream environmental features (Corkum, 1992; Allan & Castillo, 2007). However, our results, along with others (Hawkins et al., 2000; Johnson et al., 2004; Sandin & Johnson, 2004), suggest that local environmental variables were better correlates of community structure than catchment-scale variables. For instance, one of the most important local environmental variables driving variation in different facets of macroinvertebrate beta diversity in our study were pH, conductivity, and stream physical habitat, which have previously been shown to be affected by catchment features (e.g. Corkum, 1992). In addition, climate variables may also indirectly influence local stream variables via precipitation and changes in temperature affecting in-stream water chemistry and hydrology (e.g. Pajunen et al., 2016). We suggest that the climatic variables might have been better predictors of beta diversity patterns if larger spatial extents, such as continents, had been taken in consideration.

In summary, we found that local and spatial variables were important drivers of all facets of macroinvertebrate beta diversity, whereas catchment and climate variables were less effective in explaining variation in macroinvertebrate beta diversity patterns. Analyzing different facets of beta diversity offer interesting and emergent perspectives that cannot be highlighted if only one aspect of biodiversity is considered (Devictor et al., 2010; Cai et al., 2018). For example, the details of community-environment relationships (e.g. different predictor variables) may differ among the different beta diversity facets. To complement traditional strategies focusing on species-based biodiversity only, we suggest that a multi-facetted approach could help to improve the conservation of biodiversity through generating better understanding of current patterns and environmental determinants of biodiversity.

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Biosketch

Mariana P. Rocha is interested in macro-scale patterns of aquatic organisms and their different facets, emphasizing ecological factors controlling biodiversity patterns. This paper is part of M.P.R thesis and a larger project focused on scaling biodiversity in tropical and boreal streams led by Jani Heino, Janne Soininen and Tadeu Siqueira.

Author contributions: M.P.R., J.Heino, and L.M.B. devised the study design, data analyses, and led the manuscript writing; S.D. extracted the catchment and climate variables, and commented on the manuscript; K.T.T. contributed to macroinvertebrates identification, and gathering macroinvertebrate trait data; J.J.M. provided the map of study area and comments on the manuscript. J.S and J.Hjort contributed comments to the manuscript.

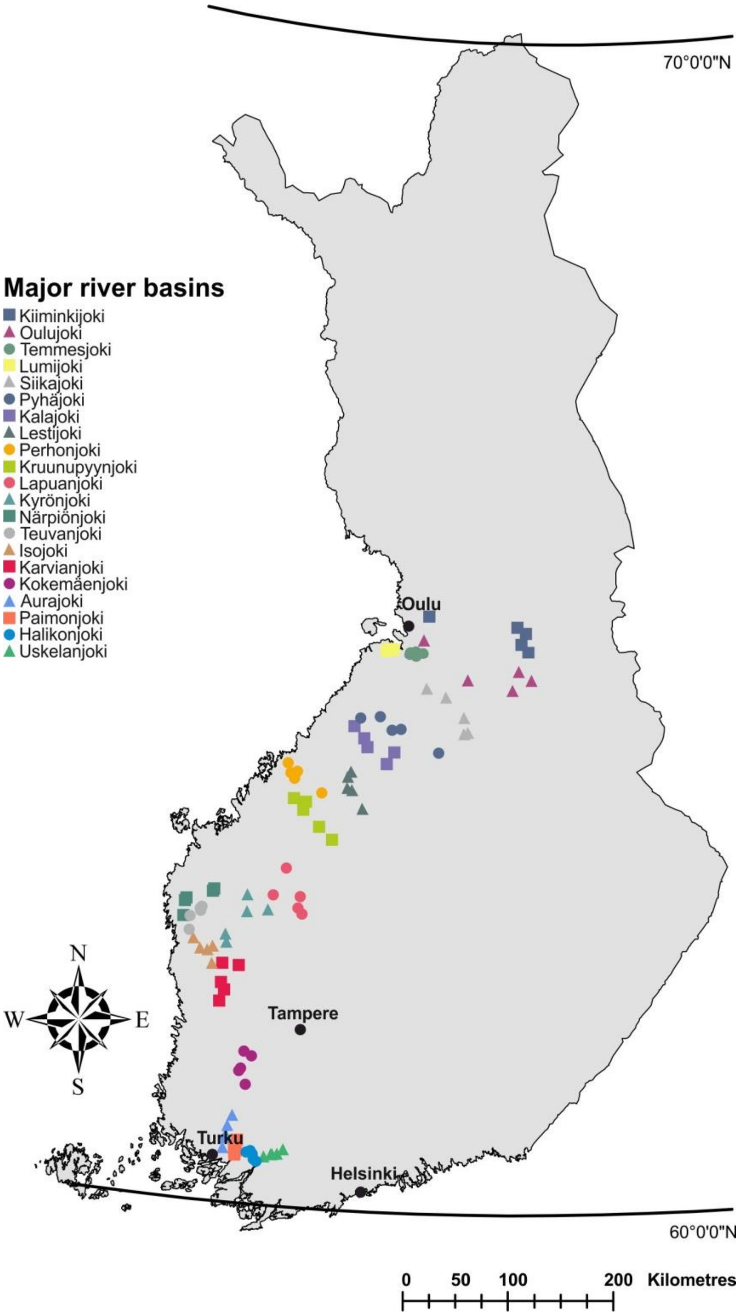

Figure 1 Map of the study area showing the locations of the 105 streams sampling sites belonging to 21 major river basins (different symbols and colors) in Finland.

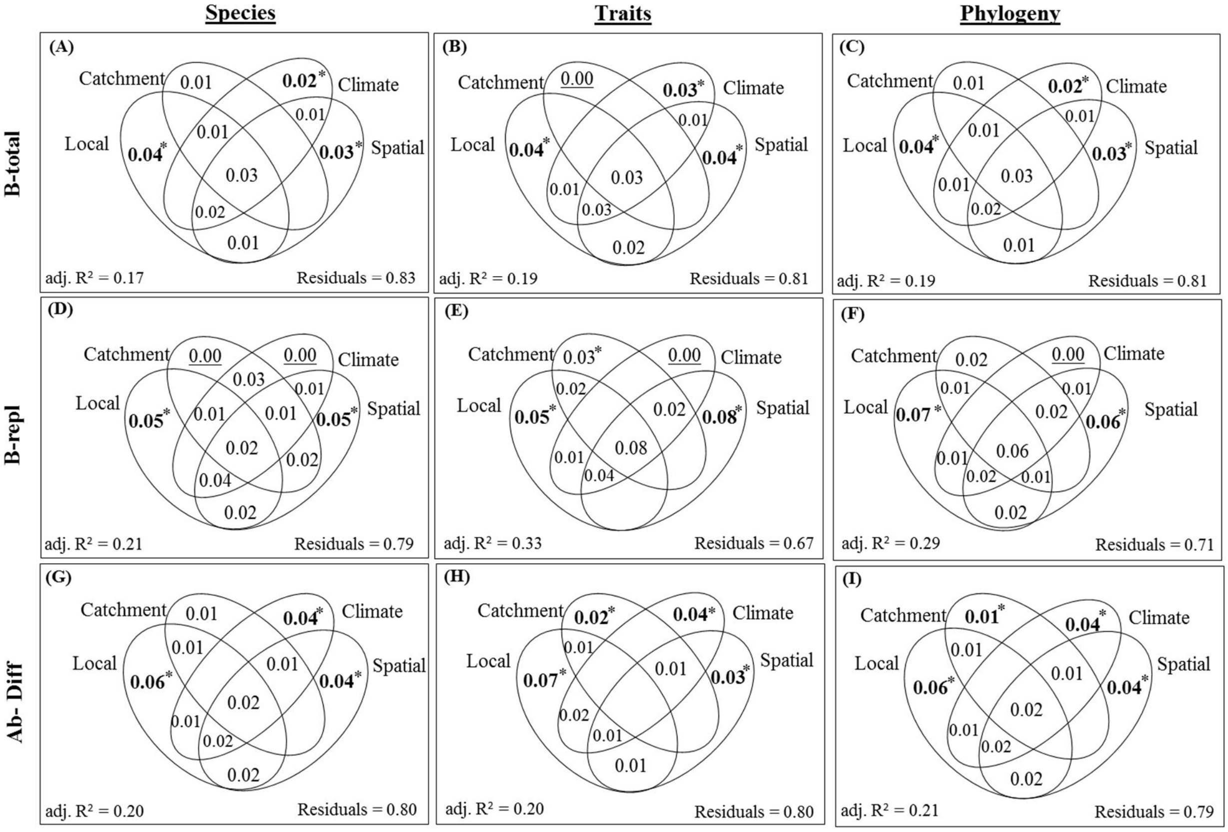

Figure 2 Variation partitioning-based Venn diagrams showing facets of beta diversity variation explained by unique and joint effects of local, catchment, climate and spatial variables. The explained variation is based on adjusted R^2 (**$* p < 0.05$**). Results indicated by 0.00 correspond to negative fractions. According to Legendre (2008), negative values should be interpreted as zeros and “they correspond to cases where the explanatory variables explain less variation than random normal variables would”. Abbreviations: Local = local environmental variables; Catchment = catchment variables; Climate = climate variables; Spatial = spatial variables (db-MEM); B-total =total beta diversity; B-repl =replacement; Ab-Diff = abundance-difference.