











Seasonal and spatial variation of stream macroinvertebrate taxonomic and functional diversity across three boreal regions

Nathan Jay Baker^{1,2}  | Ellen A. R. Welti^{1,3}  | Francesca Pilotto⁴  |
Jonas Jourdan⁵  | Burkhard Beudert⁶  | Kaisa-Leena Huttunen⁷  |
Timo Muotka⁷  | Riku Paavola⁸  | Emma Göthe⁹  | Peter Haase^{1,10} 

¹Department of River Ecology and Conservation, Senckenberg Research Institute and Natural History Museum Frankfurt, Gelnhausen, Germany

²Laboratory of Evolutionary Ecology of Hydrobionts, Nature Research Centre, Vilnius, Lithuania

³Conservation Ecology Center, Smithsonian Conservation Biology Institute, Front Royal, Virginia, USA

⁴Norwegian Institute for Nature Research, Oslo, Norway

⁵Department of Aquatic Ecotoxicology, Johann Wolfgang Goethe University Frankfurt am Main, Frankfurt am Main, Germany

⁶Department of Conservation and Research, Bavarian Forest National Park, Grafenau, Germany

⁷Department of Ecology and Genetics, University of Oulu, Oulu, Finland

⁸Oulanka Research Station, University of Oulu Infrastructure Platform, Kuusamo, Finland

⁹Water Unit, County Board of Dalarna, Falun, Sweden

¹⁰Department of River and Floodplain Ecology, University of Duisburg-Essen, Duisburg, Germany

Correspondence

Nathan Jay Baker, Department of River Ecology and Conservation, Senckenberg Research Institute and Natural History Museum Frankfurt, Clamecystrasse 12, 63571 Gelnhausen, Germany.
Email: nathan93baker@gmail.com

Funding information

Bernard and Ursula Plettner Foundation, Grant/Award Number: T0083/30772/2017/kg; eLTER PLUS project, Grant/Award Number: 871128; Rudolf and Helene Glasser Foundation

Editor: Christopher Hassall and
Associate Editor: Steve Yanoviak

Abstract

1. The exploration of biodiversity has predominantly been based on taxonomic measures, whereas functional diversity, a key component of biodiversity, is comparatively understudied. Therefore, studies simultaneously investigating patterns of taxonomic and functional diversity change in biological communities are of increasing interest.
2. We collated high-resolution macroinvertebrate and environmental data from 70 boreal headwater stream sites across three European countries (Germany, Finland, Sweden) to (1) investigate seasonal variation in taxonomic diversity, functional diversity, and redundancy, and (2) identify their potential drivers of spatial and seasonal variation.
3. Seasonal changes in boreal macroinvertebrate taxonomic diversity were decoupled from changes in functional diversity. Seasonal shifts in environmental conditions, including acidity and nutrient variability, drove fluctuations in taxonomic diversity which were far more pronounced than those of functional diversity.
4. Seasonal shifts in environmental conditions including variation in the quantity, quality, and state of organic carbon (dissolved vs particulate) facilitate an exchange of taxa, leading to taxonomically unique communities that exploit the pool of available

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2023 The Authors. *Insect Conservation and Diversity* published by John Wiley & Sons Ltd on behalf of Royal Entomological Society.

seasonal resources. Thus, similar levels of functional diversity across seasons—even as taxonomic diversity changes—suggest limited differences in interspecific changes in community function, potentially indicating functional resistance rooted in redundancy.

5. We highlight the spatial and seasonal discrepancies of freshwater communities, emphasising the need for both taxonomic and functional diversity patterns to be assessed in future biodiversity monitoring programmes.

KEYWORDS

biological traits, community ecology, environmental drivers, freshwater ecosystems, functional redundancy, inter-regional analysis, multivariate statistics, organic carbon

INTRODUCTION

Interacting environmental conditions filter species by their unique ecological requirements and tolerances, in turn shaping biological community composition in terms of both taxonomic and functional diversity. Here, taxonomic diversity describes the number and frequency of species within a given community, while functional diversity refers to the value and range of functional traits within said community (Tilman, 2001). Additionally, at the intersect between taxonomic and functional diversity, functional redundancy (hereafter ‘redundancy’) describes the degree to which species within a given community share similar traits (i.e., niche overlap) and may be linked to ecosystem resilience (Micheli & Halpern, 2005; Rosenfeld, 2002). While taxonomic diversity has historically been at the heart of ecological inquiry, it has limitations since it treats each species equally and is highly scale dependent (Borcard et al., 2018). Due to its use of traits (e.g., life cycle descriptors, physiological strategy, etc.), functional diversity aims to overcome these limitations and can be used to compare biodiversity patterns at different scales, for example via the use of null models (Múrria et al., 2020; Schmera et al., 2022). Consequently, the combined and complementary use of taxonomic and functional approaches has the potential to provide a more mechanistic understanding of the processes governing global biodiversity and holds weight for guiding policy and protection measures in the wake of global environmental change (Dolédec et al., 2021).

Global change poses a significant threat to freshwater ecosystems (Darwall et al., 2018; Dudgeon et al., 2006) which have suffered disproportionately from biodiversity loss (Strayer & Dudgeon, 2010). Changes in climate and nutrient availability have strong impacts on freshwater communities (Verberk et al., 2013). Shifting seasonal patterns and associated hydrological regimes, such as the increased frequency of extreme events (e.g., droughts, floods, extreme temperatures), exert pressure on freshwater communities both directly (e.g., hard freezes or desiccation) and indirectly (e.g., via altering resource availability; Dolédec et al., 2021). Nutrient availability can have highly variable effects on freshwater communities; major elements like carbon, nitrogen, and phosphorus are essential for life, but increases in their concentrations and ratios often only benefit a subset of species (Baker & Greenfield, 2019). In response to increased atmospheric carbon, allochthonous leaf litter

is becoming more recalcitrant (Tuchman et al., 2002; Welti et al., 2020), leading to changes in food web nutrient pathways and shifts in consumer feeding habits (Rooney et al., 2006; Sterner & Elser, 2002). Consequently, both natural and anthropogenic environmental stressors alter food web energy flow and ecosystem functioning.

Freshwater macroinvertebrate communities display seasonal turnover in community composition in response to food quantity and quality, climate, and stream type (Mouton et al., 2020, 2022; Smol et al., 2005). Boreal freshwaters experience particularly high seasonal variation in temperature and resource quality and quantity (Frainer et al., 2014). Accordingly, boreal freshwaters in forested regions (i.e., headwaters) are particularly dependent on allochthonous energy inputs (but see Brett et al., 2017), predominantly in the form of organic matter from runoff and seasonal leaf fall (da Silva et al., 2021), which are key factors responsible for shaping biological communities and food webs further down the stream continuum (Vannote et al., 1980; Woodward et al., 2010). By contrast, as global environmental change alters the seasonal variation of temperature regimes and allochthonous inputs (Woods et al., 2022), macroinvertebrate communities in headwaters, which are evolutionarily adapted to predictable seasonal conditions, are increasingly more at risk of alteration (Floury et al., 2018; Frainer et al., 2014; Tonkin et al., 2017).

Boreal freshwaters contain many rare, cold-adapted specialist taxa (Heino, 2005), making them sentinels for understanding the impacts of climate change and associated stressors (Bruno et al., 2019; Woodward et al., 2010). In Europe, boreal ecosystems are primarily confined to Finland, Sweden, and the Baltics. From a biogeographic standpoint, boreal ecosystems are restricted to northernly latitudes (~50°N to ~70°N), however, similar ecosystems are found sporadically at lower latitudes, particularly at higher altitudes (> ~500 m a.s.l.). The Bavarian Forest National Park in Germany is one such high-elevation region, characterised by high predictability and seasonality, and harbouring a high number of glacial relicts and specialised cold-adapted taxa. The Danube catchment, which drains the headwaters originating in the Bavarian Forest, is a hotspot for boreal and central and western European species (Tockner et al., 2009). Thus, the overlap between boreal and temperate species facilitates more diverse communities compared to Northern European boreal streams (Grigoropoulou et al., 2022).

Boreal freshwaters were particularly susceptible to nitrogen and sulphur induced acidification during industrialisation in the 20th century (Dangles et al., 2004). By contrast, more stringent environmental policy and cleaner industrial processes have curtailed atmospheric pollutants and freshwater ecosystems have begun to recover (Baker, Pilotto, Haubrock, et al., 2021a; Baker, Pilotto, Jourdan, et al., 2021b; van Looy et al., 2016). However, through acidification recovery and other processes (Kritzberg et al., 2020), boreal freshwaters have experienced some of the most extreme cases of brownification, whereby sustained increases (primarily) in dissolved organic carbon (DOC) and iron (Fe) have significantly darkened waters, limiting light penetration. Brownification processes affect thermal regimes, oxygen saturation, periphyton growth, and the predation efficacy of visual-reliant organisms (Arzel et al., 2020; Lehtovaara et al., 2014). Consequently, boreal ecosystems and their freshwaters continue to be vulnerable to climate change, which is more pronounced at northerly latitudes and higher altitudes (Antão et al., 2022; Høye et al., 2013; Mouton et al., 2022; Parmesan & Yohe, 2003).

Here, we examine macroinvertebrate communities from 70 sites in boreal headwater stream networks in three European countries. We use high-resolution macroinvertebrate and regionally coupled environmental data from three boreal regions located in Germany, Sweden, and Finland to (1) investigate how taxonomic diversity, functional diversity, and redundancy vary between seasons (spring and autumn) and (2) identify the potential drivers of variation in biodiversity within these regions. Given the strong interaction between regional and local richness (de Juan et al., 2013) as well as the unique yet complimentary information provided by different diversity components (Boyé et al., 2019; Chiantore et al., 2018), we explored taxonomic and functional diversity via their alpha (α ; local diversity), gamma (γ ; regional diversity), and beta (β ; compositional differences between α - and γ -diversity) decompositions. Although we tested for the effects of season and environmental drivers within these three boreal regions, we avoided direct comparisons of biodiversity between countries as sampling methods were not identical.

Given the fine-scale environmental heterogeneity (Heino, 2005) and predictably strong seasonal variation of boreal ecosystems (Frainer et al., 2014), we hypothesised that (H_1) taxonomic and functional diversity (via α - and β -diversity) as well as redundancy would show strong seasonal variations due to seasonal changes in abiotic conditions (e.g., temperature, hydrological regimes, physico-chemistry; Woods et al., 2022) and allochthonous inputs (Blarock et al., 2021). In addition to season, we expected taxonomic diversity, functional diversity, and redundancy to be driven by regional differences in geography, acidity, and nutrients and major ions (hereafter ‘nutrients’). First, through regional habitat conditions associated with higher altitudes—for example, faster flow, harsher floods, cooler temperatures, softer waters, increased oxygen concentrations (Southwood, 1977; Townsend & Hildrew, 1994)—we predicted that (H_{2a}) higher altitudes will be negatively correlated with taxonomic diversity and redundancy, but positively correlated with functional diversity, due to increased taxonomic specialisation (Clarke et al., 2008; Finn et al., 2011). Second, through the loss of acid-tolerant specialist taxa, we expected that (H_{2b}) higher

pH conditions would be associated with higher taxonomic diversity and redundancy but lower functional diversity (Baker, Pilotto, Haubrock, et al., 2021a; Baker, Pilotto, Jourdan, et al., 2021b; Masters et al., 2007). Last, given the reliance of boreal freshwaters on allochthonous energy inputs (Woodward et al., 2010), we anticipated that (H_{2c}) minor increases to instream nutrients (allo- and autochthonous energy resources) would be positively correlated with taxonomic diversity, functional diversity, and redundancy.

METHODS

Sampling sites

Sampling was conducted at 70 stream sites from near-natural headwater catchments in three densely forested areas: the Bavarian Forest National Park in southwestern Germany, the upper Krycklan River catchment in northern Sweden, and the Koutajoki catchment in north-east Finland (Figure 1).

The German Bavarian Forest National Park is a ~24,000 ha protected area with elevation ranging 650–1430 m a.s.l. and precipitation ranging 1200–1800 mm/year (Müller et al., 2009). Habitats include high montane forest (above 1150 m a.s.l.) dominated by Norway Spruce *Picea abies*, in addition to European Beech *Fagus sylvatica*, and Mountain Ash *Sorbus aucuparia*, and mixed montane forest (below 1150 m a.s.l.) of Norway Spruce, European Beech, and Silver Fir *Abies alba* (Walentowski et al., 2004). Sites are situated on the southwest section of the Bohemian Massif, composed of gneiss and granite, facilitating the formation of acidic soils (Müller et al., 2009).

The Swedish upper Krycklan River catchment ranges in elevation from 130 to 369 m a.s.l. and has an average of 600 mm/year precipitation, one third of which falls as snow (Löfvenius et al., 2003). The catchment is dominated by mixed coniferous forests—mostly Scots Pine *Pinus sylvestris* in the high, drier areas and Norway Spruce in the wetter, lower-lying areas—and patchy, interspersed *Sphagnum*-dominated wetlands (Buffam et al., 2007). Catchment geology is primarily solid gneiss bedrock, with moraine and iron-podsol soils (Göthe et al., 2013).

The Finnish Koutajoki catchment is mostly plateaued with elevations of 200–300 m a.s.l. and 520–550 mm/year precipitation, of which one third falls as snow (Malmqvist et al., 2009). The catchment is mostly forested with highly variable vegetation including old-growth forests of Norway Spruce and Scots Pine, mixed deciduous woodlands, and wetlands (Heino et al., 2009). The geology is highly variable, consisting of Proterozoic shists, nutrient-poor acidic rocks, and moraine (Malmqvist et al., 2009).

Data collection

At each of the 70 sampling sites, macroinvertebrate community composition (i.e., α - and β -diversity) and environmental conditions were determined in spring and autumn. In Sweden, sampling was conducted

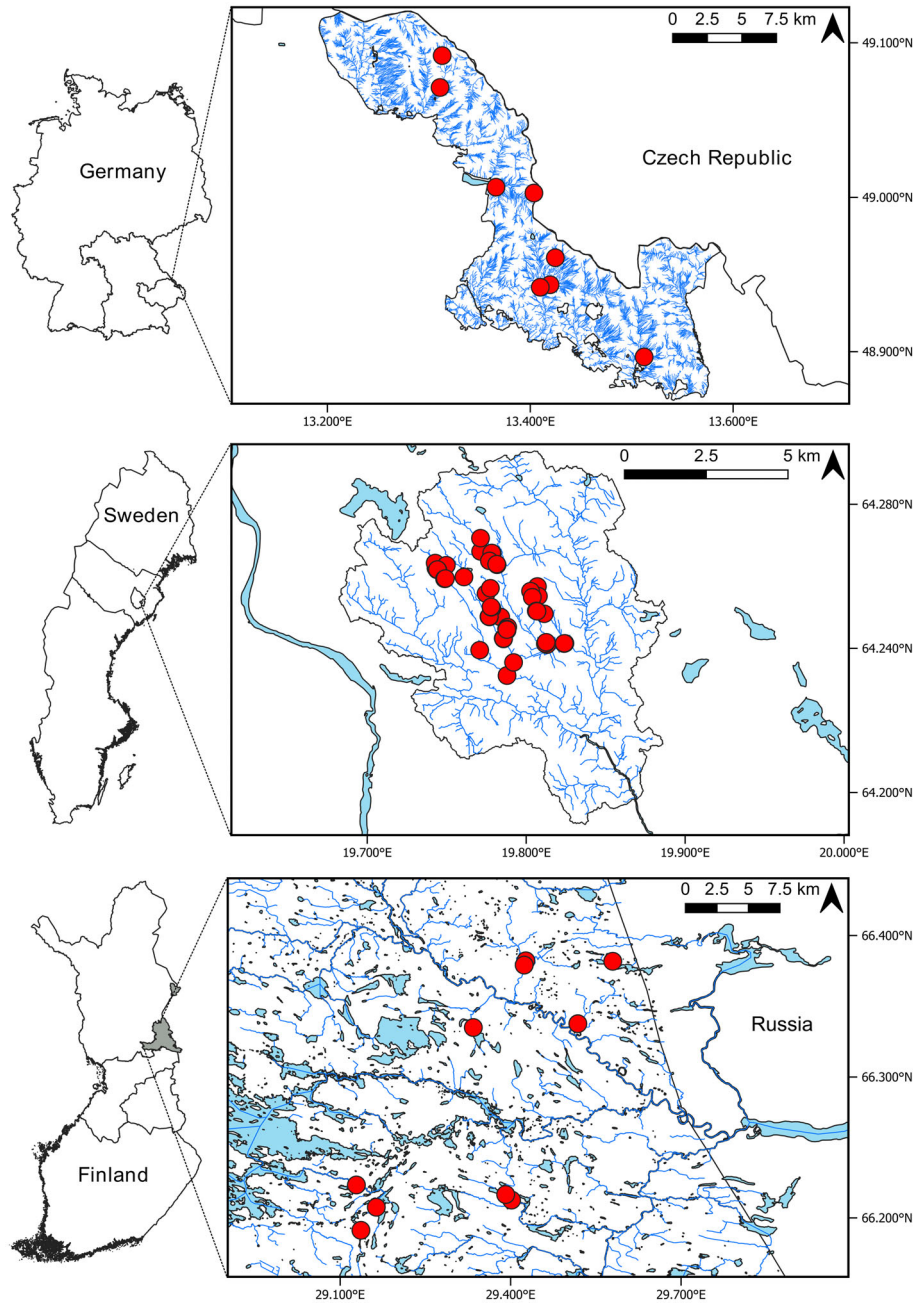


FIGURE 1 Map illustrating the sampling sites across the three study regions. Sampling sites are indicated by red dots (Germany $N = 8$; Sweden $N = 52$; Finland $N = 10$). The coordinate system used was WGS 84/Pseudo-Mercator (Datum: World Geodetic System 1984). For site-specific details, see Table 1.

in 2009; in Germany and Finland, sampling was conducted in 2016. Stream orders in each of the study regions ranged between one (upstream) and three (downstream). The availability of environmental data (i.e., explanatory variables) varied with region. To deal with these differences and reduce complexity, we generated four explanatory variable groups, namely: *season* (spring, autumn), *geography* (altitude, geographic coordinates), *acidity* (pH), and *nutrients* (region-specific nutrient and major ion concentrations). In addition to the summaries below, see Supplement 1 for details regarding regional macroinvertebrate sampling methods and Supplement 2

for descriptive statistics of region-specific environmental variables.

In Germany, macroinvertebrates were sampled at eight stream sites from five catchments within the Bavarian Forest National Park (Table 1) using standardised multi-habitat kick-net sampling (Haase et al., 2004) and taxonomic processing procedures (Haase et al., 2006). Macroinvertebrate sampling surveys were conducted in May (spring) and late August to early September (autumn). Stream-specific environmental data at the time of macroinvertebrate sampling were extracted from nearby gauging stations (on average 657 m away

TABLE 1 Site details.

Region	Drainage basin	Catchment/sub-catchment	Sites per catchment	Site identity
Germany	Danube	Forellenbach	1	1–8 (spring), 9–16 (autumn)
		Grosse Ohe	2	
		Kleine Regen	2	
		Kolbersbach	2	
		Sagwasser	1	
Sweden	Umeälven	Krycklan	52	17–68 (spring), 69–120 (autumn)
Finland	Koutajoki	Kitkajoki	3	121–130 (spring), 131–140 (autumn)
		Kuusinkijoki	2	
		Oulankajoki	4	
		Sovajoki	1	

Note: Site identities correspond to the labels used in all further analyses.

in stream distance) and included altitude (Alt), pH, dissolved organic carbon (DOC), sulphate (SO_4^{2-}), ammonium (NH_4^+), and nitrate (NO_3^-).

In Sweden, macroinvertebrate and environmental data were collected from 52 sites within the Krycklan River catchment (Table 1). These sites were part of a previous study of cross-scale distribution of feeding groups across seasons (Göthe et al., 2014). Macroinvertebrates were collected using a Surber sampler as per the multihabitat sampling methods described in Göthe et al. (2013). Sampling surveys were conducted in May (spring) and October (autumn). Included environmental data were: Alt, pH, total organic carbon (TOC), SO_4^{2-} , nitrate and nitrite as nitrogen (NO_3^- -N + NO_2^- -N), total nitrogen (Tot-N), and total phosphorus (Tot-P).

In Finland, macroinvertebrate and environmental data were collected from 10 sites within the Koutajoki catchment (Table 1). Macroinvertebrates were collected using a hand net and followed standardised multi-habitat sampling and processing procedures (Mykrä et al., 2006). Sampling surveys were conducted in early June (spring) and October (autumn). Included environmental data were: Alt, pH, DOC, Tot-N, and Tot-P.

Species and trait data

Regional macroinvertebrate datasets had high taxonomic resolution (mainly genus and species level). To ensure consistency with contemporary scientific nomenclature (Grenié et al., 2021, 2022), all taxon names were harmonised using the *Taxa Validation Tool* (www.freshwaterecology.info; Schmidt-Kloiber & Hering, 2015).

Functional trait data derived from Tachet et al. (2010) were extracted from the online database www.freshwaterecology.info (Schmidt-Kloiber & Hering, 2015). Eleven biological trait groups representing 62 trait modalities (sensu Schmera et al., 2015) were selected, namely: maximal body size (size1:7), life cycle duration (life1:2), potential number of cycles per year (cycl1:3), aquatic developmental stages (aqua1:4), reproductive technique (repr1:8), dispersal (disp1:4), resistance forms (resi1:5), respiration technique (resp1:4), substrate

relation and locomotion (loco1:8), type of food (food1:9), feeding habits (fhab1:8) (Tachet et al., 2010). For more details regarding trait abbreviations and coding, see Supplement 1. When species-level trait data were not available, species were unified to genus-level complexes; if necessary, taxa were rarely moved to the sub-family or tribe level. As a result, the number of taxa within each regional dataset were reduced: Germany—from 138 taxa to 62 taxa-complexes, Sweden—from 59 taxa to 26 taxa complexes, and Finland—from 91 taxa to 61 taxa-complexes. Despite these necessary taxonomic adjustments, abundances remained unchanged. All trait data were fuzzy coded following Chevenet et al. (1994).

Data analysis

All data analyses were conducted in the R statistical environment version 4.2.1 (R Core Team, 2022).

Community indices

To explore macroinvertebrate diversity across seasons (H_1), we computed 10 taxonomic and functional community indices (Table 2): total abundance (*Abun*), species richness (*TRic*), Shannon diversity (*Shan*), Shannon evenness (*TEve*), taxonomic turnover between seasons (*Tturn*), functional richness (*FRic*), functional evenness (*FEve*), functional dispersion (*FDis*), functional turnover between seasons (*Fturn*), and functional redundancy (*FRed*). Paired t-tests were used to test differences in the community indices within regions between seasons.

Taxonomic diversity indices (i.e., *TRic*, *TEve*, *Shan*) were calculated using the ‘vegan’ R package (Oksanen et al., 2020). Regional taxonomic turnover between seasons (*Tturn*) was measured via the *beta.div.comp* function in the ‘adespatial’ R package (Dray et al., 2021) using Podani-family decompositions of Sørensen’s dissimilarity matrices (i.e., percentage difference dissimilarity of quantitative data).

For the calculation of functional diversity indices, a supraregional functional space (FS) was created using a taxa-trait matrix covering

TABLE 2 Definitions of the included community indices and the rationale behind their inclusion.

Community index	Abbreviation	Definition	Rationale for inclusion
Total abundance	Abun	The summed total number of individuals across all taxa within a given community.	A classical component of community ecology. Provides more nuanced information compared to presence-absence data.
Taxonomic richness	TRic	'The number of taxonomically distinct species within a given community'. ^a	The simplest and most ubiquitously used component in community ecology.
Taxonomic evenness	TEve	'The distribution of abundances across all species within a given community'. ^a	A classical ecological measure used to identify whether a given community is dominated by a few species.
Shannon diversity	Shan	A measure of taxonomic diversity, considering both the number of species (richness) and relative abundances of each species (evenness) within a given community. In other words, a dispersion measure based on the relative abundance frequency of the species within a given community. ^b	A classical ecological dispersion measure which incorporates both richness and evenness components to provide a general overview of the diversity within a given community.
Taxonomic turnover	Tturn	The proportion of species gained or lost between two time points ^c in this case between spring and autumn.	A more sensitive measure of global change than classic ecological indices such as richness and abundance. ^d
Functional richness	FRic	'The ratio between the hypervolume filled by each community in the FS and that filled by all the taxa occurring in the FS'. ^e In other words, the amount of FS occupied by all the species within a given community relative to the supraregional FS. ^f	A functional diversity index complementary to taxonomic richness. Provides information on the size of a community's FS and how it changes through time and space. ^g
Functional evenness	FEve	'A measure of the regularity of taxa across the FS'. ^e In other words, the distribution of abundances across the FS (i.e., across the traits). ^h	A functional diversity index complementary to taxonomic evenness. Measures how common or 'abundant' certain traits are within the FS and provides an indication of FS symmetry. ^g
Functional dispersion	FDis	'The mean distance of each taxon to the mean community centroid within the FS'. ^e In other words, a measure of how spread or clumped the species are within the FS and weighted by relative abundance. ⁱ	A functional diversity dispersal index complementary to Shannon diversity. Assesses the differences between species based on their traits to determine how species are organised within the FS. ^g
Functional turnover	Fturn	The proportion of traits gained or lost between two time points, ^a in this case between spring and autumn. A measure of changes in functional strategies between seasons. ^j	A functional diversity index complementary to taxonomic turnover. Provides orthogonal information to taxonomic turnover as to the loss and/or gain of traits over time.
Functional redundancy	FRed	'The relative amount of taxonomically distinct species that exhibit similar functions'. ^{a,k}	A key metric for describing the relationship between taxonomic and functional diversity. ^l Provides an understanding of ecosystem resilience to perturbation. ^k

^aBaker, Pilotto, Haubrock, et al. (2021a).^bBorcard et al. (2018).^cHallett et al. (2016).^dPilotto et al. (2020).^eMúrria et al. (2020).^fMason et al. (2005).^gMammola et al. (2021).^hPakeman (2014).ⁱMouillot et al. (2014).^jVilléger et al. (2008).^kMicheli and Halpern (2005).^lSchmera et al. (2017).

the combined pool of macroinvertebrate taxa collected within the three regions in each season (hereafter the 'global pool'). The global pool included 93 taxa-complexes, with regional taxa-complex diversity

being 62 in Germany, 26 in Sweden, and 61 in Finland. For the suprar-regional taxa-trait matrix, a Gower dissimilarity matrix adapted for fuzzy-coded traits was generated and used to construct a principal

coordinate analysis (PCoA) via the *dudi.pco* function in the ‘ade4’ R package (Dray et al., 2022). For the supraregional FS, nine of the most explanatory axes were retained based on their capacity to represent the original taxa trait dissimilarity (Múrria et al., 2020). The 9-dimensional (D) supraregional FS explained 68.1% (mean squared deviation = 0.008) of the Gower dissimilarity matrix covering the global pool of taxa. Pearson correlation was used to assess which traits were most important in driving each axis of the supraregional FS ($r \geq 0.5$). Then, to determine the probability of occurrence of different trait combinations within the supraregional FS, we used the kernel density estimation method via the ‘ks’ R package (Duong et al., 2022). The kernel densities, computed for illustration purposes, were calculated based on the first two axes of the supraregional FS which explained 23.4% of the variance (R^2).

Using the convex hull method (Villéger et al., 2008), we estimated functional diversity in each region, site, and season via distance-based functional diversity indices. Using modifications of the functions within the ‘FD’ R package (Laliberté et al., 2014), we calculated FRic, FEve, and FDis per Múrria et al. (2020). To facilitate comparability across sampling regions, the functional diversity indices for each site and season were computed from the same supraregional FS encompassing the global pool of taxa and traits (Múrria et al., 2020). Due to the computational errors derived from highly dimensional convex hulls, the number of dimensions was restricted to six following Mouillot et al. (2021). The selected functional diversity indices encompass the richness, regularity (evenness), and divergence dimensions of functional diversity (Mason et al., 2005; Mouchet et al., 2010; Pavoine & Bonsall, 2011) and describe various facets of a community’s niche through a multidimensional FS (Villéger et al., 2008). FRic, constrained between 0 and 1, represents the ratio between the convex hull filled by the taxa within a given community and the convex hull filled by all the taxa within the supraregional FS (Villéger et al., 2008). FEve represents the regularity of taxa across the FS and was estimated via the minimum spanning tree method (Villéger et al., 2008). FDis measures the mean distance between each taxon and the group mean centroid in the FS (Laliberté & Legendre, 2010). While FRic is unweighted (Villéger et al., 2008), FEve and FDis were weighted by the abundances of taxa within the FS.

Additionally, we calculated trait community-weighted means (CWMs) as a measure of functional community composition (Borcard et al., 2018) via the *dbFD* function in the ‘FD’ R package. Following Baker, Pilotto, Haubrock, et al. (2021a) and using the *beta.div.comp* function (Dray et al., 2021), CWMs were used to measure functional turnover between seasons (Fturn); Podani-family decompositions of Sørensen’s dissimilarity of quantitative CWM data were used as the input matrix. Thereafter, we calculated community-level functional redundancy (FRed) using the *uniqueness* function in the ‘adiv’ R package (Pavoine, 2020); Euclidian distances bound between 0 and 1 were used as the input distance matrix.

To assess whether the observed patterns of functional diversity provide orthogonal information to taxonomic diversity, rather than an analogue measure of taxonomic richness (i.e., functional diversity being highly correlated to taxonomic richness; Gotelli & Graves, 1996),

functional diversity indices (FRic, FEve, FDis) were compared to expected values using null models. The null models for the FDis index were constructed using the name-shuffling approach, whereby taxon names (from the site-by-taxa matrix) were randomly assigned to the trait combinations of the original taxa-trait matrix (Swenson, 2014). By contrast, for the null models of the FEve and FRic indices, we held constant the size of the supraregional FS (i.e., the PCoA), and instead randomly shuffled the position of the taxa within the FS (i.e., the coordinates of each taxon within the FS). Null distributions were created via 999 iterations of the shuffling procedures. The global taxa and trait pool was used to calculate a standardised effect size (S.E.S.) of each functional diversity index. S.E.S. at a site (i) is calculated as:

$$\text{S.E.S.} = (FDi_{obs} - \mu FDi_{null}) / \sigma FDi_{null}$$

where FDi_{obs} is the observed functional diversity index value, μFDi_{null} is the mean of the null functional diversity index distribution, and σFDi_{null} is the standard deviation null functional diversity index distribution.

Positive S.E.S. values indicate that the observed functional diversity is higher than expected given the taxonomic richness at a site; negative S.E.S. values indicate a lower-than-expected observed functional diversity. A two-tailed test was used to examine the position of the observed index values within the null distribution and test for significance. We report the observed (FRic, FEve, FDis) and standardised (FRic.SES, FEve.SES, FDis.SES) functional diversity indices, but comparisons between taxonomic and functional diversity are based on standardised functional diversity indices.

Drivers of taxonomic and functional diversity

To test the effects of environmental drivers on regional taxonomic and functional diversity ($H_{2a,b,c}$), we first conducted partial distance-based redundancy analyses (dbRDA) using the *capscale* function in the ‘vegan’ R package; dissimilarity data were ordinated using metric scaling and the ordination results were analysed through redundancy analyses (RDA; Legendre & Anderson, 1999). The inputted taxonomic and functional dissimilarity matrices were based on percentage difference dissimilarity (i.e., Bray-Curtis) with a Lingoes correction for negative eigenvalues. We accounted for spatial autocorrelation by including a conditioning factor which held constant the geographic distribution of the sites (geographic coordinates). For each region, we analysed taxonomic and functional composition separately.

First, we examined the influence of region-specific environmental conditions on taxonomic composition (i.e., taxonomic β -diversity). For each regional taxonomic dataset, we removed rare taxa (defined as abundance <2 individuals and prevalence at <5% of sites) and produced an abundance weighted (i.e., quantitative) percentage difference dissimilarity matrix. Prior to analyses, all highly collinear variables ($r > 0.7$) were removed. After initial analyses, included variables were again tested for multivariate collinearity using variance inflation factors (VIF) and variables with high (>10) VIF values were removed. To find the most parsimonious model, we forward selected predictor

variables using the *ordiR2step* function in the 'vegan' R package. Once model parsimony had been reached, we analysed the significance of the model, predictors, and canonical axes using ANOVA with 999 permutations (Supplement 3).

Second, we examined the influence of local environmental conditions on intra-regional functional composition (i.e., functional β -diversity) following Lindholm et al. (2020). For each regional functional trait dataset, we removed rare taxa, generated a functional dissimilarity matrix as described above, and then performed the same analyses as were conducted for taxonomic composition.

Then, to assess the relative importance of season (H_1), geography (altitude, geographic coordinates) (H_{2a}), acidity (pH) (H_{2b}), and nutrients (region-specific nutrients and major ion concentrations) (H_{2c}) in explaining the variation in taxonomic and functional α -diversity, we used multiple linear regression analyses (Legendre, 2008). Separate multiple linear regressions were conducted for abundance, each taxonomic index (TRic, TEve, Shan), and their corresponding standardised functional index (FRic.SES, FEve.SES, FDis.SES). We used the *varpart* function in the 'vegan' R package to decompose the total variance of the multiple linear regression among the predictor variable groups (i.e., fractions): (a) variation uniquely explained by season, (b) variation uniquely explained by geography, (c) variation uniquely explained by acidity, and (d) variation uniquely explained by nutrients (Legendre, 2008). As a measure of explained variance in each fraction, we used the adjusted variation (adj. R^2), an unbiased estimate (Heino et al., 2012). Following Legendre (2008), negative adjusted R^2 values were interpreted as zero as they occur in cases where the variable in question explains less variance than random. The significance of each variable group (i.e., fraction) was determined through ANOVA with 999 permutations. The results of each multiple linear regression are reported as the proportion of explained variance (adj. R^2) and significance (p-value) of each fraction for each region. If multiple linear regressions indicated significant drivers, driver directionality and effect size were determined via individual linear regressions in the *lm* function in the 'R Stats' package (R Core Team, 2022) (Supplement 4).

RESULTS

Taxonomic diversity

Across all regions, sites, and seasons, sampled macroinvertebrate communities contained 150,040 individuals from 221 taxa, representing 78 families, 22 orders, and 5 Phyla. Average regional taxonomic diversity was highest in Germany (gamma diversity [γ] = 138 taxa, TRic = 43 taxa \pm 8 SD, Shan = 15.01 \pm 2.89 SD), followed by Finland (γ = 91 taxa, TRic = 38 taxa \pm 6 SD, Shan = 8.99 \pm 3.86 SD), and then Sweden (γ = 59 taxa, TRic = 15 taxa \pm 4 SD, Shan = 6.83 \pm 2.40 SD) (Table 3, Figure 2a,c). In Germany and Finland, average a taxonomic richness was higher in spring than autumn; in Sweden, a taxonomic diversity was lower in spring than autumn (Figure 2a). Apart from TEve in Finland being higher in autumn than spring, seasonal differences in TEve were not observed in Germany or Sweden (Figure 2b).

The dominant taxa (>10% overall regional abundance) in Germany were *Gammarus fossarum* (Linnaeus, 1758), *Leuctra* sp., *Limnius perrisi* (Dufour, 1843), *Limnius* sp., and *Protonemura* sp.; in Sweden, *Nemoura* sp., *Nemurella pictetii* (Klapálek, 1900), Simuliidae Gen. sp.; and in Finland, *Baetis muticus* (Linnaeus, 1758), *B. niger* (Linnaeus, 1761), *B. rhodani* (Pictet, 1843), *B. subalpinus* Bengtsson, 1917, and Simuliidae Gen. sp. (Supplement 3). In Germany and Finland, average total abundance of communities did not differ statistically between seasons, whereas in Sweden, abundance was higher in spring than autumn (Figure 2g). Average taxonomic turnover between seasons (a measure of β -diversity) varied from 22% at sites in Finland (mean $T_{turn} = 0.22 \pm 0.13$ SD) to 28% at sites in Germany (0.28 ± 0.12 SD) and Sweden (0.28 ± 0.17 SD) (Table 3, Figure 2h).

Functional diversity

The first two axes of the supraregional FS explained 12.1% and 11.3% of the trait variation, respectively (Figure 3). The first PCoA axis was mostly explained by traits associated with life cycle duration, voltinism, food, and feeding habits, whereas the second axis was predominantly explained by traits related to voltinism, reproduction, locomotion, food, and feeding habits (Figure 3a). The major macroinvertebrate orders were the Coleoptera, Diptera, Ephemeroptera, Plecoptera, and Trichoptera (Figure 3b). The Coleoptera ordinated along the first axis and were characterised by long-lived, predatory taxa that feed on living microinvertebrates. Along the second axis, the Ephemeroptera, Plecoptera, and Trichoptera ordinated in the bottom right quadrant of the FS (Figure 3b) and were represented by crawling taxa with univoltine life cycles, isolated eggs cemented to substrate, which feed on plant detritus ≥ 1 mm via scraping. Oppositely, the Diptera mostly ordinated in the top left quadrant of the FS (Figure 3b) and were defined by short-lived, multivoltine taxa which are temporarily attached and feed on living microphytes via filtering. Considering the supraregional FS constructed from the *global* taxa and trait pool (Figure 3c), taxa in Germany occupied the largest proportion of the niche space, followed by Finland, and then Sweden, with no apparent differences in the FSs between seasons in each of the study regions (Figure 3d).

Based on null models of the functional diversity indices correcting for differences in taxonomic richness, average standardised functional richness was highest in Sweden (mean FRic.SES = -0.49 ± 0.39 SD) followed by Finland (-1.21 ± 0.46 SD), and then Germany (-1.27 ± 0.68 SD), but in general lower than expected given the number of taxa in the regional samples (Table 3, Figure 2d) thereby confirming a high degree of redundancy (Figure 2i). Seasonal differences in FRic.SES were most pronounced in Germany, with higher functional richness in autumn than spring. Conversely, communities in Sweden and Finland were less functionally rich in autumn than spring (Figure 2d), with only FRic.SES in Sweden significantly differing between seasons (Table 3). Functional evenness (FEve.SES) was comparable across the three sampling regions, with no observed seasonal differences (Figure 2e). In general, the communities from Germany and Sweden

TABLE 3 Descriptive statistics of community indices for each region and season (Germany: $N = 8 \times 2$; Sweden: $N = 52 \times 2$, Finland: $N = 10 \times 2$).

Index	Germany				Sweden				Finland			
	Mean	SD	Spr/Aut	Season	Mean	SD	Spr/Aut	Season	Mean	SD	Spr/Aut	Season
Abun	1743	1865	0.69	–	460	489	–3.30**	Autumn	3715	3185	1.97	–
TRic	43	8	2.40*	Spring	15	4	–5.46***	Autumn	38	6	–1.19	–
TEve	0.35	0.05	–0.92	–	0.47	0.15	0.71	–	0.24	0.10	–2.84*	Autumn
Shan	15.01	2.89	1.05	–	6.83	2.40	–2.99**	Autumn	8.99	3.86	–3.76***	Autumn
Tturn	0.28	0.12	–	–	0.28	0.17	–	–	0.22	0.13	–	–
FRic	0.15	0.04	1.11	–	0.00	0.01	–4.01***	Autumn	0.17	0.06	–0.32	–
FEve	0.53	0.10	0.57	–	0.52	0.17	1.68	–	0.51	0.06	–0.06	–
FDis	0.22	0.03	1.70	–	0.18	0.05	3.69***	Spring	0.15	0.06	–1.37	–
FRic S.E.S.	–1.27	0.68	–2.19	–	–0.49	0.39	2.49*	Spring	–1.21	0.46	1.01	–
FEve S.E.S.	0.19	1.16	0.87	–	–0.08	1.01	0.64	–	0.47	0.93	0.32	–
FDis S.E.S.	0.74	0.78	1.45	–	0.35	0.92	6.86***	Spring	–0.26	0.80	1.97	–
Fturn	0.13	0.05	–	–	0.16	0.08	–	–	0.13	0.08	–	–
FRed.	0.42	0.04	2.59*	Spring	0.40	0.06	–2.38*	Autumn	0.43	0.02	–0.86	–

Note: Mean, standard deviation (SD), *t*-value, and *p*-value significance indicated by asterisk of paired *t*-test results between seasons (Spr/Aut) and season in which the mean index value was higher (season). *p*-value significance indicated as: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Abbreviations for indices are provided in the materials and methods section. See Supplement 3 for further descriptive statistics of the community indices.

had higher than expected functional dispersion (FDis.SES) given the number of taxa in the regional samples, whereas communities in Finland had lower than expected FDis.SES. Across all three regions, FDis.SES was higher in spring than autumn (Figure 2f). Average functional turnover between seasons varied from 13% at the sites in Germany (mean $F_{turn} = 0.13 \pm 0.05$ SD) and Finland (0.13 ± 0.08 SD) to 16% at the sites in Sweden (0.16 ± 0.08 SD) (Table 3, Figure 2j).

Functional redundancy

Redundancy within the communities was similar across the three sampling regions (Table 3). In Germany, communities were significantly more redundant in spring than autumn, whereas in Sweden, communities were more redundant in autumn than spring (Figure 2i). No seasonal differences in redundancy were detected in samples from Finland.

Taxonomic and functional composition

Seasonal differences in regional taxonomic composition (Figure 4a,c,e) were more distinct than those of functional composition (Figure 4b,d,f). In addition to season, altitude, pH, and nutrients explained variation in regional taxonomic and functional composition (Figure 4).

There were strong seasonal differences in taxonomic composition within each of the study regions (Figure 4a,c,e). The explained variation of taxonomic dbRDA models was low: Germany adj. $R^2 = 0.09$ (Figure 4a), Sweden adj. $R^2 = 0.08$ (Figure 4b), and Finland adj. $R^2 = 0.03$ (Figure 4c). The spatial distribution of the sites, which was partitioned out of the dbRDA models, accounted for between 4.7% and 15.9% of the

variation in taxonomic composition within each region (Supplement 3). In Germany, variation in taxonomic composition along axis 1 ($R^2 = 0.15$, $p = 0.002$) was driven by season ($p = 0.003$), whereas pH ($p = 0.076$) was weakly linked with variation along axis 2 ($R^2 = 0.09$, $p = 0.087$). In Sweden, season ($p = 0.001$) was the most important predictor of the variation in taxonomic composition along axis 1 ($R^2 = 0.07$, $p = 0.001$), whereas variation along axis 2 ($R^2 = 0.02$, $p = 0.006$) was attributed to altitude ($p = 0.001$), SO_4^{2-} ($p = 0.018$), and TOC ($p = 0.014$). In Finland, variation in taxonomic composition on axis 1 ($R^2 = 0.09$, $p = 0.041$) was predominantly driven by pH ($p = 0.041$).

Seasonal variation in functional composition in each region was less pronounced than that of taxonomic composition (Figure 4b,d,f), with only the functional composition of the communities in Sweden varying with collected environmental predictors (Figure 4d). In Sweden, the dbRDA model explained 6% of total adjusted variation, with variation along axis 1 ($R^2 = 0.05$, $p = 0.001$) strongly linked to season ($p = 0.005$) and axis 2 ($R^2 = 0.02$, $p = 0.087$) to altitude ($p = 0.006$), SO_4^{2-} ($p = 0.041$), and TOC ($p = 0.001$). Site spatial distribution accounted for between 6% and 18.6% of the variation in functional composition. For the sites in Germany (Figure 4b) and Finland (Figure 4f), functional composition was not linked to any of environmental predictors, and the amount of total explained variation was low. For more nuanced information regarding the taxonomic and functional composition in each region, see Supplement 3.

Drivers of taxonomic and functional diversity

Multiple linear regressions decomposing the importance of each driver group (season, geography, acidity, nutrients) on taxonomic

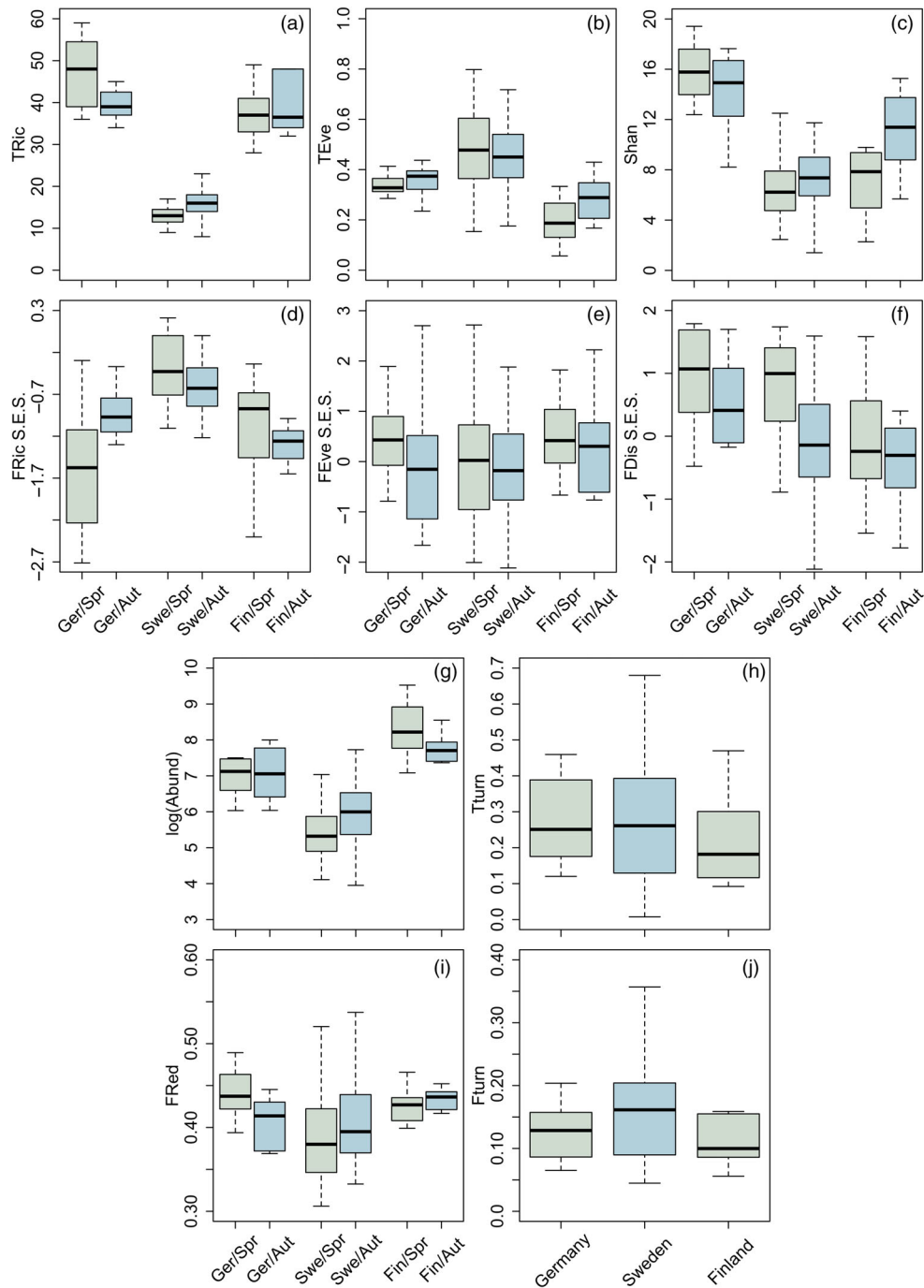


FIGURE 2 Box-and-whisker plots illustrating the variation in (a) taxonomic richness [TRic], (b) taxonomic evenness [TEve], (c) Shannon diversity [Shan], (d) standardised effect size of functional richness [FRic.S.E.S.], (e) standardised effect size of functional evenness [FEve.S.E.S.], (f) standardised effect size of functional dispersion [FDis.S.E.S.], (g) log transformed abundance [log(Abund)], (h) taxonomic turnover [Tturn], (i) functional redundancy [FRed], and (j) functional turnover [Fturn] between sampling seasons and regions. Aut, autumn; Fin, Finland; Ger, Germany; Spr, spring; Swe, Sweden.

diversity, functional diversity, and redundancy revealed regional variation in the drivers of stream macroinvertebrate communities (Table 4). See Supplement 4 for individual drivers and directionality.

Season was a key driver of taxonomic diversity, functional diversity, and redundancy across the considered study regions (Table 4). In Germany, taxonomic diversity and redundancy were higher in spring

than autumn, whereas functional diversity was higher in autumn than spring. Oppositely, in Sweden, functional diversity was higher in spring than autumn, with taxonomic diversity and redundancy being higher in autumn than spring.

Geographic variation, predominantly along an altitudinal gradient, was a key driver of redundancy in each region and explained some

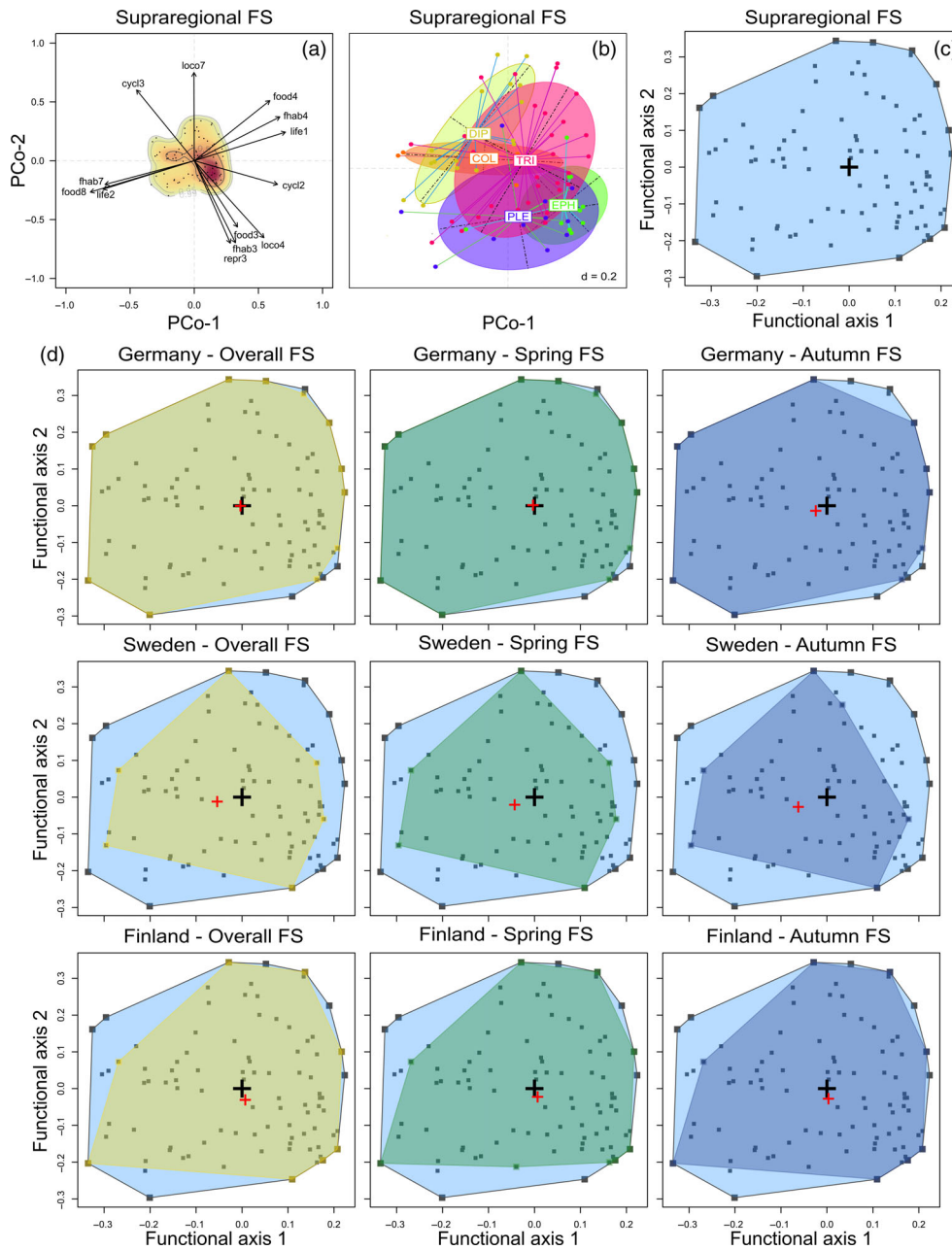


FIGURE 3 Visualisations of the supra-regional, regional, and seasonal functional spaces (FSs). (a) The probability of occurrence of trait combinations within the supra-regional FS; (b) the distribution of major taxonomic groups across the FS; (c) the supra-regional FS constructed from the global taxa and trait pool; and (d) the degree to which regional and seasonal subsets of taxa fill the supra-regional FS along functional axes 1 and 2. In (a), the 0.50, 0.95, and 0.99 probability quantiles (i.e., contour lines) are coloured according to the density of occurrence, with red indicating high probability densities and light green/yellow representing lower densities. The weightiest traits (i.e., $r \geq 0.5$ along axis 1 and 2) for each axis are represented by vector arrows. Traits are coded as: Life cycle duration ≤ 1 year (life1) and 1 year (life2); potential number of cycles per year = 1 (cycl2) and >1 (cycl3); reproductive technique via cemented, isolated eggs (repr3); substrate relation and locomotion by means of crawling (loco4) and temporary attachment (loco7); preferred food type plant detritus ≥ 1 mm (food3), living microphytes (food4), and living microinvertebrates (food8); and feeding habits such as scraper (fhab3), filter feeder (fhab4), and predator (fhab7). In (b), 'd' indicates the proportion of the scale between PCoA axes 1 and 2, whereby a 'd' value of 0.2 signifies that the scale of axis 2 is five times greater than that of axis 1. Taxonomic groups are coded as: Coleoptera (COL), Diptera (DIP), Ephemeroptera (EPH), Plecoptera (PLE), and Trichoptera (TRI). In (c) and (d), black crosses represent the supra-regional FS centroids, whereas red crosses represent regional and seasonal centroids. In light blue, the supra-regional FS combining all taxa from all regions and seasons. In yellow, the regional FS combining spring and autumn communities. In green, the FS of regional spring communities. In dark blue, the FS of the regional autumn communities.

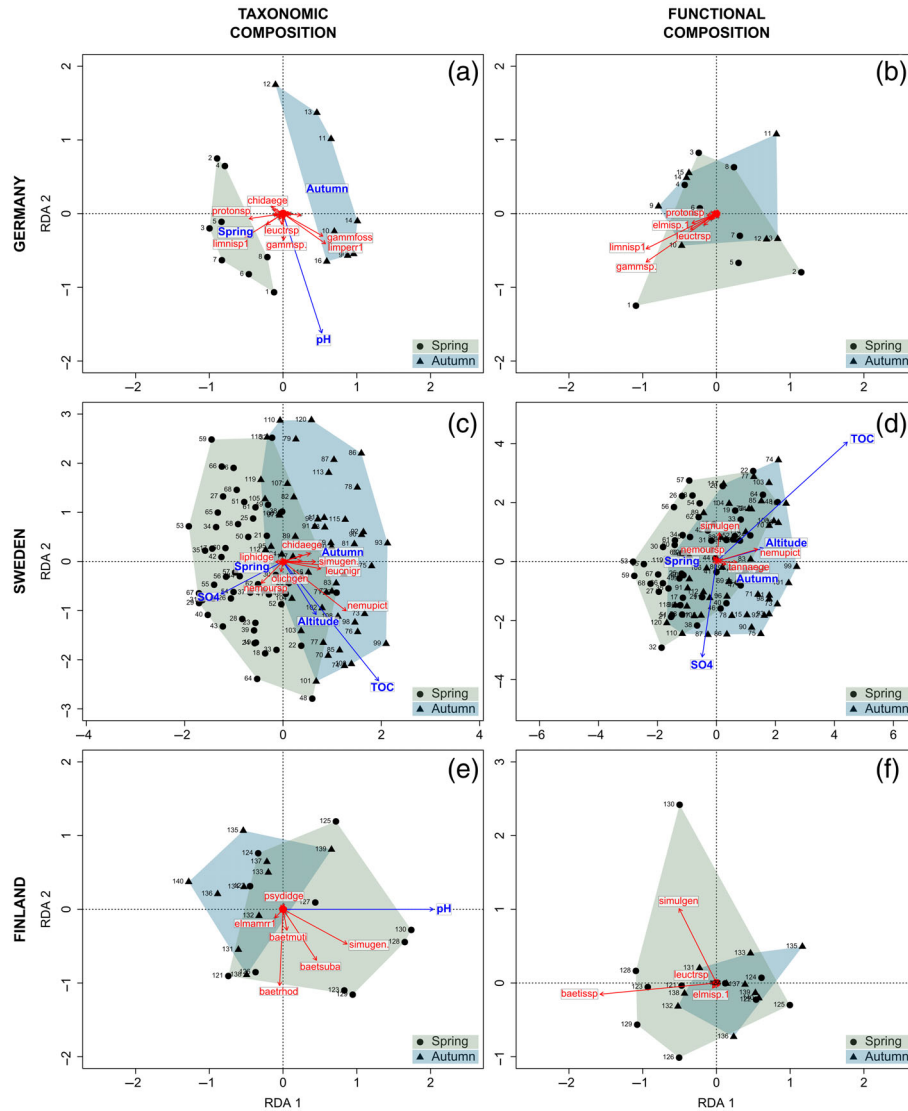


FIGURE 4 Drivers of taxonomic and functional community composition in each of the three sampling regions based on partial distance-based redundancy analyses (db-RDA). Germany: Taxonomic composition (a), functional composition (b); Sweden: Taxonomic composition (c), functional composition (d); Finland: Taxonomic composition (e), functional composition (f). Species scores of the most important species in each region (based on overall abundances across sampling sites) are indicated as red labels and vectors. When significant ($p < 0.05$), region-specific environmental variables (see section ‘Sampling sites’ for abbreviations) are displayed as blue labels and vectors. Numbers correspond to sampling site codes in Table 1. Taxon acronyms are coded as: Chironomidae Gen. sp. (chidaege), *Baetis muticus* (baetmuti), *Baetis rhodani* (baetrhod), *Baetis* sp. (beatssp.), *Baetis subalpinus* (baetsuba), *Elmis aenea/mauetii/rietscheli/rioloides* (elmamrr1), *Elmis* sp. (elmsp.1), *Gammarus fossarum* (gammfoss), *Gammarus* sp. (gammssp.), *Leuctra nigra* (leucnigr), *Leuctra* sp. (leuctrsp), Limnephilidae Gen. sp. (liphidge), *Limnius perrisi* (limperr1), *Limnius* sp. (limnisp1), *Nemoura* sp. (nemourspp), *Nemurella pictetii* (nemupict), Oligochaeta Gen. sp. (olichgen), *Protonemura* sp. (protonsp), Psychodidae Gen. sp. (psydidge), Simuliidae Gen. sp. (simugen.), Tanypodinae Gen. sp. (tannaage).

variation in overall community abundance in Germany and Sweden (Table 4).

Acidity drove taxonomic diversity and functional diversity in all three sampling regions (Table 4). Acidity was significantly positively correlated to TRic in Sweden, negatively correlated with FRic.SES in Germany, and positively correlated with FRic.SES in Finland. Although not significant, acidity additionally accounted for a substantial proportion of TEve variation in Germany.

The effect of nutrients differed widely among regions (Table 4). In Germany, nutrients significantly drove variation in abundance, with

DOC and NH_4^+ being negatively correlated with abundance, while SO_4^{2-} exhibited a positive correlation. Additionally, nutrients accounted for variation of taxonomic diversity (TRic and FEve) and functional diversity (FRic.SES) in Germany. In Sweden, abundance, functional diversity, and redundancy showed mixed responses to nutrients; abundance was positively correlated with TOC, whereas functional diversity and redundancy were positively correlated with $\text{NO}_3^- - \text{N} + \text{NO}_2^- - \text{N}$. In Finland, nutrients drove functional diversity, albeit not significantly, with FEve.SES and FDis.SES being negatively correlated with DOC and Tot-N, respectively.

TABLE 4 Drivers of macroinvertebrate taxonomic and standardised functional diversity indices in Germany, Sweden, and Finland using multiple linear regression.

	Season	Geography	Acidity	Nutrients
Germany				
Log(Abund)	0	0*	5.70	10.36*
TRic	21.92**	5.14	0	13.62
TEve	0	4.75	24.12	18.29
Shan	1.74	15.64	0	0
FRic.SES	22.18**	0	11.16*	0.64*
FEve.SES	0	8.81	0	0
FDis.SES	0.76	18.01	0	0
FRed	21.83*	22.87	0	0
Sweden				
Log(Abund)	6.79	17.21***	0.70	13.41
TRic	20.34	0	6.59*	4.28
TEve	0	2.77	0	1.91
Shan	5.63	0.96	4.72	1.60
FRic.SES	5.18	0	5.91	0
FEve.SES	0	0.66	0	3.77
FDis.SES	26.68***	0	4.57	7.83
FRed	2.90	8.67**	0	5.49
Finland				
Log(Abund)	11.93	0	0	0
TRic	0	0	4.67	0
TEve	17.63	0	0	0
Shan	27.71	0	5.30	0
FRic.SES	0	0	16.46	0
FEve.SES	0	0	2.69	18.50
FDis.SES	0.19	0	0	12.27
FRed	0	25.36	10.33	0

Note: Adjusted R^2 values are reported as percentage (%) of explained variance (i.e., adjusted $R^2 \times 100$). p -Value is highlighted in bold and indicated by asterisk when significant (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). Variable groups: Season = spring, autumn; geography = altitude, longitude, latitude; acidity = pH; and nutrients = region specific combinations of nutrient and major ion variables (DOC, TOC, SO_4^{2-} , NH_4^+ , $NO_3^- - N + NO_2^- - N$, Tot-N, Tot-P). Significant driver directionality and effect sizes are presented in Supplement 4.

DISCUSSION

Boreal freshwater communities are highly adapted to shifts in seasonal environmental conditions. While taxonomic diversity was regionally and seasonally variable, functional diversity maintained similar levels across seasons, suggesting functional resilience rooted in niche overlap and redundancy. The drivers of taxonomic diversity differed from those of functional diversity, and both varied regionally. Apart from seasonality and associated abiotic variation, geographic factors, pH, and nutrients all accounted for variation in boreal freshwater communities, albeit regionally contextualised. While variable

sampling methods did not allow for direct comparisons across regions, our study highlights spatial and seasonal discrepancies of biological communities across similar ecosystems and the importance of assessing both taxonomic and functional diversity in future monitoring (Mouton et al., 2022; Múrria et al., 2020; Pilière et al., 2016).

Seasonal and regional variation in taxonomic diversity, functional diversity, and redundancy

Over seasonal temporal scales, changes in taxonomic diversity patterns were decoupled from changes in functional diversity, with high taxonomic diversity cooccurring with periods of increased functional redundancy. Interestingly, these patterns were consistent across all three boreal regions and agree with Bêche et al. (2006) and Frainer et al. (2014) who found similar patterns of taxonomic and functional diversity from Mediterranean and boreal streams in North America and Europe, respectively. The decoupling of taxonomic and functional diversity in boreal freshwater ecosystems has been attributed to strong abiotic filters which filter taxa by the environmental conditions to which they are best adapted (Bêche et al., 2006) and are known to lead to trait under-dispersion and increasing trait similarity between seasons (Statzner et al., 2004). As boreal freshwaters are characterised by predictably strong shifts in environmental conditions between seasons (Tonkin et al., 2017; Woods et al., 2022), it is highly likely that seasonal environmental variation drives abiotic filtering and taxa turnover.

Frainer et al. (2014) argued, along with others (e.g., Dangles & Malmqvist, 2004), that taxonomic evenness has a larger effect on functional diversity than taxonomic diversity. While our null model analysis accounted for variations in taxonomic diversity among sites and seasons (i.e., scale dependence), it did not consider differences in taxonomic evenness. By contrast, and apart from TEve in Finland, none of the other study regions exhibited strong seasonal differences in evenness. In response to global change (e.g., warming temperatures, shifting seasonal patterns, biotic homogenisation; Olden, 2006; Tonkin et al., 2017), it is expected that 'slow', consistent shifts in community taxonomic α - and β -diversity will eventually lead to aggregated changes in functional diversity and ecosystem functioning (Baker, Pilotto, Haubrock, et al., 2021a; Dangles & Malmqvist, 2004; Frainer et al., 2014).

Given that the number of sites (Sweden > Finland > Germany) and catchments (Germany > Finland = Sweden) differed in each of the considered regions, spatial comparisons of biodiversity patterns were difficult. We found no generalised patterns of taxonomic and functional α - and β -diversity across the three boreal regions. By contrast, there were similar seasonal responses between northern (Finland and Sweden) and southern (Germany) boreal regions. In agreement with the habitat template theory (Southwood, 1977; Townsend & Hildrew, 1994), local factors (e.g., microhabitats, microclimates, precipitation loads, etc.) structure boreal freshwater communities. Harsh biotic and abiotic conditions in boreal regions result in high β -diversity (Clarke et al., 2008; Finn et al., 2011) and, though local adaptation and

speciation, β -diversity tends to increase proportionally to the scale of sampling considered. Therefore, the vast differences in taxonomic diversity between the three sampling regions was unsurprising.

Contrastingly, our null model approach showed that functional diversity was in fact comparable between regions, but in general lower than expected given regional taxonomic pools. Consequently, each of the considered boreal communities exhibited redundancy, the amount of which differed between regions. Additionally, redundancy was seasonally variant, implying that higher redundancy is associated with more favourable environmental conditions. Redundancy is a proxy for ecological resilience (Micheli & Halpern, 2005), with more resilient communities containing an increased number of taxa with similar traits (i.e., higher redundancy). In a study using the same 52 sites within the Swedish Krycklan catchment, Göthe et al. (2014) attributed seasonal differences in redundancy to seasonal hydrological regimes, with a higher frequency and intensity of extreme events in spring leading to a lower redundancy compared to autumnal base-flow conditions. In our study, this interpretation holds for Sweden and Finland, but not Germany. The observed heterogeneity in redundancy patterns resulted from differences in spatial factors between regions and increased with the spatial extent considered (Göthe et al., 2014). While a degree of redundancy is expected in any community, should it be driven by a gradual replacement of specialists with generalists (Olden, 2006), ecosystem resilience may eventually become negatively impaired (Belmar et al., 2019).

Drivers of taxonomic diversity, functional diversity, and redundancy

Season—an overarching driver of taxonomic and functional diversity in the here-considered boreal freshwaters—is associated with changes in many abiotic conditions, including hydrological, thermal, and light regimes (Mustonen et al., 2016). In response to varying abiotic conditions, seasonal pulses in the quality and quantity of resources drive biological communities (Verberk et al., 2013). Multiple linear regressions and redundancy analyses confirmed that seasonal variation, in association with its changes to the quality and quantity of organic carbon (DOC and TOC), had mixed effects on taxonomic diversity, functional diversity, and redundancy (partial support for H_{1a}). More specifically, periods of high organic carbon availability coincided with periods of high taxonomic diversity and redundancy, though there were regional inconsistencies regarding the season in which high carbon availability occurred. In Germany, it was in spring, coinciding with runoff and snow-melt-induced increases in DOC and fine particulate organic matter (FPOM). These spring conditions favoured taxa such as plecopterans (e.g., *Protonemoura* sp. and *Leuctra* sp.) which tend to feed on decomposing plant detritus (see Supplement 3). In contrast, autumnal leaf fall and subsequent increases in DOC and coarse particulate organic matter (CPOM) likely drove high taxonomic diversity and redundancy in Sweden and Finland. This would have favoured taxa such as Chironomids and *Nemoura* sp. in Sweden and *Baetis* spp. in Finland (see Supplement 3) which feed on larger organic material

(e.g., CPOM). A possible explanation for this observation could be that seasonal shifts in biotic conditions (i.e., thermal and hydrological regimes), and their associated effects on organic carbon dynamics, facilitate taxonomic turnover, leading to more functionally redundant communities which exploit the available pool of resources regardless of season. In agreement with the predictable shifts in macroinvertebrate community composition and function along a longitudinal carbon continuum (Vannote et al., 1980), our results support the concept of a seasonal carbon continuum, whereby community functioning is resilient to environmental change and exhibits predictable responses to shifts in seasonal carbon resources (Frainer et al., 2014; Smol et al., 2005; Verberk et al., 2013; Woods et al., 2022).

Albeit inconsistent throughout the boreal regions considered, geographic drivers—defined by altitudinal differences—decreased functional diversity but increased redundancy. In agreement with Stutzner et al. (2004), altitudinal gradients—and their direct (e.g., discharge relief energy, low temperatures) and indirect impacts (e.g., water chemistry)—have the capacity to alter macroinvertebrate diversity and function. Due to their position high up in the catchment, which often (but not always) corresponds to higher altitudes, we predicted (H_{2a}) that, through high specialisation, functional diversity would increase with altitude, reflecting low redundancy. Contrarily, our results support Bêche et al. (2006) and Frainer et al. (2014) in their notion that strong abiotic filters at higher altitudes give rise to more similar trait combinations, thereby increasing redundancy.

Variations in acidity drive changes in macroinvertebrate diversity and function through time (Baker, Pilotto, Haubrock, et al., 2021a; Baker, Pilotto, Jourdan, et al., 2021b; Dangles & Malmqvist, 2004). Accordingly, and in partial support of our hypothesis that lower acidity (higher pH) would be associated with higher taxonomic and functional diversity (H_{2b}), we found that pH drove taxonomic α -diversity (linear regression) and β -diversity (redundancy analyses), but not functional diversity. Boreal freshwaters, through their underlying geology and poor buffering capacity, have highly dynamic pH conditions (Dangles & Malmqvist, 2004) and each of the considered boreal regions had starkly different mean pH conditions; mean pH was 6.63 in Germany, 5.17 in Sweden, and 7.8 in Finland. Thus, through protracted exposure to these dynamic conditions, the effects of pH on taxonomic diversity might be reflecting the specific tolerances of different taxonomic groups to variations in pH (Dangles et al., 2004; Hall et al., 1987).

Nutrient fluctuations drove variation in abundance and functional richness. This result reflects the functional constraints taxa have to the pool of available resources. Most nutrients entering boreal headwaters stem from allochthonous sources (but see Brett et al., 2017), and although essential for life, variations in their quality and quantity can impact freshwater communities (Baker & Greenfield, 2019; Huttunen et al., 2022). In our study, the most important nutrient shaping macroinvertebrate communities was organic carbon, and as discussed above, it is essential for defining diversity and function across seasonal and longitudinal (river) gradients (e.g., Frainer et al., 2014; Vannote et al., 1980; Verberk et al., 2013). Nevertheless, a plethora of other nutrients (and major ions) have important roles in freshwater

ecosystems, with each of these nutrients being either directly or indirectly linked to organic carbon and microbial activity (Brookshire et al., 2005; Webster, 2007). By contrast, in each of the considered boreal regions, mean concentrations of PO_4^{3-} , SO_4^{2-} , and NO_3^- were very low, and while we do not negate their importance in freshwater environments (Ensign & Doyle, 2006), we did not find conclusive evidence linking them to changes in taxonomic and functional diversity. Thus, we reject our final hypothesis (H_{3c}) but acknowledge the well-known importance and impact nutrient fluctuations can have on freshwater ecosystems (Baker & Greenfield, 2019). Although we understand the limitations of funding, future monitoring efforts should consider broader spatial and temporal scales. Moreover, a wider and more consistent suite of environmental variables, particular water chemistry parameters, are needed to make more informed conservation decisions as they have been found to be critical drivers of local biodiversity (Magliozzi et al., 2020).

CONCLUSIONS

Questions of *how* and *why* biological communities are both taxonomically and functionally structured remain critical for understanding biodiversity change and for guiding conservation policy and protection (Dolédec et al., 2021). A growing body of research suggests that trait-based approaches hold more promise in realistically assessing how changes in the environment might affect ecosystem functioning (McGill et al., 2006; Múrria et al., 2020; Verberk et al., 2013). In accordance with Magliozzi et al. (2020), our study confirms that taxonomic and functional diversity are often decoupled, and that the resultant redundancy provides ecosystems with a degree of resilience to changes in environmental conditions. Despite the dependence of boreal systems on seasonal predictability (e.g., phenological synchronisations, predator prey interactions, pollination cycles, growth periods, etc.), seasonally induced shifts in environmental conditions, including the state and availability of carbon, facilitate an exchange of taxa which leads to taxonomically unique communities that exploit the pool of available seasonal resources. By contrast, if changes to seasonality and environmental conditions become more pronounced through future climate projections (IPCC, 2021), the ability of freshwater systems and their biological communities to maintain ecological functioning may become impaired. More experimental and empirical studies explicitly focussed on stressor impacts on α and β taxonomic and functional diversity are needed, particularly in ecosystems at higher latitudes and altitudes which act as sentinels for ongoing environmental change (Woodward et al., 2010).

AUTHOR CONTRIBUTIONS

Nathan Jay Baker: Conceptualization (lead); data curation (lead); formal analysis (lead); investigation (lead); methodology (lead); project administration (lead); validation (lead); visualization (lead); writing – original draft (lead); writing – review and editing (lead).
Ellen A.R. Welti: Conceptualization (supporting); formal analysis

(supporting); investigation (supporting); supervision (supporting); validation (equal); writing – original draft (supporting); writing – review and editing (equal).
Francesca Pilotto: Conceptualization (supporting); formal analysis (supporting); investigation (supporting); supervision (supporting); validation (equal); writing – original draft (supporting); writing – review and editing (equal).
Jonas Jourdan: Validation (equal); writing – original draft (supporting); writing – review and editing (equal).
Burkhard Beudert: Data curation (equal); validation (equal); writing – review and editing (equal).
Kaisa-Leena Huttunen: Data curation (equal); validation (equal); writing – review and editing (equal).
Timo Muotka: Data curation (equal); validation (equal); writing – review and editing (equal).
Riku Paavola: Data curation (equal).
Emma Göthe: Data curation (equal).
Peter Haase: Conceptualization (supporting); investigation (supporting); project administration (supporting); supervision (lead); validation (equal); writing – review and editing (equal).

ACKNOWLEDGEMENTS

The authors are grateful to the Rudolf and Helene Glasser Foundation and the Bernard and Ursula Plettner Foundation for financial support to Nathan Jay Baker (Grant No. T0083/30772/2017/kg) and to the eLTER PLUS project (Grant Agreement No. 871128) for financial support to Peter Haase. We also thank Linda Seifert from the Bavarian Forest National Park and Jindřiška Bojková from Masaryk University, Department of Botany and Zoology, Brno, Czech Republic for the extensive macroinvertebrate sampling conducted with the Bavarian Forest National Park, Germany. Lastly, we extend our gratitude to the handling editor of *Insect Conservation and Diversity* and two anonymous reviews for their comments and suggestions which greatly helped improve our manuscript. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST

The authors have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Raw biodiversity, environmental data, metadata, and R-code used to generate the results presented in this manuscript are available on GitHub: https://github.com/HeeeyNathan/Supraregional_taxonomic_and_functional_diversity.

ORCID

Nathan Jay Baker  <https://orcid.org/0000-0001-7948-106X>

Ellen A. R. Welti  <https://orcid.org/0000-0001-6944-3422>

Francesca Pilotto  <https://orcid.org/0000-0003-1848-3154>

Jonas Jourdan  <https://orcid.org/0000-0002-2745-2520>

Burkhard Beudert  <https://orcid.org/0000-0003-1434-9644>

Kaisa-Leena Huttunen  <https://orcid.org/0000-0003-0488-1274>

Timo Muotka  <https://orcid.org/0000-0002-2268-5683>

Riku Paavola  <https://orcid.org/0000-0002-4708-1413>

Emma Göthe  <https://orcid.org/0000-0002-7387-6770>

Peter Haase  <https://orcid.org/0000-0002-9340-0438>

REFERENCES

- Antão, L.H., Weigel, B., Strona, G., Hällfors, M., Kaarlejärvi, E., Dallas, T. et al. (2022) Climate change reshuffles northern species within their niches. *Nature Climate Change*, 12, 587–592. Available from: <https://doi.org/10.1038/s41558-022-01381-x>
- Arzel, C., Nummi, P., Arvola, L., Pöysä, H., Davranche, A., Rask, M. et al. (2020) Invertebrates are declining in boreal aquatic habitat: the effect of brownification? *Science of the Total Environment*, 724, 138199. Available from: <https://doi.org/10.1016/j.scitotenv.2020.138199>
- Baker, N.J. & Greenfield, R. (2019) Shift happens: changes to the diversity of riverine aquatic macroinvertebrate communities in response to sewage effluent runoff. *Ecological Indicators*, 102, 813–821. Available from: <https://doi.org/10.1016/j.ecolind.2019.03.021>
- Baker, N.J., Pilotto, F., Haubrock, P.J., Beudert, B. & Haase, P. (2021a) Multidecadal changes in functional diversity lag behind the recovery of taxonomic diversity. *Ecology and Evolution*, 11, 17471–17484. Available from: <https://doi.org/10.1002/ece3.8381>
- Baker, N.J., Pilotto, F., Jourdan, J., Beudert, B. & Haase, P. (2021b) Recovery from air pollution and subsequent acidification masks the effects of climate change on a freshwater macroinvertebrate community. *Science of the Total Environment*, 758, 143685. Available from: <https://doi.org/10.1016/j.scitotenv.2020.143685>
- Bêche, L.A., McElravy, E.P. & Resh, V.H. (2006) Long-term seasonal variation in the biological traits of benthic-macroinvertebrates in two Mediterranean-climate streams in California, U.S.A. *Freshwater Biology*, 51, 56–75. Available from: <https://doi.org/10.1111/j.1365-2427.2005.01473.x>
- Belmar, O., Bruno, D., Guareschi, S., Mellado-Díaz, A., Millán, A. & Velasco, J. (2019) Functional responses of aquatic macroinvertebrates to flow regulation are shaped by natural flow intermittence in Mediterranean streams. *Freshwater Biology*, 64, 1064–1077. Available from: <https://doi.org/10.1111/fwb.13289>
- Blaurock, K., Beudert, B., Gilfedder, B.S., Fleckenstein, J.H., Peiffer, S. & Hopp, L. (2021) Low hydrological connectivity after summer drought inhibits DOC export in a forested headwater catchment. *Hydrology and Earth System Sciences*, 25, 5133–5151. Available from: <https://doi.org/10.5194/hess-25-5133-2021>
- Borcard, D., Gillet, F. & Legendre, P. (2018) *Numerical ecology with R*, 2nd edition. New York: Springer. Available from: <https://doi.org/10.1007/978-1-4419-7976-6>
- Boyé, A., Thiébaud, É., Grall, J., Legendre, P., Broudin, C., Houbin, C. et al. (2019) Trait-based approach to monitoring marine benthic data along 500 km of coastline. *Diversity and Distributions*, 25, 1879–1896. Available from: <https://doi.org/10.1111/ddi.12987>
- Brett, M.T., Bunn, S.E., Chandra, S., Galloway, A.W.E., Guo, F., Kainz, M.J. et al. (2017) How important are terrestrial organic carbon inputs for secondary production in freshwater ecosystems? *Freshwater Biology*, 62, 833–853. Available from: <https://doi.org/10.1111/fwb.12909>
- Brookshire, E.N.J., Valett, H.M., Thomas, S.A. & Webster, J.R. (2005) Coupled cycling of dissolved organic nitrogen and carbon in a forest stream. *Ecology*, 86, 2487–2496. Available from: <https://doi.org/10.1890/04-1184>
- Bruno, D., Belmar, O., Maire, A., Morel, A., Dumont, B. & Detry, T. (2019) Structural and functional responses of invertebrate communities to climate change and flow regulation in alpine catchments. *Global Change Biology*, 25, 1612–1628. Available from: <https://doi.org/10.1111/gcb.14581>
- Buffam, I., Laudon, H., Temmerud, J., Mörth, C.-M. & Bishop, K. (2007) Landscape-scale variability of acidity and dissolved organic carbon during spring flood in a boreal stream network. *Journal of Geophysical Research*, 112, G01022. Available from: <https://doi.org/10.1029/2006JG000218>
- Chevenet, F., Dolédec, S. & Chessel, D. (1994) A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology*, 31, 295–309. Available from: <https://doi.org/10.1111/j.1365-2427.1994.tb01742.x>
- Chiantore, M., Thrush, S.F., Asnaghi, V. & Hewitt, J.E. (2018) The multiple roles of β -diversity help untangle community assembly processes affecting recovery of temperate rocky shores. *Royal Society Open Science*, 5, 171700. Available from: <https://doi.org/10.1098/rsos.171700>
- Clarke, A., mac Nally, R., Bond, N. & Lake, P.S. (2008) Macroinvertebrate diversity in headwater streams: a review. *Freshwater Biology*, 53, 1707–1721. Available from: <https://doi.org/10.1111/j.1365-2427.2008.02041.x>
- Dangles, O. & Malmqvist, B. (2004) Species richness-decomposition relationships depend on species dominance. *Ecology Letters*, 7, 395–402. Available from: <https://doi.org/10.1111/j.1461-0248.2004.00591.x>
- Dangles, O., Malmqvist, B. & Laudon, H. (2004) Naturally acid freshwater ecosystems are diverse and functional: evidence from boreal streams. *Oikos*, 104, 149–155. Available from: <https://doi.org/10.1111/j.0030-1299.2004.12360.x>
- Darwall, W., Bremerich, V., de Wever, A., Dell, A.I., Freyhof, J., Gessner, M. O. et al. (2018) The alliance for freshwater life: a global call to unite efforts for freshwater biodiversity science and conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 28, 1015–1022. Available from: <https://doi.org/10.1002/aqc.2958>
- Dolédec, S., Simon, L., Blemus, J., Rigal, A., Robin, J. & Mermillod-Blondin, F. (2021) Multiple stressors shape invertebrate assemblages and reduce their trophic niche: a case study in a regulated stream. *Science of the Total Environment*, 773, 145061. Available from: <https://doi.org/10.1016/j.scitotenv.2021.145061>
- Dray, S., Bauman, D., Blanchet, G., Borcard, D., Clappe, S., Guenard, G. et al. (2021) *Package 'adespatial': multivariate multiscale spatial analysis*. R Package Version 0.3-14. Available from: <https://doi.org/10.1890/11-1183.1>
- Dray, S., Dufour, A.-B. & Thioulouse, J. (2022) *R package "ade4": analysis of ecological data: exploratory and Euclidean methods in environmental sciences*. R Package Version 1.7-19.
- Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.-I., Knowler, D.J., Lévêque, C. et al. (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews*, 81, 163–182. Available from: <https://doi.org/10.1017/S1464793105006950>
- Duong, T., Wand, M., Chacon, J. & Gramacki, A. (2022) *R package "ks": kernel smoothing*. R Package Version 1.13.5.
- Ensign, S.H. & Doyle, M.W. (2006) Nutrient spiraling in streams and river networks. *Journal of Geophysical Research: Biogeosciences*, 111, 1–13. Available from: <https://doi.org/10.1029/2005JG000114>
- Finn, D.S., Bonada, N., Múrria, C. & Hughes, J.M. (2011) Small but mighty: headwaters are vital to stream network biodiversity at two levels of organization. *Journal of the North American Benthological Society*, 30, 963–980. Available from: <https://doi.org/10.1899/11-012.1>
- Floury, M., Souchon, Y. & Looy, K.v. (2018) Climatic and trophic processes drive long-term changes in functional diversity of freshwater invertebrate communities. *Ecography*, 41, 209–218. Available from: <https://doi.org/10.1111/ecog.02701>
- Frainer, A., McKie, B.G. & Malmqvist, B. (2014) When does diversity matter? Species functional diversity and ecosystem functioning across habitats and seasons in a field experiment. *Journal of Animal Ecology*, 83, 460–469. Available from: <https://doi.org/10.1111/1365-2656.12142>
- Gotelli, N.J. & Graves, G.R. (1996) *Null models in ecology*. Washington, D.C.: Smithsonian Institution Press.
- Göthe, E., Angeler, D.G. & Sandin, L. (2013) Metacommunity structure in a small boreal stream network. *Journal of Animal Ecology*, 82, 449–458. Available from: <https://doi.org/10.1111/1365-2656.12004>
- Göthe, E., Sandin, L., Allen, C.R. & Angeler, D.G. (2014) Quantifying spatial scaling patterns and their local and regional correlates in headwater

- streams: implications for resilience. *Ecology and Society*, 19, 15. Available from: <https://doi.org/10.5751/ES-06750-190315>
- Grenié, M., Berti, E., Carvajal-Quintero, J., Winter, M. & Sagouis, A. (2021) Matching species names across biodiversity databases: sources, tools, pitfalls and best practices for taxonomic harmonization. *Biodiversity Information Science and Standards*, 5, 1–3. Available from: <https://doi.org/10.3897/biss.5.75359>
- Grenié, M., Berti, E., Carvajal-Quintero, J., Dädlow, G.M.L., Sagouis, A. & Winter, M. (2022) Harmonizing taxon names in biodiversity data: a review of tools, databases and best practices. *Methods in Ecology and Evolution*, 1–14. Available from: <https://doi.org/10.1111/2041-210X.13802>
- Grigoropoulou, A., Schmidt-Kloiber, A., Múrria, C. & Qiao, H. (2022) Incongruent latitudinal patterns of taxonomic, phylogenetic and functional diversity reveal different drivers of caddisfly community assembly across spatial scales. *Global Ecology and Biogeography*, 31, 1006–1020. Available from: <https://doi.org/10.1111/geb.13479>
- Haase, P., Lohse, S., Pauls, S., Schindehütte, K., Sundermann, A., Rolaufts, P. et al. (2004) Assessing streams in Germany with benthic invertebrates: development of a practical standardised protocol for macroinvertebrate sampling and sorting. *Limnologica*, 34, 349–365. Available from: [https://doi.org/10.1016/S0075-9511\(04\)80005-7](https://doi.org/10.1016/S0075-9511(04)80005-7)
- Haase, P., Murray-Bligh, J., Lohse, S., Pauls, S., Sundermann, A., Gunn, R. et al. (2006) Assessing the impact of errors in sorting and identifying macroinvertebrate samples. *Hydrobiologia*, 566, 505–521. Available from: <https://doi.org/10.1007/s10750-006-0075-6>
- Hall, R.J., Driscoll, C.T. & Likens, G.E. (1987) Importance of hydrogen ions and aluminium in regulating the structure and function of stream ecosystems: an experimental test. *Freshwater Biology*, 18, 17–43. Available from: <https://doi.org/10.1111/j.1365-2427.1987.tb01293.x>
- Hallett, L.M., Jones, S.K., MacDonald, A.A.M., Jones, M.B., Flynn, D.F.B., Ripplinger, J. et al. (2016) codyn: an R package of community dynamics metrics. *Methods in Ecology and Evolution*, 7, 1146–1151. Available from: <https://doi.org/10.1111/2041-210X.12569>
- Heino, J. (2005) Functional biodiversity of macroinvertebrate assemblages along major ecological gradients of boreal headwater streams. *Freshwater Biology*, 50, 1578–1587. Available from: <https://doi.org/10.1111/j.1365-2427.2005.01418.x>
- Heino, J., Mykrä, H. & Muotka, T. (2009) Temporal variability of nestedness and idiosyncratic species in stream insect assemblages. *Diversity and Distributions*, 15, 198–206. Available from: <https://doi.org/10.1111/j.1472-4642.2008.00513.x>
- Heino, J., Grönroos, M., Soininen, J., Virtanen, R. & Muotka, T. (2012) Context dependency and metacommunity structuring in boreal headwater streams. *Oikos*, 121, 537–544. Available from: <https://doi.org/10.1111/j.1600-0706.2011.19715.x>
- Høye, T.T., Post, E., Schmidt, N.M., Trøjelsgaard, K. & Forchhammer, M.C. (2013) Shorter flowering seasons and declining abundance of flower visitors in a warmer Arctic. *Nature Climate Change*, 3, 759–763. Available from: <https://doi.org/10.1038/nclimate1909>
- Huttunen, K., Väisänen, L.O.S., Paavola, R. & Muotka, T. (2022) Partitioning of benthic biodiversity in boreal streams: contributions of spatial, inter-annual, and seasonal variability. *Freshwater Biology*, 67, 774–783. Available from: <https://doi.org/10.1111/fwb.13880>
- IPCC. (2021) Summary for policymakers. In: Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S., Péan, L.C., Berger, S. et al. (Eds.) *Climate change 2021: the physical science basis. Contribution of working group I to the sixth assessment report of the Intergovernmental Panel on Climate Change*. United Kingdom and New York: Cambridge University Press. Available at: <https://www.ipcc.ch/report/ar6/wg1/> [Accessed 2nd January 2022]
- de Juan, S., Thrush, S.F. & Hewitt, J.E. (2013) Counting on β -diversity to safeguard the resilience of estuaries. *PLoS One*, 8, e65575. Available from: <https://doi.org/10.1371/journal.pone.0065575>
- Kritzbeg, E.S., Hasselquist, E.M., Škerlep, M., Löfgren, S., Olsson, O., Stadmark, J. et al. (2020) Browning of freshwaters: consequences to ecosystem services, underlying drivers, and potential mitigation measures. *Ambio*, 49, 375–390. Available from: <https://doi.org/10.1007/s13280-019-01227-5>
- Labiberté, E. & Legendre, P. (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91, 299–305. Available from: <https://doi.org/10.1890/08-2244.1>
- Labiberté, E., Legendre, P. & Shipley, B. (2014) *Package “FD”: measuring functional diversity (FD) from multiple traits, and other tools for functional ecology*. R Package Version 1.0-12. Available at: <https://cran.r-project.org/web/packages/FD/index.html> [Accessed 15th July 2022]
- Legendre, P. (2008) Studying beta diversity: ecological variation partitioning by multiple regression and canonical analysis. *Journal of Plant Ecology*, 1, 3–8. Available from: <https://doi.org/10.1093/jpe/rtm001>
- Legendre, P. & Anderson, M.J. (1999) Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecological Monographs*, 69, 1–24. Available from: <https://doi.org/10.2307/2657192>
- Lehtovaara, A., Arvola, L., Keskkitalo, J., Olin, M., Rask, M., Salonen, K. et al. (2014) Responses of zooplankton to long-term environmental changes in a small boreal lake. *Boreal Environment Research*, 19, 97–111. Available at: <http://hdl.handle.net/10138/165171> [Accessed 14th November 2021]
- Lindholm, M., Alahuhta, J., Heino, J. & Toivonen, H. (2020) No biotic homogenisation across decades but consistent effects of landscape position and pH on macrophyte communities in boreal lakes. *Ecography*, 43, 294–305. Available from: <https://doi.org/10.1111/ecog.04757>
- Löfvenius, M.O., Kluge, M. & Lundmark, T. (2003) Snow and soil frost depth in two types of shelterwood and a clear-cut area. *Scandinavian Journal of Forest Research*, 18, 54–63. Available from: <https://doi.org/10.1080/02827581.2003.10383138>
- van Looy, K., Floury, M., Ferréol, M., Prieto-Montes, M. & Souchon, Y. (2016) Long-term changes in temperate stream invertebrate communities reveal a synchronous trophic amplification at the turn of the millennium. *Science of the Total Environment*, 565, 481–488. Available from: <https://doi.org/10.1016/j.scitotenv.2016.04.193>
- Magliozzi, C., Meyer, A., Usseglio-Polatera, P., Robertson, A. & Grabowski, R.C. (2020) Investigating invertebrate biodiversity around large wood: taxonomic vs functional metrics. *Aquatic Sciences*, 82, 69. Available from: <https://doi.org/10.1007/s00027-020-00745-9>
- Malmqvist, B., Muotka, T., Nilsson, C. & Timm, H. (2009) Rivers of the Fennoscandian shield. In: Tockner, K., Robinson, C.T. & Uehlinger, U. (Eds.) *Rivers of Europe*, 1st edition. Academic Press, pp. 297–336.
- Mammola, S., Carmona, C.P., Guillerme, T. & Cardoso, P. (2021) Concepts and applications in functional diversity. *Functional Ecology*, 35, 1869–1885. Available from: <https://doi.org/10.1111/1365-2435.13882>
- Mason, N.W.H., Mouillot, D., Lee, W.G. & Bastow Wilson, J. (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos*, 111, 112–118. Available from: <https://doi.org/10.1111/j.0030-1299.2005.13886.x>
- Masters, Z., Peteresen, I., Hildrew, A.G. & Ormerod, S.J. (2007) Insect dispersal does not limit the biological recovery of streams from acidification. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 17, 375–383. Available from: <https://doi.org/10.1002/aqc.794>
- McGill, B., Enquist, B., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, 21, 178–185. Available from: <https://doi.org/10.1016/j.tree.2006.02.002>
- Micheli, F. & Halpern, B.S. (2005) Low functional redundancy in coastal marine assemblages. *Ecology Letters*, 8, 391–400. Available from: <https://doi.org/10.1111/j.1461-0248.2005.00731.x>
- Mouchet, M.A., Villéger, S., Mason, N.W.H. & Mouillot, D. (2010) Functional diversity measures: an overview of their redundancy and their

- ability to discriminate community assembly rules. *Functional Ecology*, 24, 867–876. Available from: <https://doi.org/10.1111/j.1365-2435.2010.01695.x>
- Mouillot, D., Villegger, S., Parravicini, V., Kulbicki, M., Arias-Gonzalez, J.E., Bender, M. et al. (2014) Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. *Proceedings of the National Academy of Sciences*, 111, 13757–13762. Available from: <https://doi.org/10.1073/pnas.1317625111>
- Mouillot, D., Loiseau, N., Grenié, M., Algar, A.C., Allegra, M., Cadotte, M. W. et al. (2021) The dimensionality and structure of species trait spaces. *Ecology Letters*, 24, 1988–2009. Available from: <https://doi.org/10.1111/ele.13778>
- Mouton, T.L., Tonkin, J.D., Stephenson, F., Verburg, P. & Flourey, M. (2020) Increasing climate-driven taxonomic homogenization but functional differentiation among river macroinvertebrate assemblages. *Global Change Biology*, 26, 6904–6915. Available from: <https://doi.org/10.1111/gcb.15389>
- Mouton, T.L., Leprieur, F., Flourey, M., Stephenson, F., Verburg, P. & Tonkin, J.D. (2022) Climate and land-use driven reorganisation of structure and function in river macroinvertebrate communities. *Ecography*, 2022, 1–13. Available from: <https://doi.org/10.1111/ecog.06148>
- Müller, J., Bässler, C., Strätz, C., Klöcking, B. & Brandl, R. (2009) Molluscs and climate warming in a low mountain range national park. *Malacologia*, 51, 89–109. Available from: <https://doi.org/10.4002/040.051.0106>
- Múria, C., Iturrarte, G. & Gutiérrez-Cánovas, C. (2020) A trait space at an overarching scale yields more conclusive macroecological patterns of functional diversity. *Global Ecology and Biogeography*, 29, 1729–1742. Available from: <https://doi.org/10.1111/geb.13146>
- Mustonen, K.-R., Mykrä, H., Marttila, H., Haghighi, A.T., Kløve, B., Aroviita, J. et al. (2016) Defining the natural flow regimes of boreal rivers: relationship with benthic macroinvertebrate communities. *Freshwater Science*, 35, 559–572. Available from: <https://doi.org/10.1086/685104>
- Mykrä, H., Ruokonen, T. & Muotka, T. (2006) The effect of sample duration on the efficiency of kick-sampling in two streams with contrasting substratum heterogeneity. *SIL Proceedings*, 1922–2010(29), 1351–1355. Available from: <https://doi.org/10.1080/03680770.2005.11902901>
- Oksanen, A.J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., Mcglinn, D. et al. (2020) *Package “vegan”: community ecology package*. R Package Version 2.5-7. Available at: <https://cran.r-project.org/package=vegan> [Accessed 15th July 2022]
- Olden, J.D. (2006) Biotic homogenization: a new research agenda for conservation biogeography. *Journal of Biogeography*, 33, 2027–2039. Available from: <https://doi.org/10.1111/j.1365-2699.2006.01572.x>
- Pakeman, R.J. (2014) Functional trait metrics are sensitive to the completeness of the species' trait data? *Methods in Ecology and Evolution*, 5, 9–15. Available from: <https://doi.org/10.1111/2041-210X.12136>
- Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37–42. Available from: <https://doi.org/10.1038/nature01286>
- Pavoine, S. (2020) *Package “adiv”: analysis of diversity*. R Package Version 2.0.1. Available at: <https://cran.r-project.org/web/packages/adiv/index.html> [Accessed 15th July 2022]
- Pavoine, S. & Bonsall, M.B. (2011) Measuring biodiversity to explain community assembly: a unified approach. *Biological Reviews*, 86, 792–812. Available from: <https://doi.org/10.1111/j.1469-185X.2010.00171.x>
- Pilière, A.F.H., Verberk, W.C.E.P., Gräwe, M., Breure, A.M., Dyer, S.D., Posthuma, L. et al. (2016) On the importance of trait interrelationships for understanding environmental responses of stream macroinvertebrates. *Freshwater Biology*, 61, 181–194. Available from: <https://doi.org/10.1111/fwb.12690>
- Pilotto, F., Kühn, I., Adrian, R., Alber, R., Alignier, A., Andrews, C. et al. (2020) Meta-analysis of multidecadal biodiversity trends in Europe. *Nature Communications*, 11, 3486. Available from: <https://doi.org/10.1038/s41467-020-17171-y>
- R Core Team. (2022) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing. Available at: <https://www.r-project.org/> [Accessed 15th July 2022]
- Rooney, N., McCann, K., Gellner, G. & Moore, J.C. (2006) Structural asymmetry and the stability of diverse food webs. *Nature*, 442, 265–269. Available from: <https://doi.org/10.1038/nature04887>
- Rosenfeld, J.S. (2002) Functional redundancy in ecology and conservation. *Oikos*, 98, 156–162. Available from: <https://doi.org/10.1034/j.1600-0706.2002.980116.x>
- Schmera, D., Podani, J., Heino, J., Erős, T. & Poff, N.L. (2015) A proposed unified terminology of species traits in stream ecology. *Freshwater Science*, 34, 823–830. Available from: <https://doi.org/10.1086/681623>
- Schmera, D., Heino, J., Podani, J., Erős, T. & Dolédec, S. (2017) Functional diversity: a review of methodology and current knowledge in freshwater macroinvertebrate research. *Hydrobiologia*, 787, 27–44. Available from: <https://doi.org/10.1007/s10750-016-2974-5>
- Schmera, D., Heino, J. & Podani, J. (2022) Characterising functional strategies and trait space of freshwater macroinvertebrates. *Scientific Reports*, 12, 12283. Available from: <https://doi.org/10.1038/s41598-022-16472-0>
- Schmidt-Kloiber, A. & Hering, D. (2015) www.freshwaterecology.info—an online tool that unifies, standardises and codifies more than 20,000 European freshwater organisms and their ecological preferences. *Ecological Indicators*, 53, 271–282. Available from: <https://doi.org/10.1016/j.ecolind.2015.02.007>
- da Silva, M.P., Blarock, K., Beudert, B., Fleckenstein, J.H., Hopp, L., Peiffer, S. et al. (2021) Delineating source contributions to stream dissolved organic matter composition under baseflow conditions in forested headwater catchments. *Journal of Geophysical Research: Biogeosciences*, 126, e2021JG006425. Available from: <https://doi.org/10.1029/2021JG006425>
- Smol, J.P., Wolfe, A.P., Birks, H.J.B., Douglas, M.S.v., Jones, V.J., Korhola, A. et al. (2005) Climate-driven regime shifts in the biological communities of arctic lakes. *Proceedings of the National Academy of Sciences*, 102, 4397–4402. Available from: <https://doi.org/10.1073/pnas.0500245102>
- Southwood, T.R.E. (1977) Habitat, the templet for ecological strategies? *The Journal of Animal Ecology*, 46, 337–365. Available from: <https://doi.org/10.2307/3817>
- Statzner, B., Dolédec, S. & Hugué, B. (2004) Biological trait composition of European stream invertebrate communities: assessing the effects of various trait filter types. *Ecography*, 27, 470–488. Available from: <https://doi.org/10.1111/j.0906-7590.2004.03836.x>
- Sterner, R.W. & Elser, J.J. (2002) *Ecological stoichiometry: the biology of elements from molecules to the biosphere*. Princeton, New Jersey, NJ: Princeton University Press.
- Strayer, D.L. & Dudgeon, D. (2010) Freshwater biodiversity conservation: recent progress and future challenges. *Journal of the North American Benthological Society*, 29, 344–358. Available from: <https://doi.org/10.1899/08-171.1>
- Swenson, N.G. (2014) *Functional and phylogenetic ecology in R*. New York: Springer. Available from: <https://doi.org/10.1007/978-1-4614-9542-0>
- Tachet, H., Richoux, P., Bournaud, M. & Usseglio-Polatera, P. (2010) *Invertébrés d'eau Douce: Systematique, Biologie, Ecologie*. Paris, France: CNRS EDITIONS.
- Tilman, D. (2001) Functional diversity. In: Levin, S.A. (Ed.) *Encyclopaedia of biodiversity*. New Jersey, NJ: Academic Press, pp. 109–120.
- Tockner, K., Uehlinger, U. & Robinson, C.T. (2009) *Rivers of Europe*, 1st edition. Elsevier. Available from: <https://doi.org/10.1016/B978-0-12-369449-2.X0001-X>

- Tonkin, J.D., Bogan, M.T., Bonada, N., Rios-Touma, B. & Lytle, D.A. (2017) Seasonality and predictability shape temporal species diversity. *Ecology*, 98, 1201–1216. Available from: <https://doi.org/10.1002/ecy.1761>
- Townsend, C.R. & Hildrew, A.G. (1994) Species traits in relation to a habitat template for river systems. *Freshwater Biology*, 31, 265–275. Available from: <https://doi.org/10.1111/j.1365-2427.1994.tb01740.x>
- Tuchman, N.C., Wetzel, R.G., Rier, S.T., Wahtera, K.A. & Teeri, J.A. (2002) Elevated atmospheric CO₂ lowers leaf litter nutritional quality for stream ecosystem food webs. *Global Change Biology*, 8, 163–170. Available from: <https://doi.org/10.1046/j.1365-2486.2002.00460.x>
- Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R. & Cushing, C.E. (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, 37, 130–137. Available from: <https://doi.org/10.1139/f80-017>
- Verberk, W.C.E.P., van Noordwijk, C.G.E. & Hildrew, A.G. (2013) Delivering on a promise: integrating species traits to transform descriptive community ecology into a predictive science. *Freshwater Science*, 32, 531–547. Available from: <https://doi.org/10.1899/12-092.1>
- Villéger, S., Mason, N.W.H. & Moullot, D. (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89, 2290–2301. Available from: <https://doi.org/10.1890/07-1206.1>
- Walentowski, H., Ewald, J., Fischer, A., Kölling, C. & Türk, W. (2004) *Handbuch der natürlichen Waldgesellschaften in Bayern*. Freising, Germany: Geobotanica.
- Webster, J.R. (2007) Spiraling down the river continuum: stream ecology and the U-shaped curve. *Journal of the North American Benthological Society*, 26, 375–389. Available from: <https://doi.org/10.1899/06-095.1>
- Welti, E.A.R., Roeder, K.A., de Beurs, K.M., Joern, A. & Kaspari, M. (2020) Nutrient dilution and climate cycles underlie declines in a dominant insect herbivore. *Proceedings of the National Academy of Sciences*, 117, 7271–7275. Available from: <https://doi.org/10.1073/pnas.1920012117>
- Woods, T., Kaz, A. & Giam, X. (2022) Phenology in freshwaters: a review and recommendations for future research. *Ecography*, 2022, 1–14. Available from: <https://doi.org/10.1111/ecog.05564>
- Woodward, G., Perkins, D.M. & Brown, L.E. (2010) Climate change and freshwater ecosystems: impacts across multiple levels of organization. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 2093–2106. Available from: <https://doi.org/10.1098/rstb.2010.0055>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supplementary 1. Macroinvertebrate sampling procedures and trait coding

Supplementary 2. Descriptive statistics of region-specific environmental variables

Supplementary 3. Taxonomic and functional composition and diversity in more detail

Supplementary 4. Individual drivers and directionality

How to cite this article: Baker, N.J., Welti, E.A.R., Pilotto, F., Jourdan, J., Beudert, B., Huttunen, K.-L. et al. (2023) Seasonal and spatial variation of stream macroinvertebrate taxonomic and functional diversity across three boreal regions. *Insect Conservation and Diversity*, 1–19. Available from: <https://doi.org/10.1111/icad.12623>