Science of the Total Environment 842 (2022) 156689

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Evaluating the biological validity of European river typology systems with least disturbed benthic macroinvertebrate communities

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http://dx.doi.org/10.1016/j.scitotenv.2022.156689
Received 11 February 2022; Received in revised form 18 May 2022; Accepted 10 June 2022
Available online 17 June 2022
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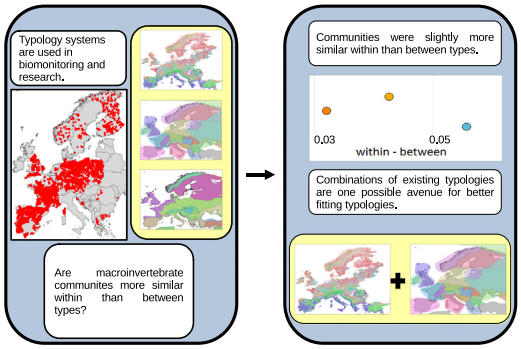
HIGHLIGHTS

- River typologies are indispensable for biomonitoring and ecological research.
- River types should delineate distinct biotic communities.
- We tested this for European river typologies using macroinvertebrates.
- Communities were dissimilar between types; only marginally more similar within.
- Our results support using typologies for studies of large-scale biodiversity trends

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Sergi Sabater

Keywords:
Water framework directive
Ecoregions
Biomonitoring
Macroinvertebrates
River typology

ABSTRACT

Humans have severely altered freshwater ecosystems globally, causing a loss of biodiversity. Regulatory frameworks, like the Water Framework Directive, have been developed to support actions that halt and reverse this loss. These frameworks use typology systems that summarize freshwater ecosystems into environmentally delineated types. Within types, ecosystems that are minimally impacted by human activities, i.e., in reference conditions, are expected to be similar concerning physical, chemical, and biological characteristics. This assumption is critical when water quality assessments rely on comparisons to type-specific reference conditions. Lyche Solheim et al. (2019) developed a pan-European river typology system, the Broad River Types, that unifies the national Water Framework Directive typology systems and is gaining traction within the research community. However, it is unknown how similar biological communities are within these individual Broad River Types. We used analysis of similarities and classification strength analysis to examine if the Broad River Types delineate distinct macroinvertebrate communities across Europe and whether they outperform two ecoregional approaches: the European Biogeographical Regions and Illies' Freshwater Ecoregions. We determined indicator and typical taxa for the types of all three typology systems and evaluated their distinctiveness. All three typology systems captured more variation in macroinvertebrate communities than random combinations of sites. The results were similar among typology systems, but the Broad River Types always performed worse than either the Biogeographic Regions or Illies' Freshwater Ecoregions. Despite reaching statistical significance, the statistics of analysis of similarity and classification strength were low in all tests indicating substantial overlap among the macroinvertebrate communities of different types. We conclude that the Broad River Types do not represent an improvement upon existing freshwater typologies when used to delineate macroinvertebrate communities and we propose future avenues for advancement: regionally constrained types, better recognition of intermittent rivers, and consideration of biotic communities.

1. Introduction

The European Water Framework Directive (WFD, European Commission, 2000) is intended to protect and restore freshwater ecosystems in the European Union (EU). Within the WFD each water body is assigned an ecological status class, spanning from high to bad status. The assignment is based on the deviation between the observed conditions and the reference conditions, which are the conditions assumed to prevail under no or minimal disturbance. Due to the large natural variation in physical, chemical, and biological conditions between rivers, reference conditions vary between rivers and between different segments of the same river (Verdonschot, 2000). Typology systems are a method to accommodate this variability. The individual river segments are assigned to river types based on selected abiotic conditions (Melles et al., 2014; Pennak, 1971). The WFD requires that type-specific reference conditions are defined for hydromorphological, physical, chemical, and biological variables, either using a spatially-based reference site network from each river type, hindcasting (e.g., Launois et al., 2011), paleoecology (e.g., Anderson et al., 2004), or expert judgment (e.g., Poikane et al., 2019).

Typology systems commonly apply one of two spatial approaches to allocate rivers to types: regional or segmental. Regional typology systems define large, spatially contiguous areas as types, which are also known as ecoregions (e.g., Abell et al., 2008). This approach is typical for terrestrial typology systems, for example, the Biogeographic Regions (EEA, 2016) are used within the Habitats (92/43/EEC) and the Birds Directive (79/409/EEC 1979). When used for lotic freshwater systems, ecoregions fail to account for changes along a river's course (e.g., Vannote et al., 1980) or its position within the dendritic river network (Campbell Grant et al., 2007). Nonetheless, regional typology systems have been proposed (e.g., Abell et al., 2008; Omernik and Griffith, 2014) and endorsed (e.g., Stoddard, 2004) for freshwater systems. Within the WFD, Illies' Freshwater Ecoregions (Illies, 1978) are used alongside catchment size, altitude, and geology, as a minimum set of criteria to define segmental river types. Segmental typology systems consider individual river segments, which commonly stretch between tributary junctions or confluences. These typologies are more commonly used for freshwater systems since they can account for longitudinal patterns and network position. Recent examples include a global typology system (Ouellet Dallaire et al., 2019), one for the conterminous United States (McManamay and DeRolph, 2019), and one for Europe (Lyche Solheim et al., 2019).

To establish reliable biological reference conditions for bioassessment, the variables used to define the types should also influence biotic community composition (Verdonschot and Nijboer, 2004). When this is the case, the relative homogeneity of environmental variables, such as climate, geology, and geomorphology, that exist within each type can engender correspondingly homogenous biocenoses. The degree to which any typology system meets this expectation can be evaluated by comparing the similarity of biotic communities from the same type (within-type similarity) to that of communities from different types (between-type similarity). For large-scale assessments of biodiversity trends and anthropogenic pressures (henceforth

biodiversity monitoring), a typology system is useful if the between-type similarity is low and exceeded by the within-type similarity. For bioassessment, however, the within-type similarity must be high, irrespective of between-type similarity. If the within-type similarity is low, no reliable type-specific conditions can be established and the type must be excluded from the status assessment (European Commission, 2000).

An evaluation of coherence between typology systems and biotic communities is known as biological validation and is a necessary consideration in the construction of a typology system (Melles et al., 2014). Biological validations that compare the variation of biological communities within types to that among types and is common practice for national WFD typology systems (e.g., Aroviita et al., 2008; Chaves et al., 2011; Lazaridou et al., 2013; Lorenz et al., 2004; Sánchez-Montoya et al., 2007; Zahrádková et al., 2005), but also regional typology systems (Feminella, 2000) and typology systems outside of Europe (Ferronato et al., 2021; Hawkins et al., 2000; Pero et al., 2019).

The national typology systems used in the WFD vary widely among EU countries in the number of river types they discern (between 1 and 367) and the features that are used to define their types (Lyche Solheim et al., 2019). Lyche Solheim et al. (2019) combined >1000 national WFD river types into twelve Broad River Types in an attempt to define a generic pan-European river typology system. The aim was to create a typology system that can aggregate type-specific data on ecological status across Europe. Furthermore, the Broad River Types were proposed and quickly adopted as a means for large scale assessments of nutrient thresholds (Nikolaidis et al., 2021; Poikane et al., 2019) and anthropogenic stressors (Birk et al., 2020; Lemm et al., 2021; Posthuma et al., 2020) and are currently being discussed as the basis of the revised European Nature Information System freshwater classification (Watson et al., 2021). However, until now, the Broad River Types have not been biologically validated.

In this paper, we evaluated the biological validity of the Broad River Types typology of European freshwater systems and thus whether they are appropriate for bioassessment and biodiversity monitoring. To contextualize the results, we compared the results to those of two other pan-European typology systems that are currently used within the EU legislature: The Biogeographic Regions and Illies' Freshwater Ecoregions. We evaluated the three typology systems by analyzing the within- and between-type similarities of riverine macroinvertebrate communities and determining whether we can derive distinct typical communities for the respective types. Specifically, we aim to answer four research questions:

- Q1: Are the similarities among biotic communities within types higher than between types, thus enabling biodiversity monitoring.
- Q2: Are the similarity among biotic communities within types sufficiently high to enable bioassessment?
- Q3: Are the segmental Broad River Types more appropriate for bioassessment and biodiversity monitoring than the two regional typology systems considered here?
- Q4: Can distinct indicator taxa and typical communities be derived for the individual types?

2. Methods

2.1. Typology systems

2.1.1. Broad river types

Lyche Solheim et al. (2019) derived 20 pan-European river types from the five descriptors catchment size, altitude, geology, region, and flow. As some of the initial 20 types were rare or deemed redundant, they aggregated them into 12 types (see Table 1). The first three descriptors are part of the System A approach outlined in Annex II of the WFD and Lyche Solheim et al. (2019) largely followed the class thresholds proposed there. While System A includes a region descriptor that recognizes 25 distinct regions throughout Europe, the region descriptor used by Lyche Solheim et al. (2019) only separates the Mediterranean and the rest of Europe. Flow is also treated as a binary variable (perennial or temporary/intermittent) and was only applied to rivers in the Mediterranean region. A digital representation of the Broad River Types was published by Globevnik (2019).

Table 1
Codes and names of the twelve Broad River Types proposed by Lyche Solheim et al. (2019). The sizes refer to catchment area: very small-small <100 km^2, medium-large 100–10.000 km^2 and very large >10.000 km^2. Lowland denotes river segments <200 meters above sea level (m.a.s.l.), mid-altitude 200–800 m.a.s.l. and highland >1.000 m.a.s.l. The geologies describe the prevailing lithological or pedological conditions in the catchments. Catchments are calcareous or siliceous if the respective soil types or minerals cover >50 % of the catchments area. If coverage is between 40 % and 50 % it is classified as mixed. Catchments with >20 % of their area covered by histosols are classified as organic.

Broad river type code	Broad river type name
RT1	Very large rivers
RT2	Lowland, calcareous or mixed, medium-large
RT3	Lowland, calcareous or mixed, very small-small
RT4	Lowland, siliceous incl. organic, medium-large
RT5	Lowland, siliceous incl. organic, very small-small
RT6	Mid-altitude, calcareous incl. organic, medium-large
RT7	Mid-altitude, calcareous or mixed, very small-small
RT8	Mid-altitude, siliceous incl. organic, medium-large
RT9	Mid-altitude, siliceous incl. organic, very small-small
RT10	Highland and glacial
RT11	Mediterranean, perennial
RT12	Mediterranean temporary and very small

2.1.2. Biogeographic regions

The Habitats Directive (92/43/EEC) references five biogeographic regions: Alpine, Atlantic, Continental, Macaronesian, and Mediterranean. These regions were based on a map of European potential natural vegetation (Noirfalse, 1987). New regions were added as additional member countries joined the EU in 1995 (Arctic & Boreal regions) and 2004 (Anatolian, Black Sea, Pannonian & Steppic regions) (Evans, 2005). Here we used the version available at https://www.eea.europa.eu/data-and-maps/data/biogeographical-regions-europe-3.

2.1.3. Illies' freshwater ecoregions

The *Limnofauna Europaea* (Illies, 1978) is a comprehensive catalog of the European freshwater fauna. As a means to describe biogeographic differences in species distributions, the author divided Europe into 25 regions following the distribution of 75 taxonomic groups but occasionally also geopolitical borders (Economou et al., 2004). These regions captured altitude, climate, and geology indirectly (Logan and Furse, 2002). The ecoregions proposed in Annex XI of the WFD (European Commission, 2000) deviate slightly from the originally proposed regions (Logan and Furse, 2002). Here we used the version also employed in the WFD and available under https://www.eea.europa.eu/data-and-maps/data/ecoregions-for-rivers-and-lakes.

2.2. Macroinvertebrate data

To evaluate the three typologies, we compiled a database of macroinvertebrate samples from lotic freshwater systems (e.g., rivers, streams, and brooks) throughout Europe (Fig. 1). The database consisted of 21 datasets (Table S1) and included 49.220 distinct sampling sites at which 163.114 samples have been collected. All samples were obtained by fully or partially proportional multihabitat sampling (Table S1) similar to the AQEM/STAR sampling method (The STAR Consortium, 2003). Most samples originate from regional or national biomonitoring campaigns. Despite extensive harmonization efforts, sampling strategies for biomonitoring differ between European countries in terms of sampling effort, sampling device, and habitat selection (Larras and Usseglio-Polatera, 2020). Even though differences between years or streams are commonly larger than between sampling methods (Borisko et al., 2007; Brua et al., 2011), the differences can bias the samples. We undertook three steps to reduce this bias. First, we removed samples from monitoring data sets that were taken

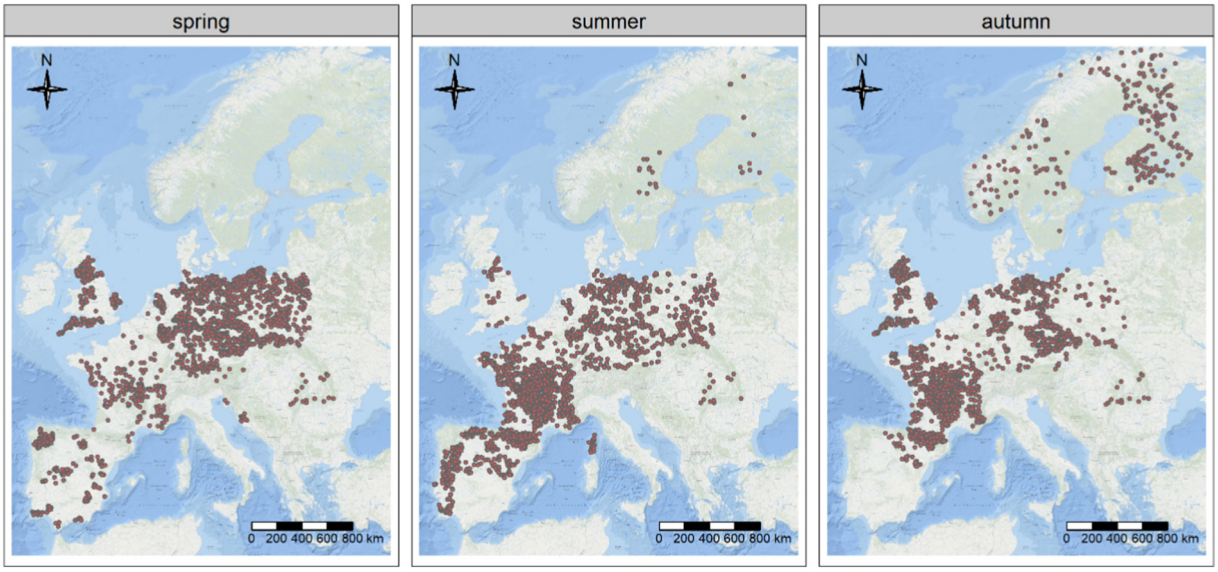


Fig. 1. The locations of macroinvertebrate sampling sites for each season. All sites shown are least disturbed sites (see text), sampled after 2005, and could be assigned a Broad River Type (see text).

before 2005. Many countries implemented the AQEM/STAR sampling method in 2005, which is deemed to significantly reduce the differences between data sets. Second, all comparisons were conducted at the family level. This was done to reduce differences between sampling schemes (Brua et al., 2011) but also because the evaluation of similarities requires the same taxonomic resolution (Cao and Hawkins, 2011). The family level was the highest taxonomic resolution for which we could achieve broad spatial coverage. However, this taxonomic harmonization likely increased the similarity between samples from the same as well as from different types (Heino, 2014; Vasconcelos et al., 2013). A higher taxonomic resolution (i.e., genus- or species-level data) could only reduce the similarities but not increase them, since members of the same family can be from different genera or species but the same species cannot be part of multiple families. Lastly, we omitted abundance information and transformed all data to presence-absence. This removed differences that arise from different counting efforts or procedures and is common in analyses of data from different sampling schemes (e.g., de Vries et al., 2020). Finding a common transformation was necessary for comparisons (Heino, 2008) and choosing presence-absence maximized the number of samples included. It should be noted that this is not consistent with the requirements of the WFD, which requires abundance data (European Commission, 2000) and several studies have found a considerable loss of information through the transformation from abundance to presence-absence (e.g., Marshall et al., 2005; Melo, 2005; Vasconcelos et al., 2013). However, different streams (Melo, 2005) and catchments (Heino, 2014) could still be discerned with presence-absence data in previous studies.

We conducted two analyses to evaluate the effect of taxonomic and numeric resolutions on the similarities. First, we conducted Mantel tests (Mantel, 1967) for all data sets. In data sets with most observations at the species level and abundance data, we compared the distance matrices of (i) species-level abundance data to genus-level and family-level abundance data as well as genus-level data to family-level abundance data, (ii) abundance to presence-absence at species, genus and family levels and lastly (iii) species abundance to genus and family occurrences as well as genus abundances to family occurrences. We used the Bray-Curtis distance to compute distance matrices for abundance data and Jaccard for presence-absence data. For a data set with data from three seasons with species-level abundances, we thus conducted 27 Mantel tests. In total, we ran 366 of 594 theoretically possible tests, as many data sets did not have sufficient species-level data or only provided presence-absence data. These tests indicated that little information was lost in the transformations to family level and presence-absence. The distance matrices of different taxonomic levels or numerical resolutions were statistically significantly correlated ($p < 0.05$ for 362 of 366 Mantel tests). A more detailed description of these results is presented in the supplementary materials (see SM4). Second, we repeated the main analyses described below for genus-level data with relative abundances. Like the Mantel tests, they indicated only minor differences between the different resolutions (see SM5).

To avoid seasonal trends from affecting the community compositions (as shown by e.g., Lorenz and Clarke, 2006; Reece et al., 2001; but see Huttunen et al., 2022), we stratified the samples by season and conducted each analysis for each season separately. We define spring as covering the months March to May, summer covering the months June to August, and autumn covering the months September to November. We did not analyze winter samples (December to February) as there were only few in the data set. Some of the sites were sampled repeatedly over the years. Samples from the same site and season are often very similar (Huttunen et al., 2022; Lorenz and Clarke, 2006), so we only used the most recent sample from each site for every season. Removing samples from before 2005, samples taken in winter, and only using the most recent sample for each site reduced the number of sites and samples to 39.252 (79.7 % remaining) and 56.894 (34.9 % remaining), respectively.

We used the Global Biodiversity Information Facility (www.gbif.org) to replace taxon synonyms with accepted names and to assign a taxonomic level to each observation. We restricted observations to the invertebrate classes Insecta, Gastropoda, Bivalvia, Malacostraca, and Arachnida which were observed in all data sets. Oligochaetes were observed in most data sets but rarely determined beyond the class level and thus removed. Within these classes, we further reduced the data to the orders Trombidiformes, Megaloptera, Isopoda, Littorinimorpha, Odonata, Sphaeriida, Hemiptera, Amphipoda, Coleoptera, Trichoptera, Diptera, Ephemeroptera, and Plecoptera. We included families that belong to the polyphyletic taxon Pulmonata (i.e., Acroloxidae, Lymnaeidae, Physidae, Planorbidae) as well as the gastropod family of Valvatidae. Lastly, we removed families that occurred in <1 % of samples. This was done separately for each season. The final data set contained 95, 104, and 97 families for spring, summer, and autumn, respectively.

2.3. Selection of sampling sites

Broad River Types were assigned to macroinvertebrate samples digitally by matching each sampling site with the next river reach in the digital representation of the Broad River Types (Globevnik, 2019, Accessed 11.12.2019). We retained only sites that we could unambiguously assign

to a specific river reach. All sites with a distance >500 m to the nearest river reach were omitted from further analyses. These sites were likely located at river reaches that were missing from the digital river network provided by Globevnik (2019). This occurs with very small or intermittent rivers and in flat areas such as coastal plains, where the derivation of river networks from digital elevation models is most error-prone. Removing sites with a distance >500 m to the nearest river reach reduced the number of sites and samples to 25.334 (51.5 % remaining) and 36.694 (22.5 % remaining), respectively.

Anthropogenic stressors are suspected to harmonize communities (Petsch, 2016; but see Petsch et al., 2021) and might thus increase the similarity among communities of different types. Therefore, we identified the least disturbed sites (sensu Stoddard et al., 2006) based on the pan-European stressor database created by Lemm et al. (2021). The database contains information on seven anthropogenic stressors (extent of urban and agricultural land use in the riparian zone, alteration of mean annual flow and baseflow index, total phosphorus and nitrogen load, and mixture toxic pressure) for over 50.000 sub-catchment units across Europe. We scaled each variable: $x_i' = \frac{x_i - min\ (x)}{max\ (x) - min\ (x)}$ where x_i' is the scaled variable, x_i the unscaled variable, $min(x)$ the minimum of the unscaled variable, and $max(x)$ the maximum of the unscaled variable. We considered all sub-catchment units as least disturbed that had scores below 0.24 for all seven stressors. The rationale for a threshold of 0.24 as well as summary statistics of least disturbed sites (Table S2) are provided in the supplementary materials (see SM2). Only least disturbed sites were retained. Sampling sites that were located outside the area covered by Lemm et al. (2021) were removed, except for data set 21 (Table S1) which only consisted of samples from least disturbed sites. The final selection included 6.965 sites (14,1 % remaining) and 9.976 samples (6,1 % remaining).

2.4. Evaluation of typologies

We only included those types in the analyses, for which we had at least 15 samples from least disturbed sites (Figs. S3 and S4 in SM3). Following this criterion, all twelve Broad River Types were covered with spring and summer samples and only RT12 was omitted for autumn samples, four of eleven Biogeographic Regions were covered for all seasons, and one for two seasons. We included ten of twenty-five Illies' Freshwater Ecoregions for all seasons, two for two seasons, and three for one season. After removing samples from types that we did not analyze, 6890 sites and 9850 samples remained. The distribution of samples between seasons and types is shown in Tables (S3–S5).

To answer the research questions Q1, Q2, and Q3 we computed and compared within- and between-type similarity with two approaches: analysis of similarity (ANOSIM, Clarke, 1993) and classification strength (CS, Van Sickle, 1997). ANOSIM computes a statistical parameter R to express the difference between the mean rank of between-type similarities to the mean rank of within-type similarities. An R value above 0.75 indicates a clear separation between groups, a value between 0.75 and 0.5 indicates a weaker separation with overlapping groups, R values between 0.5 and 0.25 indicate weak separation, and values below 0.25 indicate no discernable separation (Clark and Gorley, 2001). By permuting the type membership between samples 999 times, we computed pseudo-p-values.

The CS of a classification is the difference between the mean within-cluster similarity ($\bar{W}$) and the mean between-cluster similarity ($\bar{B}$), i.e., $CS = \bar{W} - \bar{B}$. To account for unequal cluster sizes, a weighted mean was used to compute $\bar{W}$, i.e., $\bar{W} = \Sigma_i \frac{n_i}{N} W_i$ with n_i being the number of sites in cluster i and N is the total number of sites. As with ANOSIM, a pseudo-p-value was computed by permuting the type membership of samples 999 times. Statistically significant p-values at the 0.05 significance level for ANOSIM and CS confirm Q1. To affirm Q2, we additionally required high test statistics, i.e., ANOSIM $R > 0.5$ and CS > 0.10. The former is based on the thresholds provided by Clark and Gorley (2001) and the latter on the results of previous studies (Hawkins et al., 2000; Heino and Mykrä, 2006; Snelder et al., 2004). The research question Q3 was answered by comparing the respective test statistics between the three typology systems.

To answer the research question Q4, we derived indicator taxa for each type of each typology using the Indicator Value (IndVal) approach of Dufrêne and Legendre (1997). The IndVal is the product of concentration (A) and relative frequency (F). The maximum score would be assigned to a taxon that only occurs in one type ($A = 1$) but in all samples of that type ($F = 1$). Here, we used the group-equalized version of the IndVal which accounts for the fact that the number of samples differs among types (De Cáceres and Legendre, 2009). The statistical significance of the IndVal statistic was assessed by permuting the type membership of samples 999 times. We used the number of statistically significant indicator taxa ($p < 0.05$) as well as the mean indicator value of indicator taxa as test statistics.

Lastly, we derived typical communities for each type, which consisted of all families with $F > 0.66$. We set this threshold as we regard a taxon as common if it occurs in two-thirds of samples from a type. The mean Jaccard similarity between typical communities of a typology was used as a test statistic. The Jaccard similarity can range from zero (no taxa in common) to 1 (identical community). We computed pseudo-p-values of similarities by permuting the type membership among samples 999 times.

2.5. Software

All computations were conducted in the R Statistical Environment v. 4.0.3 (R Core Team, 2020). Data were prepared using data.table 1.14.0 (Dowle and Srinivasan, 2021), tidyverse packages (Wickham et al., 2019), taxize 0.9.98 (Chamberlain and Szöcs, 2013; Chamberlain et al., 2020) and parallelDist (Eckert, 2018). Geospatial analyses were conducted using sf (Pebesma, 2018). ANOSIMs were computed with the vegan R package (Oksanen et al., 2020). The CS was computed with an R-function that is available as supplementary material (SM8). Indicator and typical communities were derived with indicspecies (De Cáceres and Legendre, 2009). Figures and maps were created with ggplot2 (Wickham, 2016), ggdist (Kay, 2021), colorspace (Zeileis et al., 2019), and tmap (Tennekes, 2018). All R scripts are available in the github repository https://github.com/JonJup/freshwater-typologies-mzb.

3. Results

All three typology systems delineated distinguishable biotic communities that were more similar within than between types (for all ANOSIM and CS: $p < 0.05$; Fig. 2). However, within-type similarities were often only marginally higher than between-type similarities (Fig. S11). The difference was most pronounced in Illies' Freshwater Ecoregions ($\overline{R_{ANOSIM}} = 0.27$; $\overline{CS} = 0.08$), followed by the Broad River Types ($\overline{R_{ANOSIM}} = 0.19$; $\overline{CS} = 0.05$) and the Biogeographic Regions ($\overline{R_{ANOSIM}} = 0.07$; $\overline{CS} = 0.03$). The performance varied across seasons. The Broad River Types were a better classification of the summer samples than of the spring or autumn samples, and Illies' Freshwater Ecoregions performed worse in spring than in summer and autumn (Fig. 2).

The within-type similarity varied considerably between the Broad River types (Fig. 3). As a general trend, we observed that mid- and high-altitude river types (RT6–10) have higher within-type similarity than low-altitude river types (RT1–5). Similarities also varied across seasons but without a general pattern.

We were able to derive distinct indicator taxa and typical communities for the individual types of all three typologies. On average, the indicator taxa were more indicative (higher mean IndVal) than those derived from random site combinations (Fig. 4A) and the number of indicator taxa was larger (Fig. 4B). The indicator families of Biogeographic Regions and Illies' Freshwater had similar indication power (mean IndVal ($\overline{Indval}$) = 0.49 *for both*). The indicator families of the Biogeographic regions were slightly more indicative in spring and autumn whereas Illies' Freshwater Ecoregions' indicator families were more indicative in summer. Indicator

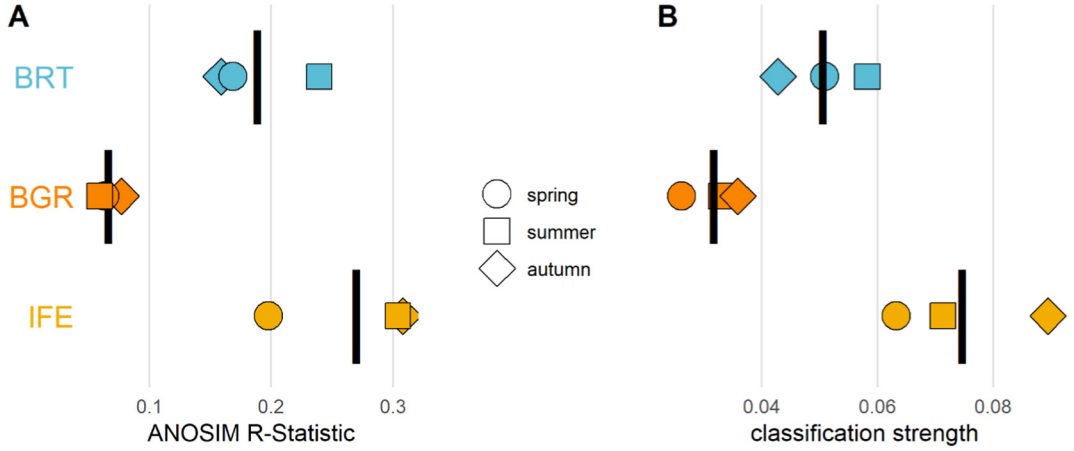


Fig. 2. Comparison of within-type and between-type. In both panels, larger values imply a larger difference between within-type and between-type similarity and hence a better classification performance. Y-axis and colors indicate the typology system: the Broad River Types (BRT), Biogeographic Regions (BGR), and Illies' Freshwater Ecoregions (IFE). The shapes indicate the season (circle = spring, square = summer, and diamond = autumn). The vertical black lines are mean values across seasons. (A) Results of the ANOSIM; (B) results of classification strength analysis.

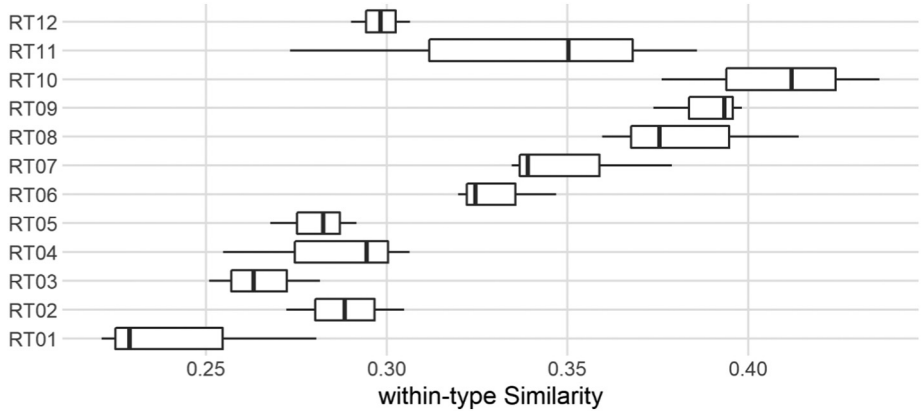


Fig. 3. The within-type similarity of Broad River Types. Each boxplot summarizes the values for the three seasons (except for RT12 where only spring and summer were analyzed). See Lyche Solheim et al. (2019) or Table 1 for a description of the types.

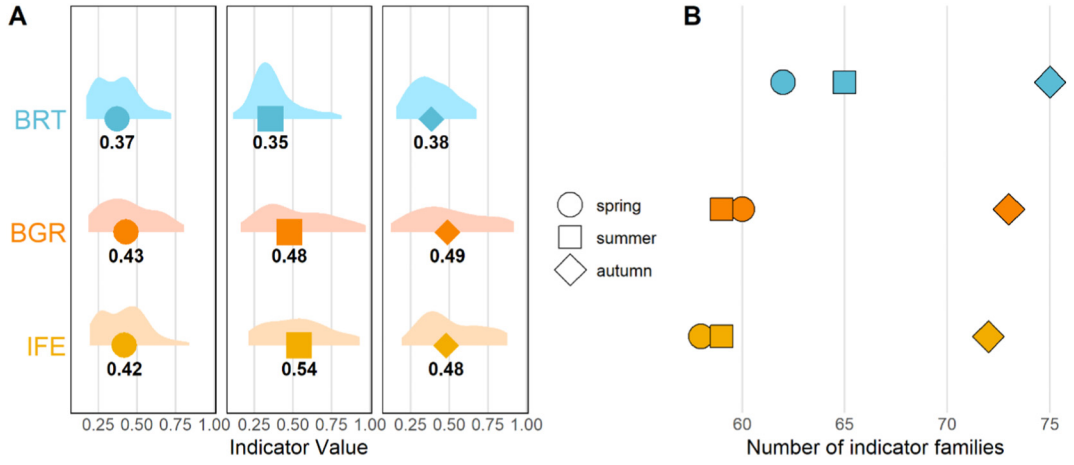


Fig. 4. Indicator taxa for the Broad River Types (BRT), the Biogeographic Regions (BGR), and Illies' Freshwater Ecoregions (IFE). (**A**) Distribution of indicator values. Values can range between 0 and 1, where 1 indicates a perfect indicator taxon. The points within the density curves highlight the median, which is also provided as a number. Three panels show the three different seasons (spring, summer, and autumn), which are also highlighted by the symbol of the median. (**B**) The number of indicator families. Point shapes indicate seasons and point colors the typology systems.

values for the Broad River Types were lower in every season ($\overline{IndVal} = 0.38$). However, the number of families that were statistically significant indicators was consistently higher in the Broad River Types than in the other two typology systems. For all three typology systems, the number of indicators was highest in autumn. Lists of indicator taxa for each season and typology system are available in the supplementary materials.

All typical communities were more distinct from each other than for random combinations of sites ($p < 0.01$). The typical communities did not show strong seasonal trends. The mean similarity was always lowest in Illies' Freshwater Ecoregions (mean similarity of 0.40), followed by the Broad River Types (0.48) and the Biogeographic regions (0.50) (Fig. 5). Lists of the typical communities are available as supplementary material (SM7) and in Figs. S12, S13 and S14.

4. Discussion

4.1. Coherence of biological communities

The three pan-European freshwater typology systems considered here did delineate more distinguishable biotic communities than random partitions of the samples. Within-type similarity always exceeded between-type similarity, but only by a small margin. The between-type similarities of all typology systems indicate that two sites from different types are likely to share between a quarter and a third of the families from the combined pool of families, while the other three-quarters to two-thirds of the families are unique to either one of the sites. Since similarity values would likely decrease with an increase in taxonomic resolution the number of shared genera and species would likely be lower. Our first research question (i.e., are the Broad River Types fit for biodiversity monitoring?) can thus be confirmed. However, the second research question (i.e., are the Broad River Types fit for bioassessment?) has to be negated. Due to the low within-type similarity, the test statistics for ANOSIM and CS were far below the ordained thresholds. They were in the low range of results obtained for national typology systems, which have ranged from 0.2 to 0.5 for ANOSIM and 0.04 to 0.19 for CS (Dodkins et al., 2005; Hawkins et al., 2000; Heino and Mykrä, 2006; Lazaridou et al., 2013; Marchant et al., 2000; Sánchez-Montoya et al., 2007; Snelder et al., 2004; Vasconcelos et al., 2013). Though Illies' Freshwater Ecoregions compared more favorably to these previous results, our results indicate a considerable overlap between the types of any of these typology systems (Clark and Gorley, 2001). These low within-type similarities suggest that it is not reasonable to assume similar communities in least disturbed sites at the type-scale.

Our third question was whether the Broad River Types are better suited for bioassessment and biodiversity monitoring than Illies' Freshwater

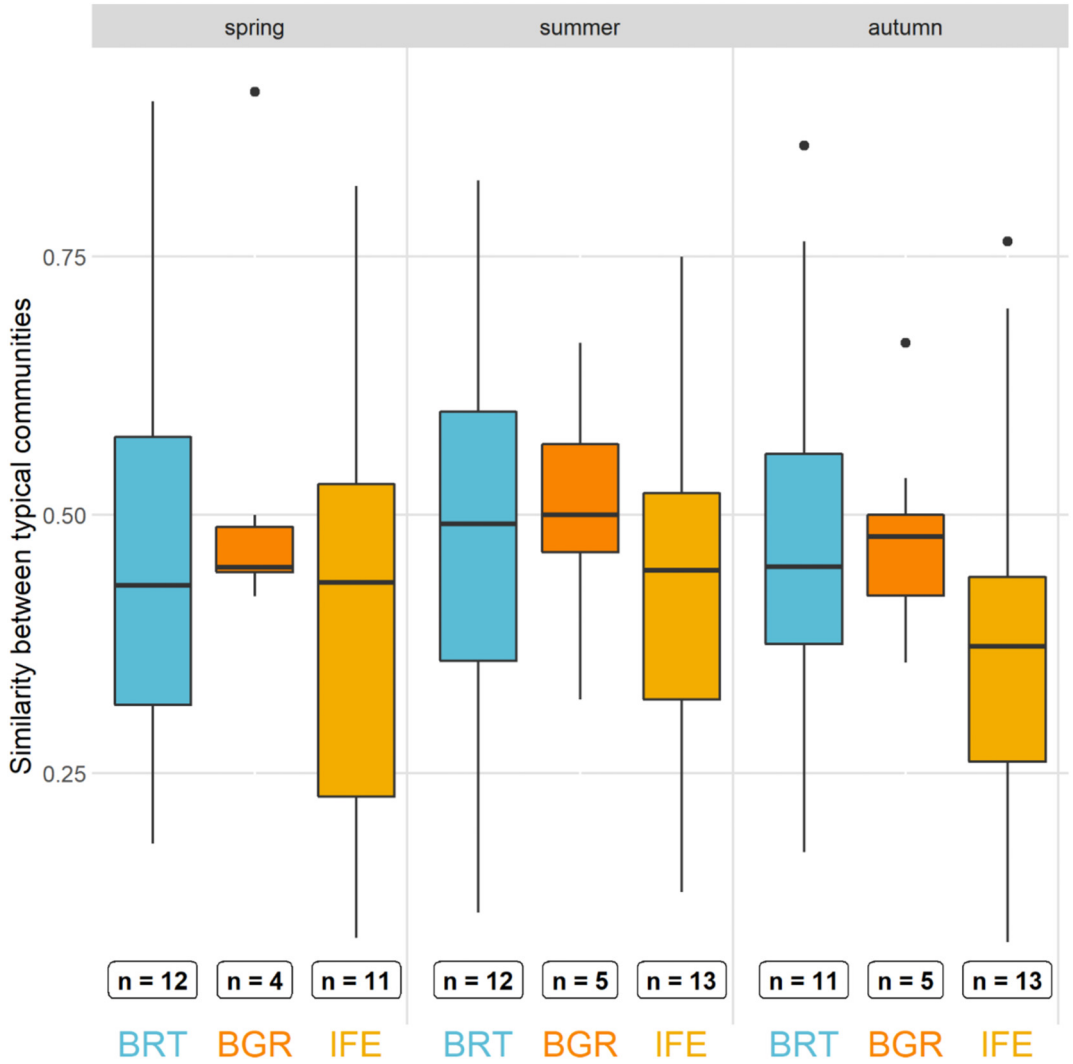


Fig. 5. Jaccard similarities between typical communities for the Broad River Types (BRT), Biogeographic Regions (BGR), and Illies Freshwater Ecoregions (IFE). A similarity of 1 implies an identical community, while a similarity of 0 implies no shared taxa. The three horizontally ordered panels show different seasons (spring, summer, and autumn). The n below the boxplots is the number of individual types in the comparison. Each density curve is derived from $\frac{n*(n-1)}{2}$ similarity values.

Ecoregions or the Biogeographic Regions. Even though we regard all typologies as suitable for biodiversity monitoring and none as suitable for bioassessment, there were noticeable differences between them. In a direct comparison, the Broad River Types performed better (higher CS and ANOSIM R) than the Biogeographic Regions but both performed considerably worse than Illies' Freshwater Ecoregions. Therefore, we also negate the third research question.

We were able to derive indicator taxa and typical communities for all three typologies and can thus confirm our fourth research question. There were more indicator taxa with higher mean indicator values for river typologies than those of random site combinations. The indicator values were generally in line with previous studies (Banks et al., 2007; Bonada et al., 2006; Heino and Mykrä, 2006; Sánchez-Montoya et al., 2007). The typical communities were less similar than would be expected by chance, indicating a change in the most common families among types.

A remarkable result was the high within-type similarity of mid- and high-altitude Broad River Types. The distinct nature of these rivers was also observed by Moog et al. (2004) and it is in line with the identification of high-altitude areas as one of the three large bioregions in Europe (Verdonschot, 2006b). The harshness of these environments (strong seasonality, high flow velocity, steep slopes) can increase the importance of dispersal for community assembly (Datry et al., 2016) and thus increase similarity among sites (Lu et al., 2019; Thompson et al., 2020; but see Lu, 2021). The lowest within-type similarities were observed for very large rivers (RT1). Their mean within-type similarity was lower than the mean between-type similarity. The biotic communities of very large rivers (catchment area > 10.000 km^2) are affected by multiple interacting stressors that were not explicitly considered in our identification of least disturbed sites. These include, among others, alien species (Arbačiauskas et al., 2008), navigation (Gabel et al., 2011; Liebmann and Reichenbach Klinke, 1967), and climate change (Caissie, 2006). Altered hydromorphology, an important stressor in very large rivers (Urbanič, 2014), is implicitly considered through the variables urban and agricultural land use as well as alteration of mean annual flow and the base flow index. Explicit information on hydromorphological alterations would be preferable, but, to our knowledge, is lacking at the pan-European scale. The magnitude of these stressors differs markedly between regions (Leitner et al., 2021) and can override regional differences leading to less indicative communities (Fittkau and Reiss, 1983), which is a possible explanation for the low similarity between the different samples from very large rivers.

We generally caution against interpreting any seasonal patterns in the results. The data were seasonally stratified to avoid a decrease in within- or between-type similarity due to seasonal dynamics. However, as not all sampling sites are present in all three seasons the observed patterns could be due to temporal or spatial variation. Most importantly, the main findings of this study do not change qualitatively between seasons.

4.2. Data constraints

Due to the taxonomic resolution of the initial data sets and the varying sampling approaches, we conducted all analyses at the family level. Analyses at the genus or species level would have included more taxa, which means more discriminating entities and thus potentially more distinct assemblages. In the analysis of Moog et al. (2004), higher taxonomic resolution led to more distinct ecoregions. Similarly, Verdonschot (2006a) showed that a small improvement in classification strength was noticeable between 'best-available' (mostly species and genus) and family-level data on a pan-European scale. This improvement is plausible since responses to environmental conditions are determined by traits, which are captured most accurately at detailed (species or individual) taxonomic resolution (Poff, 1997; Wong and Carmona, 2021). At the same time, community composition is influenced by non-environmental factors like biotic interactions, dispersal, and stochasticity (Leibold et al., 2004). If responses of congeneric species are more similar to each other than to those of more distantly related species (e.g., Hynes, 1984; Marchant et al., 1995), using genus- or family-level data might reduce this "noise" (Bowman and Bailey, 1997). However, the degree to which species niches are determined at the family level likely depends on the degree to which speciation within the family was sympatric or allopatric (Cranston, 1990; Dolédec et al., 2000). Hawkins et al. (2000) note that across taxa groups and typologies, a higher taxonomic resolution can occasionally even reduce classification strength. This notion is supported by our genus-level analyses and Mantel tests (Fig. S5) and by many studies showing that differences between differently resolved data sets are usually small (e.g., Bowman and Bailey, 1997; Feio et al., 2006; Furse et al., 1984; Godoy et al., 2019; Heino, 2008; Heino and Soininen, 2007; Melo, 2005; Rutt et al., 1990; Waite et al., 2004). Yet, some studies also find contrasting patterns, suggesting that higher taxonomic resolution confers significantly more information (e.g., Heino, 2014). Marchant et al. (1995) propose that the necessary degree of taxonomic resolution decreases with increasing spatial scale, with family-level data being sufficient for analyses that cover multiple catchments. This concurs with Moog et al. (2004), and if correct, would mean that family-level data is sufficient for our analysis.

The second measure we took to reduce the variation introduced by the varying sampling strategies was the transformation to presence-absence. Several studies have demonstrated that results can differ between presence-absence and abundance data (e.g., Heino, 2008; Marshall et al., 2005; Melo, 2005; Thorne et al., 1999; Vasconcelos et al., 2013). In comparison to abundance data, binary data put less weight on highly abundant taxa and more on rare ones, placing equal weight on each taxon, instead of each individual. The focus of the analysis thus moves from changes in relative abundances to changes in occurrences, which likely is the more important component of variation at the large spatial scales we considered in this study (Anderson et al., 2005). How large the difference between presence-absence and abundance data is, thus likely depends on the spatial scale of the study. All of the above studies have considered smaller spatial scales (often the catchment scale) and might therefore overestimate the deviation for the spatial scale of the present study. This is in line with the finding that different basins can be differentiated with family-level presence-absence data (Heino, 2014). In conclusion, using species-level and abundance data would likely affect our results. To which degree cannot conclusively be determined until such data becomes available but given the arguments above and the results of the Mantel tests as well as the genus-level analysis, we are confident that our conclusions would hold.

4.3. Next steps for freshwater typologies

We showed that currently available pan-European typology systems require improvements when they are used to define bioceonotic reference conditions. This is not a fault in their construction, as they were not primarily derived for this purpose. However, we believe they might serve as a starting point for typology systems that can be used to this end. Hence, we propose three modifications that might improve the Broad River Types' capacity to delineate coherent and distinct biotic communities. First, the combination of regional and segmental typology systems would likely improve the typologies fit to large-scale ecological patterns. Regional and segmental systems capture important but distinct scales of variation: variation among large geographic areas and longitudinal changes along the river's course, respectively. When combined, regions spatially constrain river types. Instances of the same Broad River Type are thousands of kilometers apart. At such large spatial scales, dispersal limitation is a crucial determinant of community composition (Tonkin et al., 2018). If species cannot reach favorable sites, due to historical or anthropogenic dispersal barriers (Belletti et al., 2020; Leibold et al., 2010) or due to the sheer distance between sites, within-type similarity decreases. Such spatial structuring of benthic macroinvertebrate communities has already been observed at smaller spatial scales (e.g., Astorga et al., 2012; Mykrä et al., 2007), indicating the potential benefit of spatially constrained types. The WFD System A typology system includes such a spatial constraint through the ecoregion descriptor. The Broad River Types, however, only differentiate between Mediterranean and non-Mediterranean regions. Including more elaborate regional descriptors such as Illies' Freshwater Ecoregions, the

Hydroecoregions (Wasson et al., 2007), the Biogeographic Regions, the Freshwater Ecoregions of the World (Abell et al., 2008), or the Environmental Zones of Europe (Metzger et al., 2012), would spatially constrain types and hence help to integrate dispersal limitations into the typology system. Problems can arise for rivers that run along or across ecoregion borders (Lazaridou et al., 2013) and using all types that result from such a combination produces too many types to be useful. Therefore, ways to optimally aggregate the combined types should be derived in future work.

Second, intermittent rivers and ephemeral streams (IRES) are common throughout Europe (Datry et al., 2014; Messager et al., 2021; Stubbington et al., 2018) and their prevalence is projected to increase with climate change (Jaeger et al., 2014). Intermittent flow regimes increase the importance of dispersal and network connectivity (Cid et al., 2020), reduce the importance of species sorting, and hence decrease the utility of purely environmental typology systems. The Broad River Types do not adequately account for this distinct and widespread river type by only recognizing them in the Mediterranean type. Simultaneously, they fail to capture the diversity of rivers in the Mediterranean region by aggregating them into two river types. The disregard for IRES mirrors the general lack of recognition for very small rivers (catchment size < 10 km^2) in the WFD (Stubbington et al., 2018) and their public undervaluation (Armstrong et al., 2012). This omission of very small rivers also neglects springbrooks, which are often distinct from nearby rhithral streams (Barquín and Death, 2006; Lusardi et al., 2016).

Third, while the Broad River Types are based solely on environmental attributes, biological communities can also be used as classification criteria. Doing so could help to better represent biological interactions, dispersal, and small-scale environmental variations (de Vries et al., 2020). While de Vries et al. (2020) argue for purely biological classifications, Hill et al. (2020) review numerous methods to combine biological and environmental features to this end. Among them, there are joint species distribution models (e.g., Ovaskainen and Abrego, 2020; Pichler and Hartig, 2021), generalized dissimilarity models (Ferrier et al., 2007), and regions of common profile (Foster et al., 2013). A drawback of including biotic features is their vicissitude. Classification criteria should be near immutable including by human action (e.g., altitude and bedrock geology), which is not true of biological communities. Particularly in western Europe, reference communities are often lacking and would need to be replaced by least disturbed (Stoddard et al., 2006) or modeled communities (e.g., Wright et al., 1998).

An alternative approach for pan-European biodiversity monitoring and bioassessment is the estimation of reference conditions with predictive models that use variable environmental attributes as inputs. These models are also trained with data from minimally-disturbed reference sites, but they estimate the expected value of an index or e.g., the occurrence probability of taxa for a site instead of a type. Deviations from predicted occurrences are interpreted as a sign of deterioration, as in typology-based assessments. Current iterations are restricted nationally, e.g., RIVPACS (Wright et al., 1998) to the United Kingdom and MEDPACS (Poquet et al., 2009) to Spain, or a lake profundal index in Finland (Jyväsjärvi et al., 2014). Regionalizations have been shown to increase the performance of site-specific models at large spatial scales (Yuan et al., 2008), however, ecoregions or segmental types are likely better delimiters than political borders. As model evaluations at the European scale are lacking for invertebrates (see Pont et al., 2007 for a model with fishes), optimizing typology systems to structure predictive modeling presents a further promising research topic for freshwater typology systems.

4.4. Conclusion

We evaluated three pan-European freshwater typology systems as classifications of riverine macroinvertebrate communities. All three performed better than random combinations of sites. However, the analyses also highlighted large overlaps between biocenoses of the river types. While between-type similarity was low enough for biodiversity monitoring, the within-type similarity was too small to support the use of pan-European typologies for bioassessment. A next step will be to evaluate the Broad River Types with additional taxonomic groups (e.g., macrophytes, fishes, and diatoms) to see if our findings generalize or pertain solely to benthic invertebrates.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.156689.

CRediT authorship contribution statement

Jonathan F. Jupke: Conceptualization, Writing - Original Draft Preparation, Writing - Review & Editing, Methodology, Software, Formal analysis. **Sebastian Birk**: Writing - Review & Editing, Conceptualization, Resources. **Mario Álvarez-Cabria**: Data curation, Resources, Writing - Review & Editing. **Jukka Aroviita**: Data curation, Resources, Writing - Review & Editing. **Pepe Barquín**: Data curation, Resources, Writing - Review & Editing. **Oscar Belmar**: Writing - Review & Editing. **Núria Bonada**: Data curation, Resources, Writing - Review & Editing. **Miguel Cañedo-Argüelles**: Data curation, Resources, Writing - Review & Editing. **Gabriel Chiriac**: Data curation, Resources, Writing - Review & Editing. **Emília Mišíková Elexová**: Data curation, Resources, Writing - Review & Editing. **Christian K. Feld**: Data curation, Resources, Writing - Review & Editing. **M. Teresa Ferreira**: Data curation, Resources, Writing - Review & Editing. **Peter Haase**: Data curation, Resources, Writing - Review & Editing. **Maria Lazaridou**: Data curation, Resources, Writing - Review & Editing. **Kaisa-Leena Huttunen**: Data curation, Resources, Writing - Review & Editing. **Margita Lešťáková**: Data curation, Resources, Writing - Review & Editing. **Marko Miliša**: Data curation, Resources, Writing - Review & Editing. **Timo Muotka**: Data curation, Resources, Writing - Review & Editing. **Riku Paavola**: Data curation, Resources, Writing - Review & Editing. **Piotr Panek**: Data curation, Resources, Writing - Review & Editing. **Petr Pařil**: Data curation, Resources, Writing - Review & Editing. **Edwin T. H. M. Peeters**: Data curation, Resources, Writing - Review & Editing. **Marek Polášek**: Data curation, Resources, Writing - Review & Editing. **Leonard Sandin**: Data curation, Resources, Writing - Review & Editing. **Denes Schmera**: Writing - Review & Editing. **Michal Straka**: Data curation, Resources, Writing - Review & Editing. **Philippe Usseglio-Polatera**: Data curation, Resources, Writing - Review & Editing. **Ralf B. Schäfer**: Writing - Review & Editing, Supervision, Project administration, Conceptualization, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This study was part of the GETREAL (Incorporating spatial and seasonal variability in community sensitivity into chemical risk assessment) project, which was funded by the European Chemical Industry Council long-range research initiative (CEFIC-LRi project ECO 50). Dénes Schmera was supported by the NKFIH K140352 and 471-3/2021 grants. Petr Pařil, Marek Polášek and Michal Straka were supported by the P505-20-17305S grant. We are grateful to the staff that collected and analyzed data for the AQEM (EU FP5, contract No: EVK1-CT1999-00027), BIODROUGHT, STAR (EU FP5, contract No: EVK1-CT 2001-00089), and WISER (EU FP7, contract No 226273) projects and to the various water agencies that participated in the abiotic and biotic data collection and analysis. The authors thank the CHMI and the enterprises Povodí for providing the data from the Czech state monitoring. We also thank Agnès Bouchez, Stéphanie Couprie, Lucie Clavel, Geoff Phillips, and John Murray-Bligh for pointing us toward openly available data. We also thank Sergei Sabater and three anonymous reviewers whose comments improved the clarity of the manuscript.

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