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European river typologies fail to capture diatom, fish, and macrophyte community composition



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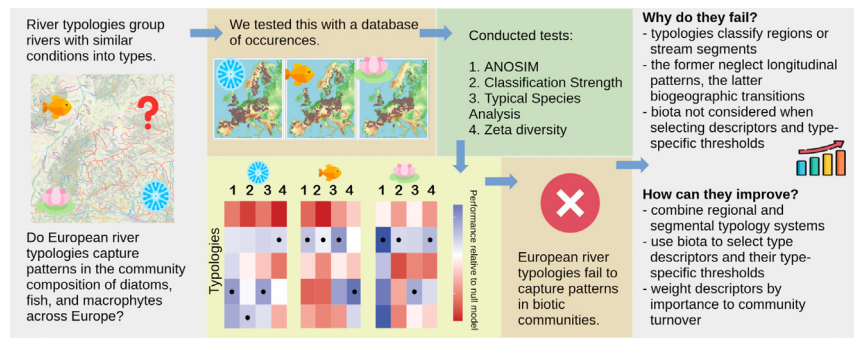
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HIGHLIGHTS

- River typologies are commonly used in applied and fundamental ecology.
- Several river typologies exist at a European scale.
- Typologies don't capture patterns in community composition of freshwater taxa.
- Combining existing typologies might improve fit to biota.
- Data on biota could be used to weight type descriptors.

GRAPHICAL ABSTRACT



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ABSTRACT

Typology systems are frequently used in applied and fundamental ecology and are relevant for environmental monitoring and conservation. They aggregate ecosystems into discrete types based on biotic and abiotic variables, assuming that ecosystems of the same type are more alike than ecosystems of different types with regard to a specific property of interest. We evaluated whether this assumption is met by the Broad River Types (BRT), a recently proposed European river typology system, that classifies river segments based on abiotic variables, when it is used to group biological communities. We compiled data on the community composition of diatoms, fishes, and aquatic macrophytes throughout Europe and evaluated whether the composition is more similar in site groups with the same river type than in site groups of different river types using analysis of similarities, classification strength, typical species analysis, and the area under zeta diversity decline curves. We compared the performance of the BRT with those of four region-based typology systems, namely, Illies Freshwater Ecoregions, the Biogeographic Regions, the Freshwater Ecoregions of the World, and the Environmental Zones, as well as spatial autocorrelation (SA) classifications.

All typology systems received low scores from most evaluation methods, relative to predefined thresholds and the SA classifications. The BRT often scored lowest of all typology systems. Within each typology system, community composition overlapped considerably between site groups defined by the types of the systems. The overlap tended to be the lowest for fishes and between Illies Freshwater Ecoregions.

In conclusion, we found that existing broad-scale river typology systems fail to delineate site groups with distinct and compositionally homogeneous communities of diatoms, fishes, and macrophytes. A way to improve the fit between typology systems and biological communities might be to combine segment-based and region-based typology systems to simultaneously account for local environmental variation and historical distribution patterns, thus potentially improving the utility of broad-scale typology systems for freshwater biota.

1. Introduction

Ecologists use typology systems to assign ecosystems to discrete types (Stoddard, 2004; Soranno et al., 2010). The degree to which real-world ecosystems are discrete entities or artificial divisions of a continuous gradient is an ongoing debate (Eliot, 2011; Liataud et al., 2019), but the utility of typology systems is less contentious (Leathwick et al., 2011; Ebach, 2021). They are used in water quality monitoring to delineate ecosystems with similar natural conditions (Reynoldson et al., 1997). Conservationists use them to identify areas with high species richness or endemism (Heiner et al., 2011; Oliveira et al., 2015), to identify ecosystem types that merit increased protection efforts (Mackey et al., 1988), or to describe desired ecosystem states (Vynne et al., 2022). In broad-scale analyses, ecosystem typologies provide spatial units for the comparison of community trait composition (Iversen et al., 2019) or temporal trends in species abundance (Powell et al., 2022).

Typology systems are models (Goodwin, 1999; Loveland and Merchant, 2004) that represent their subjects as members of discrete groups (types). In ecosystem typology systems, ecosystems are the subject and they are grouped according to their biotic and abiotic conditions. One simple, illustrative example is grouping rivers by the mean altitude of their catchment into lowland, mid-altitude, and highland rivers. Another example is grouping river segments longitudinally by the fish species that commonly occur in them, into the trout, grayling, barbel, and bream zones (Huet, 1949). Regarding each individual ecosystem as an instance of its type allows us to draw inferences and make predictions under a set of assumptions. An important assumption is that ecosystems of the same type are more similar

to each other than to ecosystems of different types, with respect to a specific property of interest. Each typology system is optimized for one property (e.g., delineating homogeneous communities of mammals) and might fail to delineate meaningful patterns in other properties (e.g., background nitrogen concentration) (Loveland and Merchant, 2004).

Ecologists commonly use ecosystem typologies to delineate ecosystems with similar biological communities. These typology systems usually define contiguous areas (regions) as mapping units and are focused on terrestrial ecosystems. Region-based typologies are appropriate for terrestrial (Olson et al., 2001) and marine ecosystems (Spalding et al., 2007), as both lack inherent geometry. However, river ecosystems are dendritic networks (Benda et al., 2004; Campbell Grant et al., 2007) and change from headwater to mouth (Vannote et al., 1980; Herlihy et al., 2021). Region-based typologies can't account for these factors, but segment-based river typologies that classify confluence to confluence sections of rivers can.

Segment-based river typologies have been proposed at national (Snelder et al., 2004) and global levels (Ouellet Dallaire et al., 2019), but until recently we lacked a unified European system. Lyche Solheim et al. (2019) filled this gap with the Broad River Types (BRT), which aggregate the disparate river typology systems created by participating countries of the European Water Framework Directive (WFD) into twelve broad types. The demand for such a typology system was demonstrated by a quick adoption from the research community (e.g., Birk et al., 2020; Lemm et al., 2021; Posthuma et al., 2020). The BRT were created to aggregate and compare information on environmental state and relevant pressures acting on the rivers (Lyche Solheim et al., 2019). As noted above, the usefulness of ecosystem

typologies hinges on the assumption that ecosystems of the same type are more similar than ecosystems of different types. For the BRT, this crucial assumption remains largely unchecked for biological communities. Jupke et al., 2022 showed that patterns in the composition of benthic macroinvertebrate communities are not well captured by the BRT. The concordance between ecosystem typologies and biological communities differs between taxonomic groups (Paavola et al., 2003; Infante et al., 2009; Ficetola et al., 2021), and should therefore be evaluated for multiple taxonomic groups.

Diatoms, fishes, and aquatic macrophytes are each commonly used to monitor the status of freshwater systems (Aguilar et al., 2011; Masouras et al., 2021; Pont et al., 2021). They are complementary in the stressors they identify (Johnson et al., 2006; Hering et al., 2006; Cellamare et al., 2012; Marzin et al., 2012), partly as they represent an ecosystem's state at different trophic levels and spatio-temporal scales (Lainé et al., 2014). Diatoms have short generation times (days to weeks), disperse via passive drift in water or air (e.g., Liu et al., 2013) and attached to animals (Maguire, 1963; Manning et al., 2021). Their community composition reflects the current environmental conditions (water conductivity, pH, nutrients, organic pollution). Fishes are long-lived and mobile. Their community composition represents the state of a riverscape (temperature, connectivity, and hydromorphology) over larger spatio-temporal scales (Hoeinghaus et al., 2007). Macrophytes are also long-lived but, due to their mostly sessile nature, respond most strongly to environmental conditions (water chemistry, light availability, substrate) in their direct vicinity (Alahuhta et al., 2014), and hence integrate environmental fluctuations over long temporal but fine spatial scales.

Here, we aim to evaluate the fit between the BRT and the community composition of diatoms, fish, and aquatic macrophytes. We evaluated the coherence between community composition and the BRT with analysis of similarities, classification strength, typical species analyses, zeta diversity analyses. To contextualize the BRT's performance, we compared it to those of four region-based typology systems (Illies Freshwater Ecoregions (IFE, Illies, 1978), Biogeographic Regions (BGR, EEA, 2016), Freshwater Ecoregions of the World (FEoW, Abell et al., 2008), and Environmental Zones (EnZ, Metzger et al., 2005)), and to spatial autocorrelation (SA) classifications. The SA classifications are naïve typology systems, consisting of simple geometric forms spread over Europe (Fig. 1). We aim to answer two

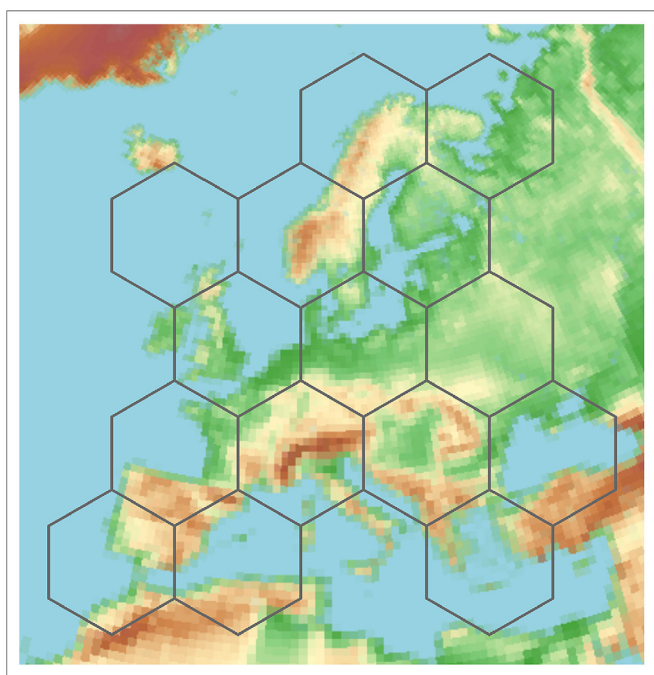


Fig. 1. Hexagonal spatial autocorrelation (SA) classification with 15 cells. Each cell is a separate type. The SA classification is a naïve approach to classification capturing spatial autocorrelation but uninformed by ecologically relevant variables.

questions: (Q1) Do the site groups delineated by the BRT host communities of diatoms, fish, and macrophytes whose composition is more similar within than among types? (Q2) Are the BRT a better classification of diatom, fish, and aquatic macrophyte communities, with regard to their composition, than the four region-based approaches?

2. Material and methods

2.1. The typology systems

The BRT reduce the number of national WFD river types (1247) to a workable set, which can be used to compare water body status data across Europe (Lyche Solheim et al., 2019). National types were combined based on altitude, catchment size, geology, region, and flow regime. Rare types were merged with the most similar type. The final BRT categorize 12 river types, as detailed in Table 1. We utilized the digital version of the BRT published by Globevnik (2019).

The typology systems we used as reference points are shortly introduced below (for details and maps see S11). All reference typologies are region-based typologies as no other segment-based typologies are available for all of Europe. IFE divide between 25 regions based on the distribution of macroinvertebrate fauna, the BGR partition Europe into 12 regions based on their potential natural vegetation, the FEoW are a global system that classifies catchments based on their fish faunas, and the EnZ are 12 zones derived from principal component analysis of 22 environmental variables.

We created classifications that capture the spatial autocorrelation inherent in community composition data but are otherwise uninformed by biogeographic transition zones. These spatial autocorrelation (SA) classifications were created by laying regular, grids over Europe (Fig. 1), where each grid cell represents one type. We created four grids differing in cell size and form. The first SA classification has 15 hexagonal cells (Fig. 1), the second 36 hexagonal cells, the third 12 square cells, and the fourth 33 square cells. We chose 15 types as this approximately matches the average number of types from the other typology systems. The results of the four SA classifications agreed qualitatively and hence only the results of the 15 cell hexagonal classification are shown in the results section. Maps of and results for the additional SA classifications are provided in the supplementary information.

2.2. Data preparation

We compiled 21, 23, and 25 datasets for diatoms, fish, and macrophytes, respectively (Fig. 2, Tables S1, S2, and S3). All sampling was

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 km², medium-large 100–10.000 km² and very large >10.000 km². Lowland denotes river segments <200 m above sea level (m.a.s.l.), mid-altitude 200–800 m.a.s.l. and highland >800 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. Mediterranean rivers are treated separately. For them the flow regime (perennial/temporary) is considered additionally.

ID	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

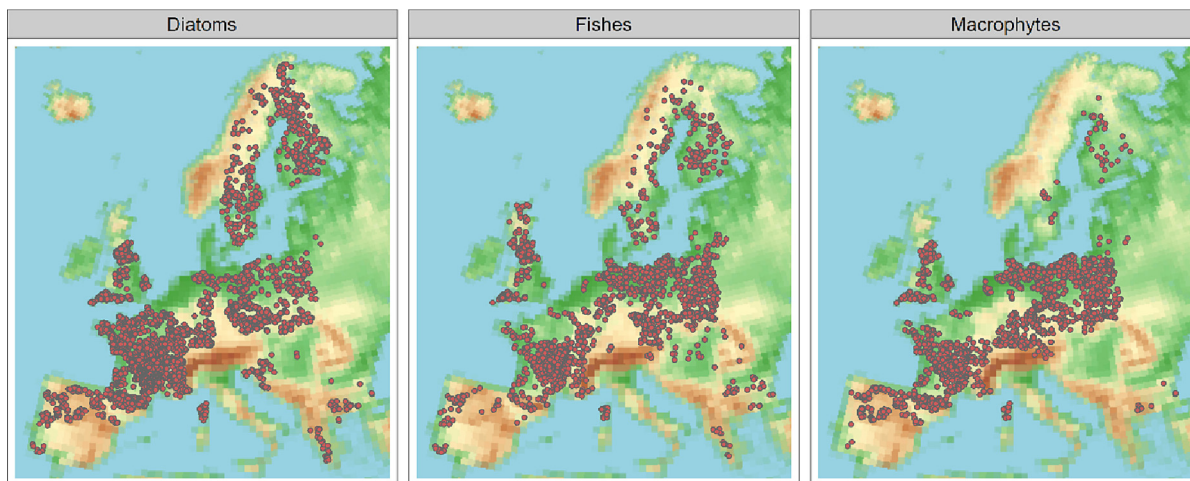


Fig. 2. Spatial distribution of sampling sites for diatoms, fishes, and aquatic macrophytes. The map only shows sampling sites that we deemed least disturbed and could assign unambiguously to one stream in the digital representation of the Broad River Types. The spatial distribution of samples is driven by data availability and the extent of anthropogenic impacts and hence not balanced.

conducted according to EU norms (EN 13946, EN 14407, and EN 15708 for diatoms, EN 14011 for fishes, and EN 14184 for macrophytes). We harmonized the datasets by transforming all data to presence-absence. This harmonization was necessary because abundance information was included in different formats or missing in the original datasets. However, analyses of the community structure (i.e., using abundance data) might come to different conclusions (Mueller et al., 2013) than ours. The samples were taken between 2000 and 2021, 1986 and 2021, and 2006 and 2021 for diatoms, fishes, and macrophytes respectively. The composition of communities has likely changed during these periods (Tison-Rosebery et al., 2022) which might bias our results as within-type similarity is decreased by temporal fluctuations. However, the magnitude of this bias is small and it is unlikely to change our results quantitatively (see SI3 for analysis). We reduced the effect of seasonal variations in community composition (e.g., Aberle and Wiltshire, 2006) by only including samples taken in summer. We use a broad definition of summer (May to September) to account for latitudinal differences in seasonal timing and phenology (e.g., Dunn et al., 2023; Woods et al., 2022).

For each sampling site, we only used one sample (the most recent), since repeated measurements can spuriously increase the similarity within types (Fig. 3).

The diatom data required extensive harmonization because of varying nomenclatures, identification errors (Morales et al., 2001; Kahlert et al., 2009), and ongoing changes to the accepted nomenclature (e.g., Mann and Vanormelingen, 2013). We updated names to current synonyms and grouped often misidentified taxa into complexes. We updated names with the taxonomic database from the OMNIDIA software (Lecointe et al., 1993) and the algaebase website (Guiry et al., 2014). We used Table S2 from Kahlert et al. (2020) to group contentious taxa into complexes. For fish and macrophytes, we replaced taxonomic synonyms with accepted names as indicated by the Global Biodiversity Information Facility (www.gbif.org). We removed taxa that only occurred in one sample. For macrophytes, we included true hydrophytes, helophytes, and mosses but no riparian vegetation. All analyses were conducted with species- or complex-level data. Harmonization tables providing original names and synonyms for all three taxonomic groups are available in the accompanying Zenodo folder (Jupke et al., 2023).

To prevent anthropogenic stressors from harmonizing communities across river types (McKinney and Lockwood, 1999; Petsch, 2016), we analyzed only the least disturbed sites (Stoddard et al., 2006) (Fig. 3). We identified the least disturbed sites with a European database including the stressors total phosphorus and nitrogen load, alterations of mean and base flow, mixture toxic pressure, and extent of agricultural and urban

land use at a sub-catchment scale (Lemm et al., 2021). We standardized each stressor to the range from 0 to 1 and categorized all sub-catchment units where all scores were ≤ 0.24 as least disturbed (see SI4 for rationale). In addition, we removed samples with ≤ 10 diatom species, ≤ 2 fish or macrophyte species, because we took the low richness as an indicator of a disturbance not covered by the approach described above. The thresholds are adjusted to average species richness of communities, which was notably higher for diatoms than for fish or macrophytes. Lastly, we visually validated the assignment of samples to BRT by comparing the position of the sampling sites with the digital river network and the CarDB.Positron base map through the mapview R package (Appelhans et al., 2021) and removed samples from erroneous assignments. As a result of data availability and our data preparation the spatial distribution of samples in the analyzed dataset is not fully balanced. Some contiguous areas (e.g., parts of western

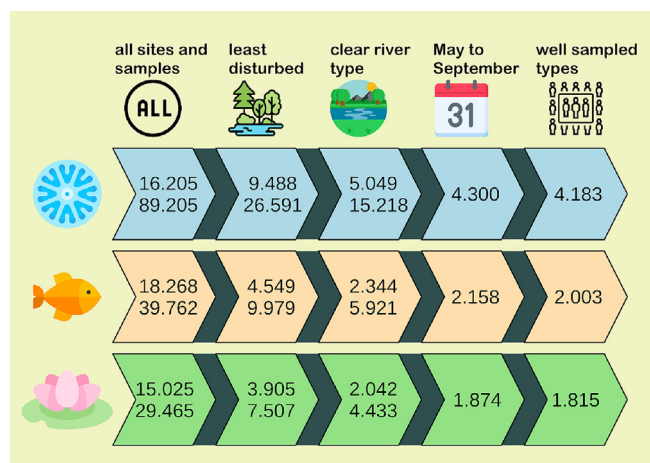


Fig. 3. Overview of data processing and the resulting number of sites and samples. The rows are the taxonomic groups diatoms, fishes, and macrophytes. Within each box the upper number gives the number of sites and the lower is the number of samples. The first column gives the numbers before data processing. The second column gives the numbers after only least disturbed and not impoverished sites are retained. The third column provides the numbers after removing samples that could not unambiguously assigned a specific broad river type. The fourth column gives the number of samples after only the most recent sample and only samples between May and September were retained. As only one sample is kept per site, the number of samples and sites is the same. The last column gives the number of sites after those that were in ecosystem types with <20 samples were removed.

Germany and the Netherlands, as well as eastern United Kingdom) have a high proportion of agricultural and urban land use and are consequently underrepresented in the final selection.

2.3. Evaluation of typologies

For each taxonomic group, we evaluated the river types for which we had at least 20 samples from the respective group (see SI5) using analysis of similarities (ANOSIM, Clarke, 1993), classification strength (CS, Van Sickle, 1997), typical species analysis (TSA, Jupke et al., 2022), and the area under the zeta diversity decline curve (AUC ζ), a method proposed in this paper.

ANOSIM compares the ranked similarities within and among types. The resulting R statistic ranges from -1 to 1 . The best classification, in which all within-type similarities are higher than all among-type similarities, corresponds to an R of 1 . To confirm our first research question, whether community composition is more similar with BRT-types than between them, they would need to obtain an ANOSIM R-value ≥ 0.5 (Clarke and Gorley, 2006) and to outperform the SA classifications. CS is the difference between mean similarity within-types (W) and mean similarity among-types (A). The means are weighted by the number of samples per ecosystem type. Values range between -1 (samples are equal among types but share no taxa within types) and 1 (samples are equal within types but share no taxa among types). We affirm research question one if the CS is above 0.1 (Hawkins et al., 2000; Soininen et al., 2004) and above the CS of the SA classifications. We used TSA to determine typical species/complexes for the types of each typology system. In TSA, a typical species/complex of a type is one that occurs in 33 % of samples from that type. To test if the TSA communities, i.e., all typical species/complexes of a type, differ between types, we computed the Jaccard dissimilarities between TSA communities of the same typology system. These dissimilarities range from 0 (identical communities) to 1 (no taxa in common). A good typology system would have high dissimilarity between the TSA communities. Finally, we determined the area under the zeta diversity decline curve. Zeta diversity is the average number of shared species between a given number of sites (Hui and McGeoch, 2014). Zeta diversity extends to multi-site comparisons through the number of considered sites, the zeta degree. For example, ζ_3 is the average number of species shared between three sites. Zeta diversity decreases monotonically with increasing zeta degree and the rate of decline is steeper when fewer species are shared between sites. Therefore, zeta diversity decline should be slower within types than among types. To evaluate declines, we used the area under the zeta diversity decline curve (AUC ζ). This metric is derived by computing the zeta diversities for the zeta degrees 1 to 10 , scaling all zeta diversities so that $\zeta_1 = 1$ and then computing the area under the curve that is created by drawing a line through all zeta diversities. Higher AUC ζ values imply a slower decline, i.e., more similar communities and thus a better typology system.

To evaluate the performance of individual typology types, we analyzed the type-specific classification strengths, TSA dissimilarities, and AUC ζ . ANOSIM does not provide type-specific results and hence was omitted here. The type-specific CS were the difference between within-type similarity of a single type and between type similarity, which always considered all types. In contrast to the CS computed for the complete typology systems, this metric was not adjusted for sample size. For TSA dissimilarity, we computed the median dissimilarity of each type toward all others. For AUC ζ , we used the zeta diversities computed for each type. For each taxon, typology system, and test, we scaled the results by their range. The best-performing type in each combination of typology system and taxonomic group had a range score of 1 , while the worst-performing type had a range score of 0 .

Each type received nine range scores: one for each combination of taxon and test. For each type, we added these nine range scores. The highest possible range score is a nine, indicating that a type performed best for all taxonomic groups and tests. The worst possible range score is a zero, implying that a given type performed worst of all types in its typology system for all taxonomic groups and tests. Only types that were tested for all three taxa were considered for this analysis.

2.4. Software

All analyses were conducted with R 4.2.2 (R Core Team, 2022). Data were prepared with data.table 1.14.2 (Dowle and Srinivasan, 2022), tidyverse 1.3.2 (Wickham et al., 2019), and sf 1.0–9 (Pebesma, 2018). Analyses were conducted with zetadiv 1.2.0 (Latombe et al., 2018), vegan 2.6–2 (Oksanen et al., 2022) and parallelDist 0.2.6 (Eckert, 2022). Maps and figures were created with ggplot2 3.4.0 (Wickham, 2016), wesanderson 0.3.6 (Ram and Wickham, 2018), maptiles 0.4.0 (Giraud, 2022), and tmap 3.3–3 (Tennekes, 2018).

3. Results

The diatom data set comprised 1110 species and species complexes, from 176 genera and 60 families at 4183 least disturbed sites. The most common species/complexes were the *Achnanthydium minutissimum* complex (3835 occurrences, 92 % of samples), the *Gomphonema parvulum* complex (2894 occurrences, 69 % of samples), and *Planorhynchium lanceolatum* (2734 occurrences, 65 % of samples). The average species/complex occurred in 105.7 ± 340.6 (arithmetic mean \pm standard deviation) samples and the average diatom species/complex richness per sample was 28.1 ± 11.0 . The 265 singletons (24 % of the species/complexes) were omitted from further analyses. 87 % of observations had species/complexes-level information, > 99 % genus and family-level observations. Observations that lacked genus-level data were largely observations of undetermined *Achnanthales* (< 0.1 % of total observations).

The fish data included 105 species from 69 genera and 21 families at 2003 least disturbed sites. The most common species were *Salmo trutta* (1208 occurrences, 60 % of samples), *Barbatula barbatula* (1029, 51 % of samples), and *Gobio gobio* (893, 45 % of samples). The mean number of occurrences was 140 ± 253 . The average fish species richness was 7.3 ± 4.3 . 17 species (16 % of species) were singletons and thus removed from subsequent analyses. 99 % of observations were at the species level. Most observations that were lacking species-level data were of Petromyzontidae (0.5 %) or *Lampetra* sp. (0.5 %).

Lastly, macrophyte data included 299 species, 131 genera, and 67 families at 1815 least disturbed sites. The most common species were *Fontinalis antipyretica* (719 occurrences, 40 % of samples), *Lemna minor* (677 occurrences, 38 % of samples), and *Leptodictyum riparium* (567 occurrences, 32 % of samples). The mean number of occurrences was 44.1 ± 97.8 . The average macrophyte species richness was 7.3 ± 4.2 . The 63 singletons (21 % of taxa) were removed from further analyses. 98 % of observations had information at the species level. *Callitriche*, *Carex*, and *Rorippa* (all < 0.01 %) are most frequent among observations without species-level data.

For all three taxonomic groups, the results of the different SA classifications differed minimally and without a discernible pattern. Below, we present the results of the 15-type hexagonal SA classification (see SI6 for the results of the other SA classifications).

For diatoms and fish, all ANOSIMS indicated weak separation between the types ($R < 0.5$, Fig. 4) and most typology systems performed similar to the SA classifications. For macrophytes, IFE, FEOW, and EnZ were good classifications ($R > 0.5$) and all typology systems outperformed the SA classifications, though the BRT only slightly. CS was low (< 0.1) for all analyses, except for IFE and fish (Fig. 4). The SA classification outperformed most typology systems for fish and macrophytes and always performed better than the BRT. The dissimilarity between TSA communities was lowest in macrophytes but the SA model outperformed most combinations of taxonomic group and typology systems, including the BRT for all the taxonomic groups. The complete list of typical communities is available in the accompanying Zenodo folder (Jupke et al., 2023). The median AUC ζ was lowest for macrophytes and the median AUC ζ s of the SA classification generally had a similar magnitude as those of the actual typology systems. The BRT's AUC ζ was always lower than that of the SA classifications. The typologies performance relative to the SA classifications and the best performing typology systems for each evaluation method and taxonomic groups are shown in Fig. 5.

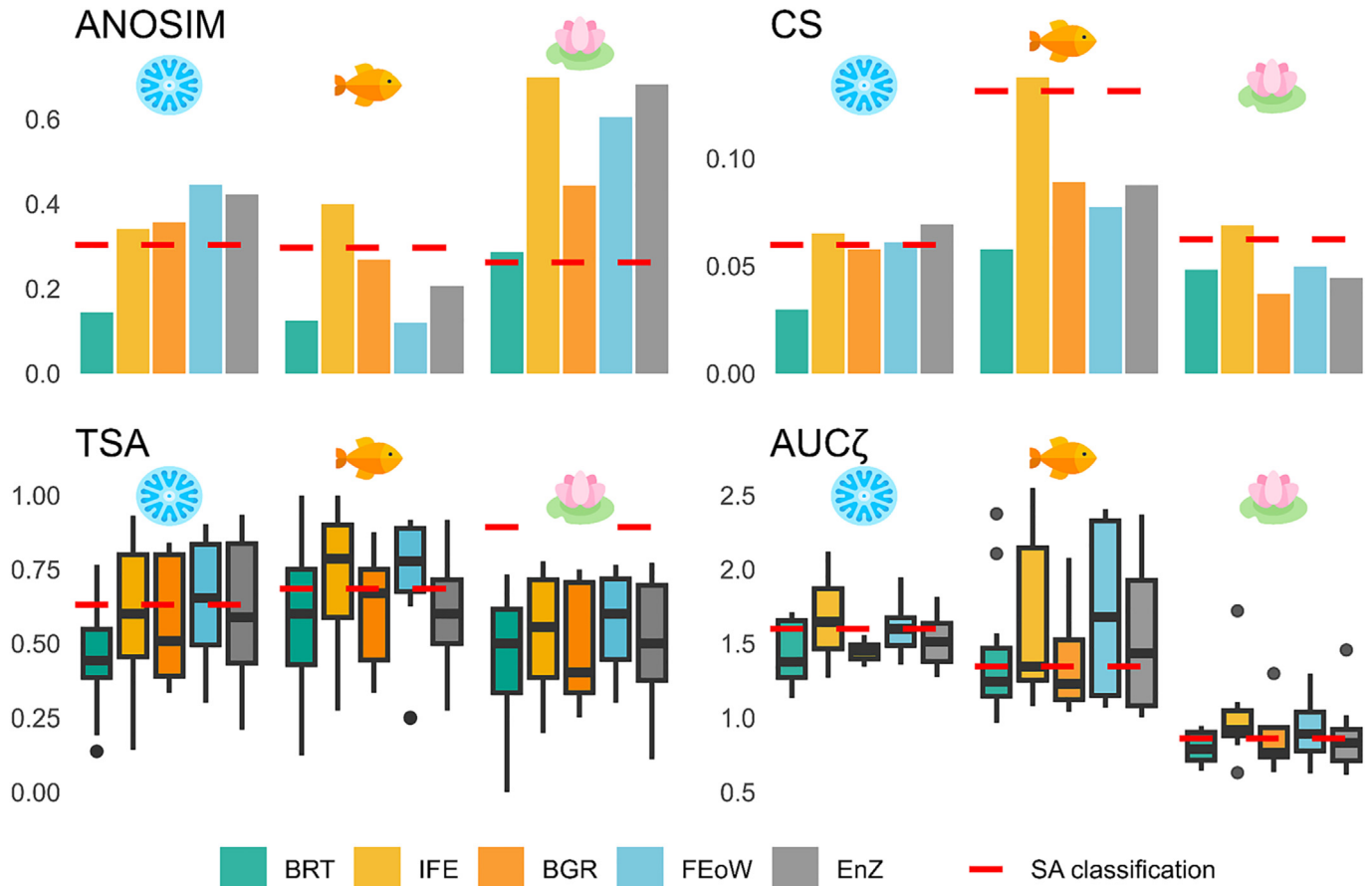


Fig. 4. Results of the four cluster analyses, Analysis of similarities (ANOSIM), Classification Strength (CS), Typical Species Analysis (TSA), and area under the zeta diversity decline curve (AUCz), for the Broad River Types (BRT), Illies Freshwater Ecoregions (IFE), Biogeographic Regions (BGR), Freshwater Ecoregions of the World (FEoW), and Environmental Zones (EnZ) across diatoms, fishes, and macrophytes. For all four analyses, higher values imply a better classification. The dashed red line indicates the results for the 15-type hexagonal spatial autocorrelation (SA) classification. For ANOSIM, the R-statistic is shown. An R of 1 corresponds to a perfect classification where within-type similarities exceed among-type similarities. For the CS, the classification strength is shown. A high dissimilarity between the TSA communities of two types implies that the different species are common in each of the two types. Therefore, a good typology system would have high dissimilarities between TSA communities. For AUCz, the area under the zeta diversity decline curve is shown. If communities share fewer species, their zeta diversity decline curves will be steeper and hence enclose a smaller area over a fixed number of orders. A good typology would aggregate ecosystems with similar communities and hence with slowly declining zeta diversity curves and large areas under the decline curve. This analysis returns one area under the curve per type and taxonomic group. The distribution of these areas is shown here.

The observed type-specific scores ranged from 6.6 (type *boreal* from BGR) to 0.3 (type *Mediterranean* from BGR) with a mean score of 3.1 (Fig. 6). Overall, we observed that the high latitude and altitude types tended to perform better than low latitude types across typology systems and taxa.

4. Discussion

We compiled datasets of diatom, fish, and macrophyte occurrences from rivers throughout Europe to determine whether spatial patterns in community composition follow broad-scale environmental covariates as captured by different ecosystem typologies. Our first research question was whether the site groups delineated by the BRT host communities of diatoms, fish, and macrophytes whose composition is more similar within than among types. This is not the case for any of the three taxonomic groups. The BRT failed to meet the predefined quality threshold for ANOSIM and CS and performed worse than the SA model in 11 out of 12 tests. Our second research question was whether the communities within BRT were more homogeneous and distinct than those of the types of IFE, BGR, FEoW or EnZ. Here, the opposite was the case. In most analyses, the BRT were least reflected by the community compositions. Our analyses were based on presence-absence data. The results therefore pertain solely to the composition of communities and not their structure, i.e., the abundance of different taxa.

Since patterns in community structure can deviate from those in community composition (Mueller et al., 2013) we advise against generalizing our results to community structure. Further, we wish to emphasize again that our sampling sites are not uniformly distributed across types or within types. As such data do not exist on broad-scales we cannot evaluate the magnitude or direction of bias this might induce.

Differences between diatom assemblages in ecoregions have been shown on a national (Mykrä et al., 2009; Rimet and Bouchez, 2012; Soininen et al., 2004; Tison et al., 2005; Tornés et al., 2007, 2022) and international level (Kelly et al., 2012), but are often small. Our CS and ANOSIM values for diatoms are comparable to literature values between 0.03 and 0.09 for CS (Soininen et al., 2004; Mykrä et al., 2009) and 0.34 to 0.43 for ANOSIM (Kelly et al., 2012; Soininen et al., 2016). No single typology system emerged as having a considerably higher fit to the diatom community compositions.

Fish assemblages often exhibit a spatial structure (Jackson and Harvey, 1989; Kilgour and Barton, 1999) and accordingly several studies indicated that fish assemblages are well described by a priori typology systems at fine (Hoeinghaus et al., 2007; Vehanen et al., 2020) and broad scales (Frimpong and Angermeier, 2010). This partly reflects the fact that modern-day fish distributions are still strongly influenced by historical patterns (Vargas et al., 1998; Reyjol et al., 2007) but also that, among the taxa studied here, fish are the only group that disperses strictly within the river network,

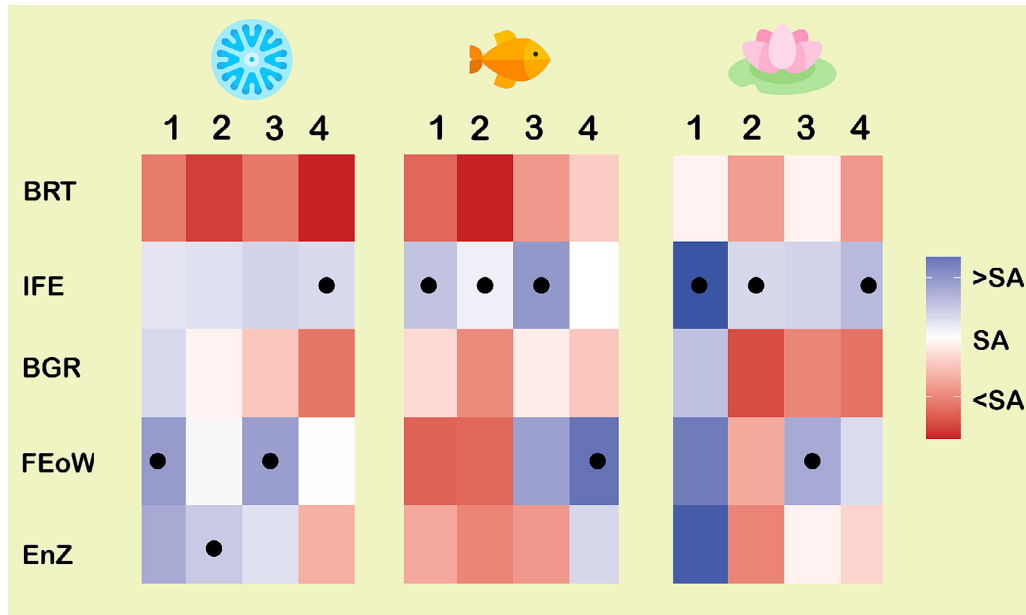


Fig. 5. Summary of all results relative to the 15-type hexagonal spatial autocorrelation (SA) classification. The rows indicate the typology systems: Broad River Types (BRT), Illies Freshwater Ecoregions (IFE), Biogeographical Regions (BGR), Freshwater Ecoregions of the World (FEoW), and Environmental Zones (EnZ). The columns are the different analyses: Analysis of similarities (1), classification strength (2), Jaccard dissimilarity between typical species analysis communities (3), and area under the zeta diversity decline curve (4). All results are relative to the SA classification. Blue cells indicate that the typology received a higher score than the SA classification, red cells indicate the opposite. White cells show that the performance is similar to the SA classification. Black dots highlight the typology system that performed best for a given combination of taxonomic group and evaluation method.

though we lack empirical data on possible zoochory in fish (Hirsch et al., 2018). Assuming that zoochory plays a subordinate role, dispersal between basins is only possible for euryhaline taxa such as *Anguilla anguilla*, *Alosa alosa*, or *Lampetra fluviatilis*, during river captures (Burrige et al., 2006), or with declining sea levels. The IFE capture fish community composition best of the evaluated typology systems. The bad performance of the BRT

is surprising, given that longitudinal patterns, which only segment-based typology systems capture, are common in fish assemblages (Vila-Gispert et al., 2002). The influence of broad-scale factors and historical distribution patterns seems to override these longitudinal types.

Macrophyte community composition tended to be more similar within types (high ANOSIM R) but the absolute differences in similarity were

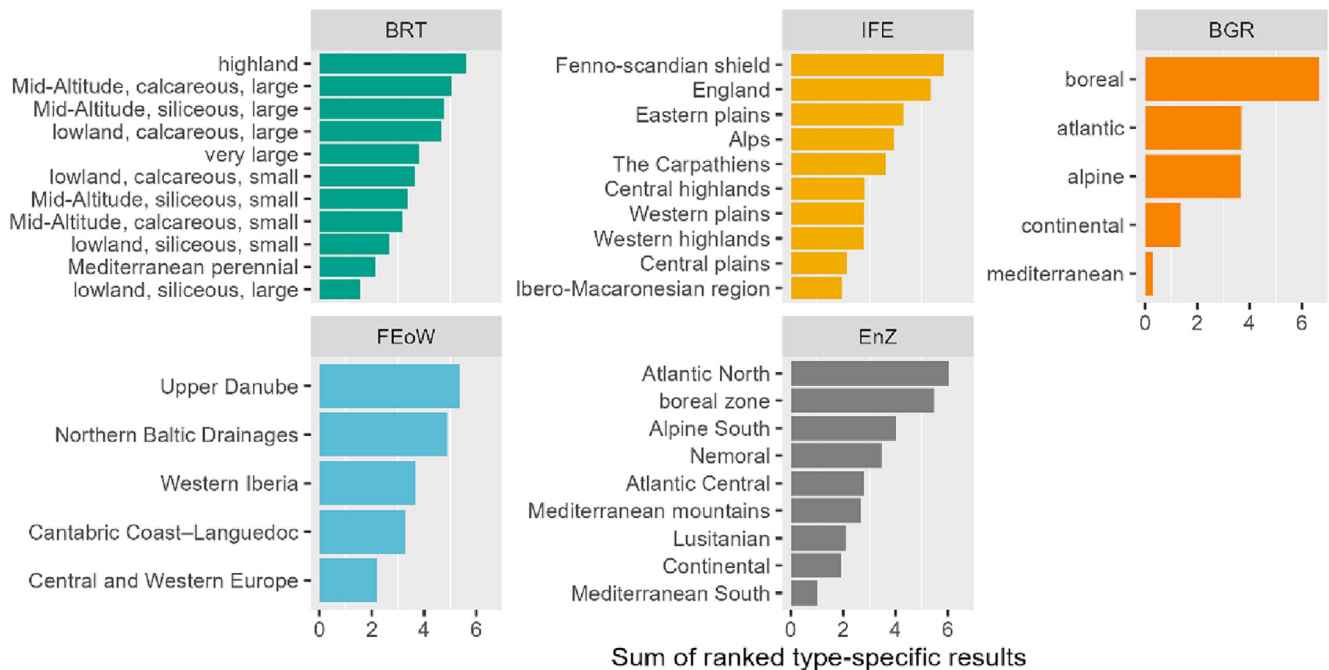


Fig. 6. Performance of individual types across taxonomic groups and evaluation metrics for the Broad River Types (BRT), Illies Freshwater Ecoregions (IFE), Biogeographic Regions (BGR), Freshwater Ecoregions of the World (FEoW), and Environmental Zones (EnZ). Each score is the sum of scaled results across taxonomic groups and test. Scaling was conducted separately for each combination of taxonomic group, typology system, and test. The highest and best possible score is 9, the lowest and worst is 0. Only types that were evaluated for all three taxa are included.

small (low CS) and the most common taxa tended to occur across types (similar TSA communities). This is in agreement with previous studies that found considerable overlap between the macrophyte communities of different river types (Baattrup-Pedersen et al., 2006; Alahuhta and García-Girón, 2021). Aquatic macrophytes display a wide range of autoecological variability, and therefore seem to occur across regions, therefore increasing similarly of types and rendering pressure responses uncertain (Szozkiewicz et al., 2006). However, the biogeography of aquatic macrophytes is less well-studied than that of diatoms or fish. Existing studies tend to focus on lentic systems (Alahuhta et al., 2021) and the driving factors of macrophyte community composition are known to differ between lentic and lotic systems (Iversen et al., 2019; Gillard et al., 2020). As for fish, the IFE were the best typology system for macrophytes in our study.

In the type-specific analysis, northern European and high-altitude types tended to perform better than low altitude and southern types, i.e., communities at high latitudes and altitudes were compositionally more distinct and homogenous than those observed at lower latitudes and altitudes. This is in concert with frameworks that predict larger geographic range sizes at higher latitudes (Rapoport's rule; Stevens, 1989) and a stronger role of environmental species sorting relative to dispersal processes or biotic interactions (Dobzhansky-MacArthur hypothesis (Brown, 2014); Harsh-Benign hypothesis (Menge, 1976)). Communities composed of taxa with large geographic ranges will vary less across space and are hence captured better by large contiguous areas such as ecoregions. Further, the effects of environmental sorting are likely more easily captured by environmentally determined regions than the imprints of either biotic interactions or dispersal.

In our three focal taxonomic groups, support for these frameworks is mixed. For diatoms, studies on the relationship between latitude and geographic range size are lacking. Mruzek et al. (2022) found no support for Rapoport's rule in algae (including but not restricted to diatoms) in the conterminous USA. For fish, Carvajal-Quintero et al., 2019 have shown that aridity, which is more prevalent at lower latitudes, has a negative effect on species' geographic ranges and Mruzek et al., 2022 found a weak but consistent increase of range size with latitude. For macrophytes, Murphy et al., 2020 show an increase in geographic range with latitude globally, but this pattern seems less pronounced in Europe than in North America (Alahuhta et al., 2020). Few studies have investigated latitudinal gradients in the relative importance of environmental species sorting. Mruzek et al., 2022 found a clear increase with latitude in the variation of species richness of algae and fish explained by environmental variation accompanied by a less pronounced decrease in the variation explained by dispersal. However, these patterns were absent for beta diversity. Hence, while the strength and form of latitudinal patterns in geographic range size and relative strength of environmental species sorting likely vary between taxonomic groups, such patterns represent a possible explanation for our type-specific results. For future efforts to derive broad-scale typology systems, we therefore recommend using finer-scaled types for low-latitude systems compared to high-latitude systems.

4.1. Relevance of typology systems and ways forward

The availability of well-fitting typology systems matters. Typology systems are useful heuristics for researchers. Recent studies have used river typology systems to investigate type-specific temporal biodiversity trends (Powell et al., 2022), inter-type differences in pollution pressure caused by man-made chemicals (Posthuma et al., 2020), and the relevance of multiple stressors for different types of rivers (Birk et al., 2020). Further, typology systems are crucial to the practical implementation of environmental policy. Policies need to define quantifiable standards and targets which requires distinct groups (Mau, 2017) to render complex matters legible to institutions (Scott, 2008). As a practical example, consider the environmental risk assessment of pesticides, which commonly derives a predicted exposure concentration and a, presumably safe, regulatory acceptable concentration. While exposure concentrations are predicted considering different

types of ecosystems, the acceptable concentration does not take the receiving ecosystems into account. Introducing a typology system delineating biotic communities with different sensitivities represents a straightforward possibility to include spatial variation in sensitivity. If we neglect the potentially international nature of environmental issues, e.g., by relying on national tools to implement international policies, we risk being blindsided by transboundary harm (Knox, 2002) and transboundary crises (Boin, 2009). Together with Jupke et al. (2022), we show that European river typology systems fail to capture patterns in the community composition of aquatic biota considerably better than arrangements of simple geometric forms. It is important to note that the typology systems evaluated here were not designed for the specific purpose we evaluated them on. Hence, we do not wish to argue against the use of typology systems in general. Rather, we wish to highlight this research gap and encourage future efforts to close it.

To improve the concordance between community composition and river typologies, we suggest combining segment-based and region-based approaches. Region-based systems do not capture taxonomic turnover along a rivers course (Vannote et al., 1980, Baattrup-Pedersen et al., 2006), while segment-based systems may fail to account for regional climatic and geological differences (Omernik and Bailey, 1997). The BRT include a region variable, but additional regional differences may be relevant in Europe. Watson et al. (2021) and Jupke et al. (2022) have previously suggested integrating the BRT into a region-based system. Based on our results, we recommend combining the BRT with IFE, which were superior to other typology systems for fish and macrophytes.

Further, we might consider biological type descriptors in addition to abiotic ones, as is done in the IFE, BGR, and FEoW. While these three systems are based on expert knowledge about species ranges, others have created typology systems directly from observations. Several authors have derived diatom typologies for the evaluation of ecological indices (e.g., Goldenberg Vilar et al., 2014, Grenier et al., 2006, Lavoie et al., 2010, Tang et al., 2016). However, these typologies are at the subnational scale and were not meant to be generalized beyond their specific studies. For both macrophytes and fish, biotypes or -regions are commonly derived based on community composition and structure (e.g., Alahuhta and García-Girón, 2021; Holmes et al., 1998; Loewen et al., 2021; Pont et al., 2007; Riis et al., 2000). If the purpose of the typology system is to define types with similar reference communities though, biotic type descriptors should not be used to avoid circularity (Bailey et al., 2004; Stoddard et al., 2006). A way to circumvent this circularity would be to use Generalized Dissimilarity Models (GDM, Ferrier et al., 2007, Latombe et al., 2017). These models use spline functions to model the relationship between beta diversity (measured as dissimilarity metric, e.g.; Jaccard dissimilarity) and environmental variables. We can train such models to predict beta-diversity for the area of interest with the variables we want to use as type descriptors in our typology system. The predicted beta diversity, which is a function of the environmental variables, can then be clustered, instead of the environmental variables themselves. Effectively, this weights the variables by their importance for the taxonomic turnover of the focal taxon.

5. Conclusion

Our study is the most comprehensive evaluation of European river typology systems to date. Despite variation across evaluation metrics and taxonomic groups, we showed that current broad-scale typology systems fail to capture the community composition of different taxonomic groups beyond their spatial autocorrelation. We propose several avenues for advancing the field. Most notably by combining existing segment- and region-based systems. In an age of increasing data availability, the context becomes scarce and context is what ecosystem typologies can provide. Therein lies their great value for ecological research and environmental policy. When science and policy are restricted to national, fine-scale tools they remain blind toward issues that transcend political borders. Therefore, we encourage future work on broad-scale river typologies specifically catered toward delimiting distinct biotic communities.

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. Apostolos Apostolou: Data curation, Resources, Writing - Review & Editing. Jukka Aroviita: Data curation, Resources, Writing - Review & Editing. Annette Baatrup-Pedersen: Data curation, Resources, Writing - Review & Editing. Peter Baláži: Data curation, Resources, Writing - Review & Editing. Libuše Barešová: Data curation, Resources, Writing - Review & Editing. Saúl Blanco: Data curation, Resources, Writing - Review & Editing. María Borrego-Ramos: Data curation, Resources, Writing - Review & Editing. Herman van Dam: Data curation, Resources, Writing - Review & Editing. Elias Dimitriou: Data curation, Resources, Writing - Review & Editing. Christian K. Feld: Data curation, Resources, Writing - Review & Editing. Maria Teresa Ferreira: Data curation, Resources, Writing - Review & Editing. Gana Gecheva: Data curation, Resources, Writing - Review & Editing. Joan Gomà: Data curation, Resources, Writing - Review & Editing. Nikola Hanžek: Data curation, Resources, Writing - Review & Editing. Ida Marie Haslev: Data curation, Resources, Writing - Review & Editing. Tsvetelina Isheva: Data curation, Resources, Writing - Review & Editing. Aurélien Jamoneau: Data curation, Resources, Writing - Review & Editing. Jenny Jyrkänkallio-Mikkola: Data curation, Resources, Writing - Review & Editing. Maria Kahlert: Data curation, Resources, Writing - Review & Editing. Ioannis Karaouzas: Data curation, Resources, Writing - Review & Editing. Satu Maaria Karjalainen: Data curation, Resources, Writing - Review & Editing. Adriana Olenici: Data curation, Resources, Writing - Review & Editing. Piotr Panek: Data curation, Resources, Writing - Review & Editing. Petr Paril: Data curation, Resources, Writing - Review & Editing. Edwin T.H.M. Peeters: Data curation, Resources, Writing - Review & Editing. Marek Poláček: Data curation, Resources, Writing - Review & Editing. Didier Pont: Data curation, Resources, Writing - Review & Editing. Audrone Pumpulyte: Data curation, Resources, Writing - Review & Editing. Leonard Sandin: Data curation, Resources, Writing - Review & Editing. Lucia Sochuliaková: Data curation, Resources, Writing - Review & Editing. Janne Soininen: Data curation, Resources, Writing - Review & Editing. Igor Stanković: Data curation, Resources, Writing - Review & Editing. Michal Straka: Data curation, Resources, Writing - Review & Editing. Mirela Šušnjara: Data curation, Resources, Writing - Review & Editing. Tapio Sutela: Data curation, Resources, Writing - Review & Editing. Juliette Tison-Rosebery: Data curation, Resources, Writing - Review & Editing. Marija Gligora Udovič: Data curation, Resources, Writing - Review & Editing. Michiel Verhofstad: Data curation, Resources, Writing - Review & Editing. Petar Žitinić: Data curation, Resources, Writing - Review & Editing. Ralf B. Schäfer: Writing - Review & Editing, Supervision, Project administration, Conceptualization, Funding acquisition.

Data availability

We cannot make the complete database available. We published supplementary data on Zeondo (<https://doi.org/10.5281/zenodo.7751344>). R code is available in the associated Github repository <https://github.com/JonJup/European-river-typologies-and-community-compositi>

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.165081>.

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