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

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67 Abstract

Typology systems are frequently used in applied and fundamental ecology and are relevant 68 69 for environmental monitoring and conservation. They aggregate ecosystems into discrete 70 types based on biotic and abiotic variables, assuming that ecosystems of the same type are 71 more alike than ecosystems of different types with regard to a specific property of interest. We 72 evaluated whether this assumption is met by the Broad River Types (BRT), a recently proposed 73 European river typology system, that classifies river segments based on abiotic variables, 74 when it is used to group biological communities. We compiled data on the community 75 composition of diatoms, fishes, and aquatic macrophytes throughout Europe and evaluated 76 whether the composition is more similar in site groups with the same river type than in site 77 groups of different river types using Analysis of Similarities, classification strength, typical 78 species analysis, and the area under zeta diversity decline curves. We compared the 79 performance of the BRT with those of four region-based typology systems, namely, Illies 80 Freshwater Ecoregions, the Biogeographic Regions, the Freshwater Ecoregions of the World, 81 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

- 85 groups defined by the types of the systems. The overlap tended to be the lowest for fishes and
- 86 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.

93 Keywords

- 94 Typology systems, ecoregions, freshwater ecosystems, typology evaluation, biological quality
- 95 elements, biomonitoring
- 96

1 1. Introduction

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3 Ecologists use typology systems to assign ecosystems to discrete types (Stoddard 2004, 4 Soranno et al. 2010). The degree to which real-world ecosystems are discrete entities or 5 artificial divisions of a continuous gradient is an ongoing debate (Eliot 2011, Liautaud et al. 6 2019), but the utility of typology systems is less contentious (Leathwick et al. 2011, Ebach 7 2021). They are used in water quality monitoring to delineate ecosystems with similar natural 8 conditions (Reynoldson et al. 1997). Conservationists use them to identify areas with high 9 species richness or endemism (Heiner et al. 2011, Oliveira et al. 2015), to identify ecosystem 10 types that merit increased protection efforts (Mackey et al. 1988), or to describe desired 11 ecosystem states (Vynne et al. 2022). In broad-scale analyses, ecosystem typologies provide 12 spatial units for the comparison of community trait composition (Iversen et al. 2019) or 13 temporal trends in species abundance (Powell et al. 2022).

14 All typology systems are models (Goodwin 1999, Loveland and Merchant 2004) that simplify 15 their subjects to permit inference and prediction under a set of assumptions. Ecosystem 16 typologies bundle ecosystems into a set of discrete groups characterized by selected biotic 17 and abiotic variables (e.g., altitude, temperature, and bedrock geology). These models are 18 based on the assumption that ecosystems of the same type are more similar to each other 19 than to ecosystems of different types, with respect to a specific property of interest. Each 20 typology system is optimized for one property (e.g., delineating homogeneous communities of 21 mammals) and might fail to delineate meaningful patterns in other properties (e.g., background 22 nitrogen concentration) (Loveland and Merchant 2004).

Ecologists commonly use ecosystem typologies to delineate ecosystems with similar biological communities. These typology systems usually defined contiguous areas (regions) as mapping units and 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 not account for these factors, but
segment-based river typologies that classify confluence to confluence sections of rivers can.

31 Segment-based river typologies have been proposed at national (Snelder et al 2004) and 32 global levels (Ouellet Dallaire et al 2019), but until recently we lacked a unified European 33 system. Lyche Solheim et al. (2019) filled this gap with the Broad River Types (BRT), which 34 aggregate the disparate river typology systems created by participating countries of the 35 European Water Framework Directive (WFD) into twelve broad types. The demand for such a 36 typology system was demonstrated by a quick adoption from the research community (e.g., 37 Birk et al., 2020; Lemm et al., 2021; Posthuma et al., 2020). The BRT were created to 38 aggregate and compare information on environmental state and relevant pressures acting on 39 the rivers (Lyche Solheim et al. 2019). As noted above, the usefulness of ecosystem 40 typologies hinges on the assumption that ecosystems of the same type are more similar than 41 ecosystems of different types. For the BRT, this crucial assumption remains largely unchecked 42 for biological communities. Jupke et al. 2022 showed that patterns in the composition of 43 benthic macroinvertebrate communities are not well captured by the BRT. The concordance 44 between ecosystem typologies and biological communities differs between taxonomic groups 45 (Paavola et al. 2003, Infante et al. 2009, Ficetola et al. 2021), and should therefore be 46 evaluated for multiple taxonomic groups.

47 Diatoms, fishes, and aquatic macrophytes are each commonly used to monitor the status of 48 freshwater systems (Aguiar 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, 49 Cellamare et al. 2012, Marzin et al. 2012), partly as they represent an ecosystem's state at 50 51 different trophic levels and spatio-temporal scales (Lainé et al. 2014). Diatoms have short 52 generation times (days to weeks), disperse via passive drift in water or air (e.g., Liu et al. 2013) 53 and attached to animals (Maguire 1963, Manning et al. 2021). Their community composition 54 reflects the current environmental conditions (water conductivity, pH, nutrients, organic 55 pollution). Fishes are long-lived and mobile. Their community composition represents the state 56 of a riverscape (temperature, connectivity, and hydromorphology) over larger spatio-temporal 57 scales (Hoeinghaus et al. 2007). Macrophytes are also long-lived but, due to their mostly 58 sessile nature, respond most strongly to environmental conditions (water chemistry, light 59 availability, substrate) in their direct vicinity (Alahuhta et al. 2014), and hence integrate 60 environmental fluctuations over long temporal but fine spatial scales.

61 Here, we aim to evaluate the fit between the BRT and the community composition of diatoms, 62 fish, and aquatic macrophytes. We evaluated the coherence between community composition 63 and the BRT with Analysis of similarities, classification strength, typical species analyses, zeta 64 diversity analyses. To contextualize the BRT's performance, we compared it to those of four 65 region-based typology systems (Illies Freshwater Ecoregions (IFE, Illies 1978), Biogeographic Regions (BGR, EEA 2012), Freshwater Ecoregions of the World (FEoW, Abell et al. 2008), 66 67 and Environmental Zones (EnZ, Metzger et al. 2005)), and to spatial autocorrelation (SA) 68 classifications. The SA classifications are naïve typology systems, consisting of simple 69 geometric forms spread over Europe (Figure 1). We aim to answer two questions: (Q1) Do the 70 site groups delineated by the BRT host communities of diatoms, fish, and macrophytes whose 71 composition is more similar within than among types? (Q2) Are the BRT a better classification 72 of diatom, fish, and aquatic macrophyte communities, with regard to their composition, than 73 the four region-based approaches?

74 **2. Material and Methods**

75 2.1 The typology systems

The BRT reduce the number of national WFD river types (1,247) to a workable set, which can be used to compare water body status data across Europe (Lyche Solheim e 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).

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 meters 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			

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The typology systems we used as reference points are shortly introduced below (for details and maps see SI1). All reference typologies are region-based typologies as no other segmentbased 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.

97 We created classifications that capture the spatial autocorrelation inherent in community 98 composition data but are otherwise uninformed by biogeographic transition zones. These 99 spatial autocorrelation (SA) classifications were created by laying a regular, hexagonal grid with 15 cells (types) over Europe (Figure 1). We chose 15 types as this approximately matches
the average number of types from the other typology systems. To evaluate whether size or
form impact the results, we created multiple SA classifications. Besides the 15-cell hexagonal
classification, we created a square classification with the same cell size (12 types), as well as
hexagonal and square classifications with half the cell size (36 and 33, types, respectively).
Maps of the additional SA classifications are provided in the supplementary information.



Figure 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.

109 2.2 Data preparation

110 We compiled 21, 23, and 25 datasets for diatoms, fish, and macrophytes, respectively (Figure 111 2, Table S1, S2, and S3). All sampling was conducted according to EU norms (EN 13946, EN 112 14407, and EN 15708 for diatoms, EN 14011 for fishes, and EN 14184 for macrophytes). We 113 harmonized the datasets by transforming all data to presence-absence. The samples were 114 taken between 2000 and 2021, 1986 and 2021, and 2006 and 2021 for diatoms, fishes, and 115 macrophytes respectively. The composition of communities has likely changed during these 116 periods (Tison-Roseberry et al. 2022). However, the magnitude of this bias is small and it is 117 unlikely to change our results quantitatively (see SI3 for analysis). We included samples taken 118 between May and September and only included the most recent sample at each site (Figure 119 3).



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Figure 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.

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The diatom data required extensive harmonization because of varying nomenclatures, 125 126 identification errors (Morales et al. 2001, Kahlert et al. 2009), and ongoing changes to the 127 accepted nomenclature (e.g., Mann & Vanormelingen 2013). We updated names to current 128 synonyms and grouped often misidentified taxa into complexes. We updated names with the 129 taxonomic database from the OMNIDIA software (Lecointe et al. 1993) and the algaebase 130 website (Guiry et al. 2014). We used Table S2 from Kahlert et al. (2020) to group contentious 131 taxa into complexes. For fish and macrophytes, we replaced taxonomic synonyms with 132 accepted names as indicated by the Global Biodiversity Information Facility (www.gbif.org). 133 We removed taxa that only occurred in one sample. For macrophytes, we included true 134 hydrophytes, helophytes, and mosses but no riparian vegetation. Harmonization tables 135 providing original names and synonyms for all three taxonomic groups are available as 136 supplementary material.



138 Figure 3: Overview of data processing and the resulting number of sites and samples. The rows are the taxonomic groups 139 diatoms, fishes, and macrophytes. Within each box the upper number gives the number of sites and the lower is the number 140 of samples. The first column gives the numbers before data processing. The second column gives the numbers after only 141 least disturbed and not impoverished sites are retained. The third column provides the numbers after removing samples 142 that could not unambiguously assigned a specific broad river type. The fourth column gives the number of samples after 143 only the most recent sample and only samples between May and September were retained. As only one sample is kept per 144 site, the number of samples and sites is the same. The last column gives the number of sites after those that were in 145 ecosystem types with less than 20 samples were removed.

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147 To prevent anthropogenic stressors from harmonizing communities across river types 148 (McKinney and Lockwood 1999, Petsch 2016), we analyzed only the least disturbed sites 149 (Stoddard et al., 2006) (Figure 3). We identified the least disturbed sites with a European 150 database including the stressors total phosphorus and nitrogen load, alterations of mean and 151 base flow, mixture toxic pressure, and extent of agricultural and urban land use at a sub-152 catchment scale (Lemm et al 2021). We standardized each stressor to the range from 0 to 1 153 and categorized all sub-catchment units where all scores were ≤ 0.24 as least disturbed (see 154 SI4 for rationale). In addition, we removed samples with \leq 10 diatom species, \leq 2 fish or 155 macrophyte species. Lastly, we visually validated the assignment of samples to BRT by 156 comparing the position of the sampling sites with the digital river network and the 157 CaroDB.Positron base map through the mapview R package (Appelhans et al. 2021) and 158 removed samples from erroneous assignments.

159 2.3 Evaluation of typologies

We evaluated all combinations of taxonomic groups and river types for which we had at least 20 samples 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.

164 ANOSIM compares the ranked similarities within and among types. The resulting R statistic 165 ranges from -1 to 1. The best classification, in which all within-type similarities are higher than 166 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 167 168 would need to obtain an ANOSIM R-value ≥ 0.5 (Clark & Gorley 2006) and to outperform the 169 SA classifications. CS is the difference between mean similarity within-types (W) and mean 170 similarity among-types (A). The means are weighted by the number of samples per ecosystem 171 type. Values range between -1 (samples are equal among types but share no taxa within 172 types) and 1 (samples are equal within types but share no taxa among types). We affirm 173 research question one if the CS is above 0.1 (Hawkins et al. 2000, Soininen et al. 2004) and 174 above the CS of the SA classifications. We used TSA to determine typical species/complexes 175 for the types of each typology system. In TSA, a typical species/complex of a type is one that 176 occurs in 33% of samples from that type. To test if the TSA communities, i.e. all typical 177 species/complexes of a type, differ between types, we computed the Jaccard dissimilarities 178 between TSA communities of the same typology system. These dissimilarities range from 0 179 (identical communities) to 1 (no taxa in common). A good typology system would have high 180 dissimilarity between the TSA communities. Finally, we determined the area under the zeta 181 diversity decline curve. Zeta diversity is the average number of shared species between a

182 given number of sites (Hui and McGeoch 2014). Zeta diversity extends to multi-site 183 comparisons through the number of considered sites, the zeta degree. For example, $\zeta 3$ is the average number of species shared between three sites. Zeta diversity decreases 184 monotonically with increasing zeta degree and the rate of decline is steeper when fewer 185 186 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 187 decline curve (AUC ζ). This metric is derived by computing the zeta diversities for the zeta 188 degrees 1 to 10, scaling all zeta diversities so that $\zeta 1 = 1$ and then computing the area under 189 190 the curve that is created by drawing a line through all zeta diversities. Higher AUCζ values 191 imply a slower decline, i.e., more similar communities and thus a better typology system.

192 **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).

199 **3. Results**

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).



Figure 4: Results of the four cluster analyses, Analysis of similarities (ANOSIM), Classification Strength (CS), Typical Species 205 Analysis (TSA), and area under the zeta diversity decline curve (AUCZ), for the Broad River Types (BRT), Illies Freshwater 206 Ecoregions (IFE), Biogeographic Regions (BGR), Freshwater Ecoregions of the World (FEoW), and Environmental Zones (EnZ) 207 across diatoms, fishes, and macrophytes. For all four analyses, higher values imply a better classification. The dashed red line 208 indicates the results for the 15-type hexagonal spatial autocorrelation (SA) classification. For ANOSIM, the R-statistic is shown. 209 An R of 1 corresponds to a perfect classification where within-type similarities exceed among-type similarities. For the CS, the 210 classification strength is shown. A high dissimilarity between the TSA communities of two types implies that the different 211 species are common in each of the two types. Therefore, a good typology system would have high dissimilarities between TSA 212 communities. For AUCZ, the area under the zeta diversity decline curve is shown. If communities share fewer species, their 213 zeta diversity decline curves will be steeper and hence enclose a smaller area over a fixed number of orders. A good typology 214 would aggregate ecosystems with similar communities and hence with slowly declining zeta diversity curves and large areas 215 under the decline curve. This analysis returns one area under the curve per type and taxonomic group. The distribution of 216 these areas is shown here.

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218 For diatoms and fish, all ANOSIMS indicated weak separation between the types (R<0.5, 219 Figure 4) and most typology systems performed similar to the SA classifications. For 220 macrophytes, IFE, FEoW, and EnZ were good classifications (R>0.5) and all typology systems 221 outperformed the SA classifications, though the BRT only slightly. CS was low (< 0.1) for all 222 analyses, except for IFE and fish (Figure 4). The SA classification outperformed most typology 223 systems for fish and macrophytes and always performed better than the BRT. The dissimilarity 224 between TSA communities was lowest in macrophytes but the SA model outperformed most 225 combinations of taxonomic group and typology systems, including the BRT for all the 226 taxonomic groups. The complete list of typical communities is available in the supplementary

materials. 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 Figure 5.



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Figure 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.

241 **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. 249 Our second research question was whether the communities within BRT were more 250 homogenous and distinct than those of the types of IFE, BGR, FEoW or EnZ. Here, the 251 opposite was the case. In most analyses, the BRT were least reflected by the community 252 compositions. Our analyses were based on presence-absence data. The results therefore 253 pertain solely to the composition of communities and not their structure, i.e., the abundance 254 of different taxa. Since patterns in community structure can deviate from those in community 255 composition (Mueller et al. 2013) we advise against generalizing our results to community 256 structure. Further, we wish to emphasize that our sampling sites are not uniformly distributed 257 across types or within types. As such data do not exist on broad-scales we cannot evaluate 258 the magnitude or direction of bias this might induce.

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Differences between diatom assemblages in ecoregions have been shown on a national (Mykrä et al. 2009, Rimet & Bouchez 2012; Soininen et al. 2004; Tison et al. 2005; Tornés et al. 2007) 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 (Kelly et al. 2012, Soininen et al. 2016). None of the tested typology systems performed well or considerably better than the others.

266 Fish assemblages often exhibit a spatial structure (Jackson and Harvey 1989, Kilgour and 267 Barton 1999) and accordingly several studies indicated that fish assemblages are well 268 described by a priori typology systems at fine (Hoeinghaus et al. 2007, Vehanen et al. 2020) 269 and broad scales (Frimpong and Angermeier 2010). The IFE capture fish community 270 composition best of the evaluated typology systems. The bad performance of the BRT is 271 surprising, given that longitudinal patterns, which only segment-based typology systems 272 capture, are common in fish assemblages (Vila-Gispert et al. 2002). The influence of broad-273 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 small (low CS) and the most common taxa 276 tended to occur across types (similar TSA communities). This is in agreement with previous 277 studies that found considerable overlap between the macrophyte communities of different river 278 types (Baattrup-Pedersen et al. 2006, Alahuhta and García-Girón 2021). However, the 279 biogeography of aquatic macrophytes is less well-studied than that of diatoms or fish. Existing 280 studies tend to focus on lentic systems (Alahuhta et al. 2021) and the driving factors of 281 macrophyte community composition are known to differ between lentic and lotic systems 282 (Iversen et al. 2019, Gillard et al. 2020). As for fish, the IFE were the best typology system for 283 macrophytes in our study.

284 Relevance of typology systems and ways forward

285 The availability of well-fitting typology systems matters. Typology systems are not merely 286 useful heuristics for researchers but crucial to the practical implementation of environmental 287 policy. Policies need to define quantifiable standards and targets which requires distinct 288 groups (Mau 2017) to render complex matters legible to institutions (Scott 2008). For example, 289 a river type-specific risk assessment of chemicals is not achievable on a river by river basis 290 but would be feasible with a workable set of river types. If we neglect the potentially 291 international nature of environmental issues, e.g. by relying on national tools to implement 292 international policies, we risk being blindsided by transboundary harm (Knox 2002) and 293 transboundary crises (Boin 2009). Together with Jupke et al. (2022), we show that European 294 river typology systems fail to capture patterns in the community composition of aquatic biota 295 considerably better than arrangements of simple geometric forms. It is important to note that 296 the typology systems evaluated here were not designed for the specific purpose we evaluated 297 them on. Hence, we do not wish to argue against the use of typology systems in general. 298 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 1990, Baattrup-Pedersen et al. 2006), while segment-based systems may fail to account for regional climatic and 303 geological differences (Omernik and Bailey 1997). The BRT include a region variable, but 304 additional regional differences may be relevant in Europe. Watson et al. (2021) and Jupke et 305 al. (2022) have previously suggested integrating the BRT into a region-based system. Based 306 on our results, we recommend combining the BRT with IFE, which were superior to other 307 typology systems for fish and macrophytes.

308 Further avenues are alternative type descriptors and different ways to derive the types. None 309 of the typology systems we considered integrate human influences (e.g., land use, pollution, 310 or hydromorphological alterations). While this would be counterproductive for the delineation 311 of ecosystems with similar least disturbed conditions, they might improve the fit, if the purpose 312 is to predict differences in actually occurring communities. Another class of potential type 313 descriptors are biotic data. They can be used as type descriptors, as is done in the IFE, BGR, 314 and FEoW. While these three systems are based on expert knowledge about species ranges, 315 others have created typology systems directly from observations. Several authors have 316 derived diatom typologies for the evaluation of ecological indices (e.g., Goldenberg Vilar et al. 317 2014, Grenier et al. 2006, Lavoie et al. 2011, Tang et al. 2016). However, these typologies are 318 at the subnational scale and were not meant to be generalized beyond their specific studies. 319 For both macrophytes and fish, biotypes or -regions are commonly derived based on 320 community composition and structure (e.g., Alahuhta & García-Girón 2021, Holmes et al. 321 1998, Loewen et al. 2021, Pont et al. 2007, Riis et al. 2000). If the purpose of the typology 322 system is to define types with similar reference communities though, biotic type descriptors 323 should not be used to avoid circularity (Bailey et al. 2004, Stoddard et al. 2006). A way to 324 circumvent this would be to use Generalized Dissimilarity Models (Ferrier et al. 2007, Latombe 325 et al. 2017) to weight abiotic variables according to the intensity of turnover along their 326 gradients.

327 **5. Conclusion**

328 Our study is the most comprehensive evaluation of European river typology systems to 329 date. Despite variation across evaluation metrics and taxonomic groups, we showed that 330 current broad-scale typology systems fail to capture the community composition of different 331 taxonomic groups beyond their spatial autocorrelation. We propose several avenues for 332 advancing the field. Most notably by combining existing segment- and region-based systems. 333 In an age of increasing data availability, the context becomes scarce and context is what 334 ecosystem typologies can provide. Therein lies their great value for ecological research and 335 environmental policy. When science and policy are restricted to national, fine-scale tools they 336 remain blind toward issues that transcend political borders. Therefore we encourage future 337 work toward broad-scale river typologies specifically catered toward delimiting distinct biotic communities. 338

Declaration of competing interest

340 The authors declare that they have no known competing financial interests or personal 341 relationships that could have appeared to influence the work reported in this paper.

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374 Data availability

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

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