Invertebrates in pigeonholes: Evaluating pan-European freshwater typologies in light of their macroinvertebate communites

Jonathan F. Jupke[1] Pepe Barquín[2] Núria Bonada[3]
Christian K. Feld[4,6] Peter Haase[5,6] Kaisa-Leena Huttunen[7]
Miguel Cañedo-Argüelles[3] Timo Muotka[7,8] Riku Paavola[9]
Edwin T. H. M. Peeters[10] Leonard Sandin[11] Denes Schmera[12]
Philippe Usseglio-Polatera[13] Ralf B. Schäfer[1]

[1] iES Landau, Institute for Environmental Sciences, University Koblenz-Landau, Fortstrasse 7, 76829 Landau, Germany

[2] Environmental Hydraulics Institute, University of Cantabria, C/ Isabel Torres 15, Parque Científico y Tecnológico de Cantabria, 39011 Santander, Spain.

[3] Grup de Recerca "Freshwater Ecology, Hydrology and Management" (FEHM), Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Facultat de Biologia, Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona (UB), Diagonal 643, 08028, Barcelona, Catalonia, Spain.

[4] Centre for Water and Environmental Research, University of Duisburg-Essen, 45141 Essen, Germany

[5] Department of River Ecology and Conservation, Senckenberg Research Institute and Natural History Museum Frankfurt, Gelnhausen 65371, Germany

[6] Faculty of Biology, University of Duisburg-Essen, Essen 45141, Germany

[7] Department of Ecology and Genetics, University of Oulu, P.O. Box 3000, FI-90014 Oulu, Finland

[8] Finnish Environment Institute, Freshwater Centre, P.O. Box 413, FI-90014 Oulu, Finland

[9] Oulanka Research Station, University of Oulu Infrastructure Platform, Liikasenvaarantie 134, Kuusamo 93900, Finland

[10] Aquatic Ecology and Water Quality Management Group, Wageningen University, P.O. Box 47, 6700 AA Wageningen, The Netherlands

[11] Norwegian Institute for Water Research, Gaustadalléen 21, NO-0349 Oslo, Norway

[12] Centre for Ecological Research, Balaton Limnological Institute, Tihany, Hungary

[13] Université de Lorraine, CNRS, LIEC, F-57000 Metz, France

Acknowledgements

This work was supported by ~~the ENTER GETREAL DETAILS HERE~~. We are grateful to the staff that collected and analyzed data for the AQEM, STAR, WISER and ECOSURV projects and of the various water agencies that participated in the abiotic and biotic data collection.

1 Data Availability

Some of the monitoring data sets are freely available. Data from the Ebro Hydrographic Confederation under www.datossuperficiales.chebro.es:81/WCASF/?rvn=1
Data from Naides under www.naiades.eaufrance.fr/france-entiere#/ Data from the RIVPACS data base under www.ceh.ac.uk/services/rivpacs-reference-database Data from the Dutch monitoring agencies under waterkwaliteitsportaal.nl

2 Abstract

Human actions are altering the composition and functioning of ecological communities globally. This transformation is especially rapid and intensive in freshwater ecosystems. Comprehensive and international regulatory frameworks are necessary to slow down and halt the current biodiversity crisis. Like all such frameworks, the Water Framework Directive (WFD) needs to reduce the inherent complexity of its subjects by categorizing them. A pan-European typology for freshwater systems was recently proposed and has already prompted exciting research. However, until now it lacks biological validations, which are critical given the reference state approach employed by the WFD. Using cluster validity analyses, we evaluated the classification that resulted from grouping macroinvertebrate samples across Europe by river types. The results were compared against three other freshwater classification systems, a classification of the biological data and a null model. In addition, we provide the first list of typical and indicator taxa for the new typology. The results differed widely between validity metrics. Classifications that were based on contiguous regions overall achieved better scores than classifications that are based on single stream-reaches. Though performance differed between validity metrics, the newly proposed typology never ranked among the best. These findings indicate that superior alternatives to the new pan-European typology of rivers exist but also that none reliably delineate demarcations between internally homogeneous macroinvertebrate reference communities. Further development of freshwater classifications remains an important goal to facilitate freshwater conservation.

3 Introduction

Freshwater ecosystems provide humanity with clean drinking water and food, they ensure livelihoods for fisheries and farms, and they are places of high recreational and aesthetic value to many (Youn *et al.* 2014; Béné *et al.* 2016; Börger *et al.* 2021). Combined, these contributions to people are estimated to have an annual worth of more than four trillion dollars (Costanza *et al.* 2014) which is approximately a twentieth of the global GDP as of 2017 (World Bank 2021). Despite this exceptional value, humans are currently causing a biodiversity crisis in freshwater ecosystems (Darwall *et al.* 2018; WWF 2020) and are thereby endangering these systems' capacities to provide ecosystem services (e.g. Cardinale 2011; Duffy *et al.* 2017; Grizzetti *et al.* 2019).

The Living Planet Index indicates that populations of freshwater vertebrates on average declined by 84% relative to their 1970 levels (but see Leung *et al.* (2020)). Based on the same data, He *et al.* (2019) found a slightly stronger decline (88%) in freshwater megafauna. Declining abundances have also been recorded for invertebrates (e.g. Cumberlidge *et al.* 2009; Baranov *et al.* 2020), however, most studies find stable or fluctuating patterns in abundance and richness (Floury *et al.* 2013; Outhwaite *et al.* 2020; van Klink *et al.* 2020) but also strong taxonomic and functional turnover (Jourdan *et al.* 2018; Haubrock *et al.* 2020; Mouton *et al.* 2020). The main stressors are well known and can be summarized as overexploitation, water pollution, flow modification, habitat degradation and species invasions (Dudgeon *et al.* 2006; Vörösmarty *et al.* 2010). Addressing these problems is complicated by the emergence of new stressors such as microplastics and light pollution (Reid *et al.* 2018) and interactions between co-occurring stressors (Schinegger *et al.* 2012; Birk *et al.* 2020; Comte *et al.* 2021). To prevent unacceptable harm to freshwater ecosystems and secure the supply of ecosystem services, internationally coordinated action and regulatory frameworks are necessary (Darwall *et al.* 2018; Rees *et al.* 2020; Tickner *et al.* 2020).

The Water Framework Directive (WFD) is among the major regulatory frameworks that aim to protect freshwater systems in the European Union. It aims to reach or maintain a 'good ecological status' for all water bodies in the European Union (European Commission 2000). Since its implementation in 2000, the WFD has motivated improvements in methods for biomonitoring (Birk *et al.* 2012; Carvalho *et al.* 2019), advanced our knowledge of the ecological status of freshwater systems throughout Europe (EEA 2018) and has stimulated relevant research at the science-policy interface (Reyjol *et al.* 2014). It has not, however, reached its explicit aim, to achieve 'good ecological quality' for all surface and groundwater bodies by 2015. As of 2018, only 40% of surface water bodies had reached this status (EEA 2018). Multiple criteria determine the underlying status assessment: biological quality elements (benthic invertebrates, phytoplankton, benthic flora and fish fauna), physicochemical

variables like nutrient and pollutant concentrations, and hydromorphology.

The participating states use national methods to assess their water bodies. An intercalibration process tries to ensure a coherent notion of 'good ecological quality' and to harmonize the national assessment methods. A recent output of the intercallibration process is a pan-European typology of lentic and lotic freshwater systems (Lyche Solheim *et al.* 2019). While the WFD required the participating states to create stream typologies for the assessment, these typologies differ widely in the number and kind of streams they recognize. As these diverging classification schemes impeded the comparison of assessments between states, intercalibration types have been established (Birk *et al.* 2013; Poikane *et al.* 2014). However, many national stream types (42%) are not associated with any of the intercalibration types while others are linked to multiple types (European Commission 2019). The recent effort by Lyche Solheim *et al.* (2019) combined the national classifications and connected the new, broad river types (BRT) with the established intercalibration types. This pan-European typology has already been used to compare nutrient threshold values across river types (Poikane *et al.* 2019), to investigate interaction types of multiple stressors (Birk *et al.* 2020) and to show that chemical pollution currently limits the ecological status of European surface waters (Posthuma *et al.* 2020).

Until now, it has not been evaluated, whether biological assemblages at least-impacted sites differ between the proposed broad river types and whether they are homogeneous within them. While this is generally among the most important considerations when creating a typology (Melles *et al.* 2014), it is especially important for the WFD because it relies on the reference condition approach. In this approach, a site's ecological status is evaluated by comparing it with that of least-impacted reference sites within the same stream type (Resh & Rosenberg 1993; Wright *et al.* 2000). The larger the difference between the reference and the test site, the worse the assessment. Therefore, the spatial stability of reference states is crucial to the validity of this approach (Statzner *et al.* 2001).

The typology of Lyche Solheim *et al.* (2019) largely follows the System A approach of the WFD in which ecoregion, altitude, geology and catchment size are used to classify river segments. Earlier studies (e.g. Verdonschot 2006b) suggest that other variables might be more strongly related to the distribution of different taxa and Borgwardt *et al.* (2019) showed that one of the proposed categories (BRT1-Very Large rivers) could be further divided into seven different types with distinct assemblages of benthic invertebrates.

In this paper, we evaluate whether assemblages of freshwater macroinvertebrates at least-impacted sites follow the classifications proposed by Lyche Solheim *et al.* (2019). To this end, we evaluate its merits as a classification of sampling sites and compare it to other classification schemes based on cluster validity criteria. Additionally, we provide lists of very

common (henceforth typical) and indicator taxa for the individual broad river types. The difference between the two categories is that good indicators are often rare species (Chytry *et al.* 2002; Tichy & Chytry 2006; Caceres & Legendre 2009) which are not well suited to describe reference states. Thus, while the indicator taxa are indicative of a river type the typical taxa are closer to what one might reasonably expect to find within a sample from the river type. Note that Lyche Solheim *et al.* (2019) first derived 20 BRTs and then reduced them to 12 by combining several river types with few realizations. As previous publications have used both (e.g. Posthuma *et al.* (2020) used BRT12 and Poikane *et al.* (2019) used BRT20) we will consider both in the following.

4 Methods

4.1 Preparation of macroinvertebrate data

We compiled a large data set of macroinvertebrate samples from rivers throughout Europe. The data included 152572 samples (Figure 1) taken between 1968 and 2020. The samples were assigned the BRT20-type of the nearest river segment or removed if this segment was further away than 500 m. As geospatial representation of the BRTs we used the data provided by Globevnik (2019). This step reduced the number of samples to 76621 (50% of all samples). Next, we removed all samples from sites that were considerably ~~affected by humans. To identify these non-reference sites, we used different criteria. The respective criterion depended on the data set, as some provided detailed information on environmental conditions while other solely included biological information. If no~~ environmental information ~~were included or the information did not cover~~ all sites, we identified ~~non-reference~~ sites using the catchment landcover. Sampling sites from catchments ~~in which~~ the combined area of urban and agricultural land exceeded 20% of the catchment area ~~w~~here considered ~~non-reference sites~~. We used the Catchment Characterization and Modeling database for geospatial data on catchments (Vogt *et al.* 2007) and the Corine Landcover data from 2018 for landcover information (CLC 2018). We provide detailed information on variables and thresholds used to determine the reference sites in Table 1. We removed ~~non-reference~~ sites because differences between stream types are more pronounced ~~between reference sites~~ (Verdonschot 2006a) and because we wanted to compare the typologies capability to delineate spatially stable reference assemblages. Removing non-reference sites further decreased the number of samples to 23284 (15% of all samples). Lastly, we only considered the 21169 samples that were taken in or after the year 2000 (14% of all samples).

The data originated from different sources and required adjustments to ensure taxonomic

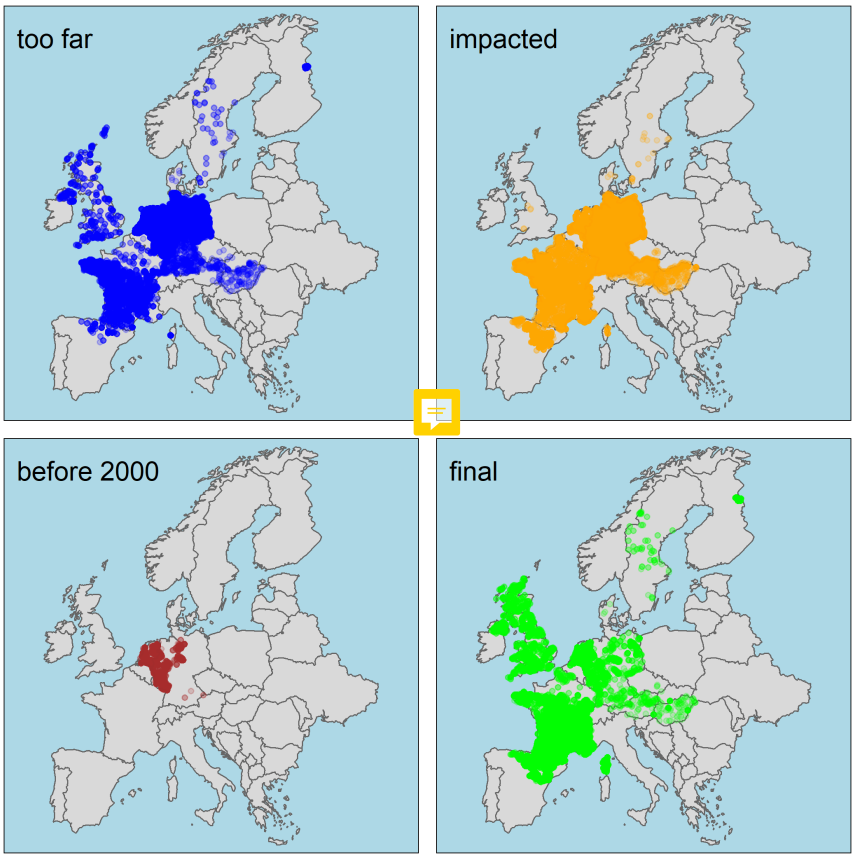

Figure 1: Map of sampling sites. The first map (too far) shows sites that were more than 500 meters removed from the closesed stream segement. The second map (impacted) shows sites that were categorized as not in referene condition. The third map (before 2000) shows sites that were sampled before 2000. The fourth map (final) shows all samples that were used for the analyses.

consistency. We used the Global Biodiversity Information Facility (GBIF) to replace synonyms with accepted names and assign a taxonomic level to each observation. To integrate the different data types we transformed all data to presence-absence. Next, we removed all observations that did not belong to one of the following classes: Clitellata, Insecta, Malacostraca, Bivalvia or Gastropoda. From here on, we will differentiate between two data sets: *data genus* and *data all*. We used *data genus* to compare the different classifications and to derive indicator taxa. This data set was harmonized to the genus level. All observations from lower taxonomic resolutions (i.e. family, order, etc.) were removed. This resulted in a data set with observations from 786 genera. We used *data all* to derive the typical assemblages. This data set does no have a common taxonomic level, so that some taxa are represented at the family level and others at the species level. Instead, we aimed to represent each taxon with a taxonomic level that would be optimal for it, given the data available for the river type. We thereby increased the number of observations that we could use but decreased the comparability between river types. Since river types do not influence the typical assemblages of other river types, comparability was not necessary. Using different levels posed the challenge of finding an optimal level for each taxon given a data set and river type. We established the optimal level with a hierarchical approach. For each taxon, we calculated the percentage of observations represented at each higher taxonomic level. If this value was below 50 %, we harmonized all observations to this, optimal, level. If it was above 50%, we repeated the procedure with the next higher level. We also included all observations with lower than optimal resolutions. The final *data all* contained 405 taxa represented at the species level, 592 taxa represented at genus level and 192 taxa represented at family or lower taxonomic levels.

After removing samples that did not meet our criteria, we did not have sufficient data to adequately represent all river types. We considered the data for a river type insufficient if it contained too few sites (< 20) or the distribution of sites was not representative of the river type.
Maps of the sampling locations for the individual river types are provided in the Supplementary Materials. We were not able to represent the river types: BRT6, 7, 12, 13, 17, 19 and 20. Samples from these river types were removed.

4.2 Comparison of typoglogies

To evaluate the two typologies proposed by Lyche Solheim *et al.* (2019), we compared them with the three other typologies: i) the k-means typology of the global river classification framework (GloRiC, Ouellet Dallaire *et al.* 2019); ii) the freshwater ecoregions proposed by Illies (1978); and iii) the biogeographical regions proposed by the European Environmental

Agency (BGR, EEA 2016). These typologies ~~represent two different kinds of freshwater typologies:~~ reach-based typologies (BRT and GloRiC) and regional typologies (Illies and BGR). Reach-based typologies classify single stream reaches. The instances of individual types are not spatially contiguous ~~but~~ can be far apart ~~and~~ are commonly very close to instances of different types. Regional typologies classify large contiguous areas and ~~there always is only one~~ instance ~~of each~~ type. ~~The~~ different types are only adjacent at the ~~regional margins~~. In addition to these five established typologies, we also evaluated BRTred, a reduced version of BRT20. In BRTred, we combined the river types with redundant typical assemblages (see section Indicator and typical assemblages for more details). Only genus-level data (*data genus*) were used for this analysis. We removed all observations from types that were represented by less than twenty sites from the data set. See table 2 for the remaining types per typology.

In order to be able to judge the results, we created two additional typologies. As an upper bound of what to expect, we created a classification of biological data using flexible beta clustering (Lance & Williams 1967) with the β parameter set to -0.25 and the common parameterization ($\alpha_1 = \alpha_2 = \alpha, \beta = (1 - \alpha)/2, \gamma = 0$). We chose the number of groups that maximized the average silhouette width (9). Since this typology is not constrained by environment or space but only represents patterns in the biological data, we expect it to delineate more clearly between different biological assemblages than the other typologies.
As a lower bound, we created 100 random partitions of the data. For each partition, we first drew the number of classes as a random variable from the interval between the lowest number of types in any of the typologies tested (6 in BGR) and the highest number (14 in BRT20 and GloRiC). Then we assigned each observation randomly to one of the groups.

We calculated four cluster quality metrics for each typology: the average silhouette width, the Calinski-Harabasz index, an indicator value score and the classification strength. We used the Jaccard distance between sites as a distance metric.

The average silhouette width (ASW, Kaufmann & Rousseeuw 1990) is computed as

$$ASW = \frac{1}{n}\Sigma_{i=1}^{n}\frac{a_i - b_i}{max(a_i, b_i)}$$

where a_i is the average dissimilarity of point i to points from its type, b_i is the average dissimilarity of point i to points from the closest other type and n is the number of observations. Positive values indicate that on average points are more similar to observations from their own type than to those ~~of~~ the most similar one. Therefore, high scores imply better typologies. Lengyel & Botta-Dukát (2019) recently proposed a generalized version of the ASW. ~~By using the~~ arithmetic average to compute a_i and b_i, spherical clusters are assumed

to be optimal. Using a generalized mean instead, we can flexibly adjust our validity metric to put a stronger emphasis on compactness (a_i) or separation (b_i). The generalized mean of degree p (M^p) is computed as:

$$M^p(\mathbf{x}) = \left(\frac{1}{n}\Sigma_{i=1}^{n} x_i^p\right)^{1/p}$$

The generalized mean can take the value of common summary statistics such as the minimum ($p = -\infty$), the maximum ($p = \infty$) or the harmonic mean ($p = -1$). For example, for $p = -\infty$ the silhouette width is the difference between the minimum distance of observation i to any other observation from the same type and the minimum distance from that observation to any observation from the next closest type. This perspective excludes outliers and values separation over compactness. The weighting shifts towards compactness as we increase p. We evaluated the silhouette width for $p \in \{-\infty, -2, -1, 1, 2, \infty\}$. If not further specified, ASW refers to the common average silhouette width (i.e. $p = 1$) in the remainder of the text.

The Calinksi-Harabasz Index (CH, Caliński & Harabasz 1974) is computed as

$$CH = \frac{BGSS}{WGSS} \times \frac{n-k}{k-1}$$

where $BGSS$ is the squared sum of distances between group centroids and the overall centroid (between group sum-of-squares), $WGSS$ is sum of squares of distances between observations of one group (within group sum-of-squares), k is the number of clusters. High values indicate that variation within types is smaller than between types. As the second term controls for the degrees of freedom, it can be understood as an analog to the F-Statistic. The algorithm assumes Euclidean data but good performance with a similar metrics was shown for binary data in the context of fMRI-scans (Dimitriadou *et al.* 2004).

The indicator value score (IVS) is based on the indicator value (IndVal) proposed by Dufrêne & Legendre (1997). The IndVal itself will be explained in detail below. Here, we only note that we used 999 permutations to compute p-values and in contrast to the latter application ~~did not control~~ the family-wise error rate. IVS is the fraction of taxa that are statistically significant indicators (at a significance level of 0.01) for some type of a typology. Higher scores indicate a better classification.

Lastly, we computed the classification strength (CS, Van Sickle 1997). Classification strength is the difference between mean within cluster similarity ($\overline{W}$) and mean between cluster ($\overline{B}$) similarity. As such it ranges between 0 ($\overline{W} = \overline{B}$) and 1 ($\overline{B} = 0$), where higher values indicate a stronger classification. ~~A similar and recently applied metric is the partition analysis (Roberts 2019) which is the ratio of $\overline{W}$ and $\overline{B}$. Here, we opted for the former~~

~~as is~~ has been used in similar analyses (e.g. Gerritsen *et al.* 2000; Van Sickle & Hughes 2000; Vasconcelos *et al.* 2013) which enables us to directly compare our results with those of previous studies. ~~Note that results did not differ qualitatively between CS and partition analysis (data not shown).~~ Similarities were calculated as 1 - Jaccard distance.

Based ~~on these four~~ cluster ~~criteria, each typology was assigned a score~~. We used these scores to evaluate the overall performance of the typologies. ~~The typology that performed best in some metric received 6 points, the second 5, the third 4 and so on.~~ Differences smaller than 5% of the range between biological and random partitions were regarded as ties. When typologies were tied, they all received the mean of their untied scores. For example, if three typologies are tied for the first place, instead of 6, 5 and 4 points ~~respectively,~~ each receives a score of 5.

4.3 Indicator and typical assemblages

Both indicator and typical assemblages were derived for BRT20. We used the IndVal approach of Dufrêne & Legendre (1997) to identify indicator taxa. For this analysis, we used *data genus* ~~which~~ consists of genus-level presence-absence data. The IndVal ~~can be understood as the~~ product of the two quantities A and B. For our purposes, A is the relative number of observations of taxon i that are within type j. It was initially described as specificity (Dufrêne & Legendre 1997) but is better understood as concentration (Podani & Csányi 2010) because ~~it~~ is independent of the total number of types. B is the relative frequency with which species i occurs in type j. The maximum score is assigned to a species that only occurs in one type ($A = 1$) and occurs in all samples of that type ($B = 1$). Here, we used the group-equalized version of the IndVal ~~which~~ accounts for the fact that the number of samples differs between types. The statistical significance of the IndVal statistic was assessed with a permutation test that computes IndVal values for random permutations of sites and types and compares the observed IndVal against this empirical distribution. We used $2 * 10^5$ permutations. We controlled the family-wise error rate with Bonferroni's correction (Bonferroni 1935). This correction is conservative and has low statistical power (García 2004; Nakagawa 2004). Hence, we regard the hypothesis, that a genus is an indicator for a broad river type, strongly supported by our data if we find the indication to be statistically significant. We used 0.05 as the base significance level.

These indicator species ~~provide valuable insight into the~~ communities ~~but~~ miss the ubiquitous generalist species that occur in many types (tramp species *sensu* McGeoch *et al.* (2002)). Even if these taxa are common within a type (high B), they will typically have low concentrations in most types (low A) and hence low and statistically non-significant indicator

values. ~~Hence, the indicator assemblages do not represent a typical sample, in the sense that these taxa can reasonably be expected to occur in samples of the type.~~ We derived such typical assemblages by setting ~~explicit~~ thresholds for B. ~~We used *data all* to derive typical assemblages. These data have different taxonomic levels and we set different thresholds for different taxonomic levels.~~ All species that occurred in more than 25% of samples of a river type (i.e. $B > 0.25$) were considered typical. The value increased to 33% for genera and 66% for families or lower taxonomic levels. Others used alterations of the indicator value before, even if this was implicit. For example, Wagner & Edwards (2001) considered only the A component. McGeoch *et al.* (2002) discusses the advantage of different combinations of A and B.

After deriving typical assemblages, we evaluated their similarity using the Jaccard similarity. A similarity of 0.5 indicates that half of the taxa ~~in the combined taxa pool~~ occur in both typical assemblages. If the similarity between two typical assemblages exceeded 0.8, we deemed the river types redundant and combined them. For example, the broad river types BRT2 and BRT3 (medium to large and very small to small siliceous lowland rivers) might be found to be redundant and combined into BRT2_3 (very small to large siliceous lowland rivers). All sites belonging to either of these river types would also be reclassified and the typical assemblages would be derived again. This is repeated until no similarity exceeded 0.8. We ~~did not do the same with~~ indicator assemblages as they are explicitly ~~being~~ optimized for being different from one another (through the equal weighting of A and B). This way we can evaluate whether the ad-hoc combinations of river types used to derive the BRT12 typology are justified by biological homogeneity.

4.4 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 & Srinivasan 2021), tidyverse packages (Wickham *et al.* 2019) and taxize 0.9.98 (Scott Chamberlain & Eduard Szocs 2013; Chamberlain *et al.* 2020). Geospatial analyses were conducted using sf (Pebesma 2018). Clusters were created and evaluated with fpc (Hennig 2020), indicspecies (Caceres & Legendre 2009), labdsv (Roberts 2019), optpart (Roberts 2020). Generalized silhouette widths were computed with the R functions provided in the supplementary materials of Lengyel & Botta-Dukát (2019). Figures and maps were created with ggplot2 (Wickham 2016) and tmap (Tennekes 2018).

5 Results

5.1 Comparison of classifications

The ASW was highest in the biological classification (0.04) followed by BGR (0) and Illies (-0.01)(Figure 2a). All reach-based typologies had negative ASWs (BRTred: -0.03; BRT12: -0.02; BRT20: -0.03; GloRiC: -0.05) below or equal to those of the random partitions (0 ± 0.001). The CH was highest in the biological classification (342.04). Both regional approaches had higher CH (BGR: 188.94; Illies: 142.44) than the reach-based typologies (BRT12: 111.67; BRT20: 96.03; GloRiC: 77.4), with the exception of BRTred (158.3), which had a higher CH than Illies' ecoregions. All typologies had higher scores than the random partitions (1 ± 0.1). The CS was highest in the biological classification (0.1) and lowest in the random partitions (0 ± 0). Most typologies had very similar scores, of approximately 0.04. Only Illies' ecoregions exceeded 0.5 with a score of 0.07.
The biological classification had the largest IVS (0.14) closely followed by Illies (0.14) and GloRiC (0.14). These two were followed by BRTred (0.12), BRT12 (0.11), BGR (0.1) and BRT20 (0.09). The random partitions received lower scores (0 ± 0).

The generalized silhouette width for all typologies except the random partitioning decreased with increasing degree of the mean (Figure 2b). The rank order of silhouette widths changed little between the different degrees and generally followed the pattern: biological > BGR > Illies > BRT12 > BRTred > BRT20 > GloRiC. Exceptions to this rank order were that at $p = -\infty$ GloRiC had a higher silhouette width than BRT12 and BRT20 as did BRTred. Additionally, Illies had a lower silhouette width than all BRT typologies at $p = \infty$. The difference between typologies and random partitions is most pronounced at $p = -2$ and decreases with increasing degree. At $p = -2$ GloRiC has a lower silhouette width than the random partitions and at $p = \infty$ all typologies silhouette widths below that of the random partitioning.

Overall Illies received the highest score, with 20 of 24 possible points, followed by BGR (16.5), BRTred (14), BRT12 (13.5), GloRiC (13) and BRT20 (9).

5.2 Indicator genera

Of the 786 genera included in the analysis, 463 were selected as statistically significant indicators by our analysis. Most were indicative of three or fewer river types (324, 70 %). The highest number of broad river types that a single genus was indicative of was eight.
Five genera ~~were indicative of eight broad river types~~: the damselfly Calopteryx, the beetle Oulimnius, the bivalve Pisidium, the mayfly Serratella and the alderfly Sialis. They

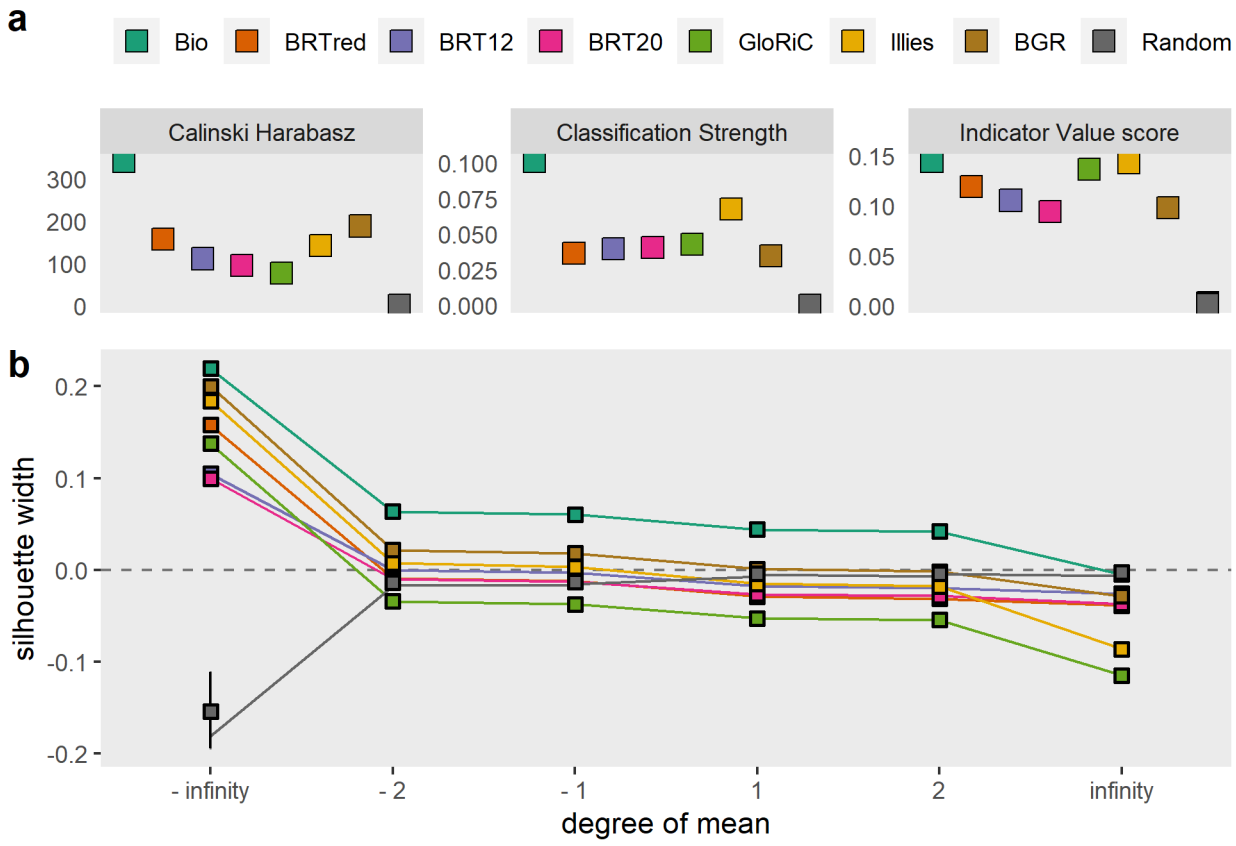

Figure 2: Cluster validity citeria for freshwater typologies. (a) Calinski Harabasz, Classification Strength and Indicator Value score of all eight freshwater typologies. (b) Generalized Silhouette width over the degrees p of the mean. The dashed horizontal line indicates a score of zero.

were generally indicative ~~for~~ all river types that were not high-altitude (BRT14-16) and not Mediterranean (BRT18). Oulimnus and Sialis were indicators for all remaining types except ~~the~~ very large rivers (BRT1). Calopteryx indicated all remaining types except for small, lowland, siliceous rivers (BRT3). However, the indicator value of Calopteryx in BRT3 (0.18) was only marginally lower than for BRT1 and 2 (0.2), while is was noticeably lower for high-altitude and Mediterranean types (0.04 - 0.11). The bivalve Pisidium was indicative of all remaining types except large, mid-altitude siliceous rivers (BRT8). As with Calopteryx, the indicator value for the exempt river type was only slightly lower than for some of significant types. Serratella is the only genus of the five that is also indicative of a high-altitude river type. It is indicative of BRT16, but not of very large (BRT1) and small, lowland, calcareous (BRT5) rivers.

Baetis was the most common genus overall, occurring in 73.1 % of sites followed by Hydropsyche (65.6 %), Gammarus (64.6 %), Elmis (62.6 %) and Limnius (57.7 %). The number of indicative genera varied strongly between river types. BRT4 had the most indicative genera (261) and BRT14 had the least (5). The mean number of indicative genera was 96 with a standard deviation of 79. Of the 261 genera that were indicative of BRT4, 34 were unique to BRT4. ~~The mean indicator value of statistically significant indicators was 0.14 with a standard deviation of 0.08.~~ Dikerogammarus in BRT1 had the highest significant indicator value with 0.63 and Notiphila in BRT4 had the lowest significant indicator value with 0.03.

Table 4 shows the indicator values for all taxa that were statistically significant indicators.

5.3 Typical assemblages

We combined the broad river types BRT4 and 5, BRT 2, 3, 8, 9, 10, 11 and 18 as well as BRT 15 and 16 because their Jaccard similarity exceeded 0.8. The BRT4_5 type represents lowland, calcareous streams irrespective of size, BRT2_3_8_9_10_11 represents low and mid-altitude streams of varying geology and BRT 15_16 represents non-siliceous high-altitude streams.

68 of 1189 taxa were included in the typical assemblages. Most at the genus level (43), followed by family or lower level (24) and species (1). On average, taxa occurred in 2.1 typical assemblages. The family Chironomidae was included in all typical assemblages. The most common genera were Ancylus, Baetis, Esolus, Hydropsyche, and Limnius all of which occurred in four typical assemblages. *Serratella ignita* was the only species included in the typical assemblages and was typical for BRT4_5, BRT2_3_8_9_10_11 and BRT15_16. The average size of typical assemblages was 23.3 with a standard deviation of 5.5. The largest typical assemblage was BRT1 with 28 taxa and the smallest was BRT18 with 15

taxa. To compare taxonomic resolution across typical assemblages, we assigned a value of three to each species, two to genera and one to lower taxonomic levels. The mean taxonomic resolution was 1.6 with a standard deviation of 0.5. The river type BRT4_5 had the highest taxonomic resolutions (2). BRT14 and BRT18 had the lowest taxonomic resolution (1.0)

6 Discussion

We used four cluster validity metrics to compare the partitioning of macroinvertebrate samples proposed by six different freshwater typologies. Four typologies were reach-based (BRTred, BRT12, BRT20 and GloRiC) and two were regional (Illies and BGR). As a reference frame for the cluster validity scores, we also computed a biological classification of the samples and 100 random partitions of the data. As we expected, the cluster validity scores for the six freshwater typologies lay in the interval between random partitioning and biological classification in most cases. The only exceptions were silhouette widths (Figure 2b).

Overall, the freshwater ecoregions proposed by Illies (1978) performed best in our assessment. The Bio-geographical regions, BRTred, BRT12, GloRiC and BRT20 followed in that order. Illies' freshwater ecoregions had the highest IVS and classification strength. While GloRiC is a close second in the IVS, it has the lowest scores in CH and ASW. Between the broad river types, BRTred performed best in two out of four metrics. All three were tied for classification strength and BRT12 had the best silhouette width across degrees.

Average silhouette widths were relatively low for all groups. No typology received positive scores for the ordinary silhouette width at $p = 1$. However, the ASW_{∞} was highest for BRT12 but still below zero. The low ASWs indicate that most observations could also be regarded as an instance of a different type, without losing much (or, in the case of negative ASWs, any) discriminatory power. $ASW_{-\infty}$ gives the largest weight to the separation of clusters without considering compactness. It clearly shows a stronger separation between the types of regional typologies than between those of reach-based ones. It is also at this level that all typologies have positive ASWs and that the difference to random partitions is largest. The differences between regions and reaches and between typologies and null-partitions decrease with increasing p. The negative ASW_{∞} indicate that for each of the typologies, there is some site within their type that is more dissimilar to it, than the most dissimilar site from the next closest type.

Overall, regional approaches that assign large contiguous areas to a single type were a better summary of our extensive data set of invertebrate occurrences than reach-scale typologies. The constrains of our study may have played in favor of regional approaches. The taxonomic

resolution of our data only allowed inferences at the genus level. Potentially, species-level data would have highlighted bigger differences at smaller scales and hence be better summarized by typologies with smaller mapping units. Along the same lines, Moog *et al.* (2004) showed that higher taxonomic resolution was necessary to delineate smaller ecoregions and the same logic could expand to reach-scale typologies. Similarly, Verdonschot (2006a) showed that differences in classification strength were noticeable between 'best-available' and family-level data on a pan-European scale. However, the difference was ~~not large~~ and their analysis ~~does not allow~~ to infer the loss of using genus- instead of species-level data. Hawkins *et al.* (2000) note that, across taxa groups and typologies, higher taxonomic resolution does not always lead to greater classification strength.

Additionally, the likelihood of assigning an observation to the wrong type due to inaccuracies in the spatial data are lower for regional typologies, where such mistakes can only happen toward the margins between types. We reduced this error by using a more stringent distance-to-stream criterion for the selection of sites than similar studies. For example, Irving *et al.* (2018) used a cutoff of 3 km to assign streamflow gauging stations to rivers. Very small rivers are largely missing from the river network representations used by GloRiC and the BRT as provided in Globevnik (2019). Hence, samples from these rivers are either omitted from the analysis if they are too far removed from the next stream or assigned to the next stream segment. In most cases, this ~~ought to be~~ a stream of a similar type (i.e. some type of small river) ~~but this is not guaranteed~~. New and highly resolved river networks (e.g. Lin *et al.* 2021) might provide more accurate mapping of stream types and resolve these problems.

~~However,~~ the patterns we observed can also be interpreted in the light of metacommunity theory. The spatial distance between the instances of different types in reach-scale typologies is often small. Typically, landscapes and catchments are made up of mosaics of different stream types. In positing that assemblages vary between instances of different reach-scale types, we implicitly assume that dispersal is strong enough for species to track variation in local conditions (Leibold *et al.* 2004) but not so strong that mass effect ~~would~~ overrule environmentally induced patterns (Mouquet & Loreau 2003). If taxa are strongly limited by dispersal e.g. through historical and anthropogenic dispersal barriers (Leibold *et al.* 2010; Belletti *et al.* 2020) or through the sheer distance between sites, they are unable to reach potentially favorable sites. In our case, stronger dispersal limitation would lead to larger differences between sites of the same type. Dispersal limitation leads to a pattern known as distance decay, which is often found at large spatial scales (Nekola & White 1999; Morlon *et al.* 2008) but varies in its magnitude between taxa, realms and degrees of latitude (Graco-Roza *et al.* 2021). Studies have found both, invertebrate communities that are predominantly structured by environment (e.g. Heino *et al.* 2012; Landeiro *et al.* 2012) and those that are structured by space (Mykrä *et al.* 2007; Astorga *et al.* 2012). However,

even for microbes, which under the Bass-Becking hypothesis ("everything is everywhere but the environment selects") were long considered to have cosmopolitan distributions, the role of dispersal limitation, at least at large spatial scales, is becoming evident (Telford *et al.* 2006; Lindström & Langenheder 2012; Soininen 2012). Our analysis of generalized silhouette widths showed that the separation between assemblages of broad river types decreases if the weight of outliers (i.e. p) is increased up to a point where the separation is lower than in random partitions. This pattern could be explained by strong dispersal limitation leading to divergent communities in comparable environments.

At the other extreme, dispersal is strong enough to allow species to persist in habitats otherwise unsuitable for growth in a process known as source-sink dynamic or mass-effect (*sensu* Wilson & Shmida (1984)). In our case, mass effects would lead to smaller differences between sites of different types. Such effects are expected to exist primarily on small spatial scales (Ng *et al.* 2009). What constitutes a small spatial scale depends on the dispersal ability of species (Heino *et al.* 2015). For many taxa the distance between reaches would fall under this category, while the distances between regions are only small at their margins. Experimental studies indicate that the immigration flows that are required to alter community composition are considerable. (Logue & Lindström 2010; Lindström & Östman 2011; Adams *et al.* 2014). Mass effect might be reduced when organisms bias their dispersal towards favorable environments (Resetarits & Binckley 2013; Haegeman & Loreau 2015) but increased if the dispersal destination is outside the control of the dispersee. Such is the case for flying insects under windy conditions (Epele *et al.* 2021). The tools to identify the imprints of mass effects in large ecological data sets remain an area of active development (e.g. Leboucher *et al.* 2020).

The better performance of regional typologies might also be taken to support the notion, that the composition of aquatic macroinvertebrate communities tracks changes in large-scale rather than small-scale variables. Many studies have investigated this question before. Among them are studies that have studied the explanatory potential of ecoregions, which might be considered as categorical combinations of large-scale environmental conditions like climate, geology and altitude. Verdonschot & Nijboer (2004) used the data compiled during the AQEM project to investigate potential drivers of macroinvertebrate community composition. They found that the distribution of macroinvertebrates follows Illies' freshwater ecoregions and that large-scale variables like geology explain most of the variation. However, using an extended data set, that included data from both AQUEM and STAR, Verdonschot (2006b) ~~did not find~~ ecoregions to be a ~~strong~~ predictor of invertebrate community composition. Similarly, ecoregions explained a negligible amount of variance in community composition in Swedish boreal streams (Johnson *et al.* 2004). The review of Hawkins *et al.* (2000) finds that ecoregion-based approaches usually outperform catchment-scale classifica-

tions. However, the classification strength was generally low. The classification strengths of the studies they considered lay between 0.07 and 0.16, which slightly exceeds the ones we found (between 0.04 to 0.07) but is in agreement with several other studies (e.g. Snelder *et al.* 2004; Heino & Mykrä 2006; Mykrä *et al.* 2009; Vasconcelos *et al.* 2013). The interplay between local and regional control cannot be considered removed from the previous discussion of dispersal limitation since the degree to which assemblages are regulated regionally or locally likely depends on the magnitude of dispersal (Ryabov & Blasius 2011). Synthesis of these findings is impeded by the fact that many of the studies relied on combinations of variance partitioning and eigenfunction analyses that have been shown to be flawed (Gilbert & Bennett 2010; Smith & Lundholm 2010; Tuomisto *et al.* 2012). An alternative method to evaluate the importance of dispersal processes for community assembly was recently proposed (Vilmi *et al.* 2020) but has yet to be extensively tested and applied.

Typologies based on environmental variables cannot account for the effects of biotic interactions on species distributions. While these received much attention in the early days of macroecology (Diamond 1975; Connor & Simberloff 1983) the focus shifted towards environmental filters (e.g. Whittaker & others 1970; Pearson & Dawson 2003) assuming that biotic interactions are only important at local scales. Recently their role for macroecology as been revisited (Wisz *et al.* 2013). Propelled by a series of new methods (e.g. Popovic *et al.* 2019; Ovaskainen & Abrego 2020) several studies have recently investigated the effect of biotic interactions on larger biogeographical patterns. While some indicate, that the role of environmental conditions is more important than that of biotic interactions (Elo *et al.* 2021), others suggest that biotic interactions modulate the response the abiotic enviornment (Abrego *et al.* 2021).

Our analyses further suggest that there are large redundancies between the typical assemblages of the broad river types. We found four different mid-altitude river types and two low altitude types to have very similar typical taxa. These river types extended across gradients in altitude, geology and stream size, though they did not include very large or high altitude rivers. This might be taken to indicate, that species-level data are necessary to show differences between these types or that even the BF typology with twenty types is too coarse. Our analysis identified mostly those taxa as common that sufficiently euryoecious that their distribution is not determined by the variables that delineate the different stream types. Within the single stream types only a few taxa were common without also being common in other stream types. This could indicate that even within a single river type environmental conditions vary so strongly that more stenooecious species do not commonly occur throughout them.

The typical assemblage of very large river (BF 1) harbors many genera that include inva-

sive species like *Dreissena polymorpha*, *Dikerogammarus villosus*, *Corbicula fluminea* and *Potamogyrus antipodarum*. The presence of these taxa within the typical assemblage thus highlights the importance of neozoa ~~as stressors~~ in large rivers (Leitner *et al.* 2020). The typical assemblage for the large combined river type BRT2_3_8_9_10_11 mainly includes Trichoptera (6), Ephemeroptera (6) and Elmidae (4) genera. These genera include several species that are typical for the rhitral, such as *Esolus parallelepipedus*, *Elmis aenea* and *Hydropsyche pellucidula*. In addition, several taxa that are more common in mid-altitude rivers are included like Rhithrogena or Ecdyonurus. The typical assemblage of siliceous and organic high altitude rivers (BRT14) only contains families or lower taxonomic levels. This is most likely what leads to the differentiation from the combined high altitude type BRT15_16. The combined high altitude river type (BRT15_16) has a higher taxonomic resolution and contains the largest number of Plecoptera genera of any typical assemblage (4), among them Isoperla which is common in high-altitude rivers. Lastly, the typical assemblage of Mediterranean mid-altitude streams also exclusively consists of families or lower taxonomic levels. Unique to this typical assemblage is only the family Gerridae.

~~The data were not suitable~~ to evaluate most of the combinations made to arrive at BRT12 from BRT20. Many of the types that were merged ~~in the reduction~~ are very rare and hence we ~~only had few or no samples for them~~. However, our analysis lends support to the combination of BRT14, 15 and 16 to a single high-altitude river type. We found the typical assemblages of BRT15 and 16 to be redundant. BRT14 possibly only differed from those two types due to the low taxonomic resolution of our data for this type. As BRT12 generally performed better than BRT20 in this study, the combinations made by ~~Lyche~~ Solheim *et al.* (2019) seem to be ~~warranted~~. We suggest that future studies should rather employ the aggregated than the full typology. However, given the low performance of stream-based typologies in general, we advise caution when assuming spatially homogeneous reference communities within them.

While there were clear and systematic differences between typologies, not one of the typologies tested in this study performed well. All cluster validity metrics had comparatively low scores. It is beyond the scope of the current study to assess whether this is a problem of the implementation or a general issue, i.e. if it is theoretically possible to create environmental typologies that capture large amounts of variation between communities or if niche processes or selection (*sensu* Vellend (2016)) generally do not explain enough variance. The latter would constitute a serious problem for the reference state approach as this would entail that spatial stability of reference communities (Statzner *et al.* 2001) should generally not be assumed. However, since several studies have found typologies to explain a significant amount of variation (e.g. Lorenz *et al.* 2004; Johnson *et al.* 2007) we deem issues with the implementation more likely.

The stream typology of the WFD must be optimized not only for macroinvertebrates but

for all four biological quality elements (macroinvertebrates, diatoms, fish and macrophytes) (Dodkins *et al.* 2005). Future studies should assess whether the conclusions drawn from this study are supported by the other taxa groups. Stream classifications must be understood as models Loveland & Merchant (2004). Alongside our growing knowledge about freshwater systems, we should strive to further improve them, as to increase their value for biomonitoring and to render them more effective tools for conservation. Our study has shown that the typologies proposed by ~~Lyche~~ Solheim *et al.* (2019) should not be the end of this effort.

7 Supplementary Materials

Table 1: Overview of data sets used for the analysis.

Data set	Area	Time Span	Number of Samples	Criterion	Connected Publications
Monitoring data from German federal agencies	Germany	1968 - 2013	65211	Land	Bhowmik & Schäfer (2015), Berger et al. (2018), Le et al. (2021)
Ebro Hydrographic Confederation	Spain	2004 - 2019	3668	IASPT > 4.5 & Land use	Escribano et al (2018)
Naiades	France	2002 - 2020	27052	BDI > 14.5 & Land use	
Cantabria	Spain	2005	55	Land use	Alvarez et al. (2010), Alvarez et al. (2011)
Picos de Europa	Spain	2015-2017	24	Land use	
Ecosurv	Hungary	2005	491	Land use	Schmera & Baur (2011), Schmera et al. (2012)
RIVPACS database	UK	1978-2004	2504	original site selection	Clark et al. (2003), Turley et al. (2014)
STAR	Europe	2002-2003	91	classific in data set & Land use	Verdonschot (2006a), Johnson et al. (2007)
WISER	Europe	2000-2008	2565	Land use	Lyche-Solheim et al. (2013)
AQUEM Sweden	Sweden	2000	150	Land use	Verdonschot (2006a)
Koutajoki drainage basin	Finnland	2000-2013	322	original site selection	Huttunen et al. (2017)
Monitoring data from the RCS national network managed by the French water agencies	France	2007-2013	2694	qualitative ratings of multiple anthropogenic stressors	Mondy & Usseglio-Polaterra (2013), Alric et al. (2021)
Monitoring data from Dutch regional water authorities	Netherlands	1978 - 2017	44702	Land use	Peters et al. (2013)
Monitoring data from the German Federal state of Hesse	Germany	2005-2018	3044	Land use	Haubrock et al. (2020)

In table 1, *Land use* refers to the 20% cutoff for relative area of agriculture or urban areas in a catchment. This criterion was applied wherever no other information was available. IASPT is short for Iberian Average score per taxon which refers to the average Iberian biological monitoring working party score (IBMWP, between 1 and 10) of a sample. The IASPT has been shown to be a reliable indicator of water quality (e.g. Leunda *et al.* 2009; Munné & Prat 2009). The Biological Diatom Index (BDI) (Lenoir & Coste 1996) is a standardized way to evaluate the quality of freshwater systems in France using diatoms.
In two of the data sets (RIVPACS and Koutajoki) the sampling sites were selected to represent reference conditions so we used all of the sites. For the data from the RCS national network several qualitative metrics were available. The measured stressors were: organic matter, nitrogen compounds (except nitrates), nitrates, phosphorous compounds, suspended matter, organic micropollutants (other), mineral micropolluants (metal), pesticides and polycyclic aromatic hydrocarbons (PAH). Each was rated on a scale of high, good, intermediate, poor and bad. All sites for which two or more categories were rated as intermediate or one more were rated as either poor or bad was removed from the analysis.

Table 2: Types of different typologies that were used in the analyses.

Typology	**Types**
BRT12	RT1, RT2, RT3, RT4, RT5, RT6, RT7, RT8, RT9, RT10, RT11
BRT20	RT1, [illegible] RT3, RT4, RT5, RT8, RT10, RT11, RT14, RT15, RT16, RT17, RT18
GloRiC	3, 4, 6, 7, 8, 14, 15, 17, 18, 22, 24, 26, 29, 30
Illies	Alps, Central highlands, Central plains, England, Fenno-scandian shield, Hungarian lowlands, Ibero-Macaronesian region, Ireland and Northern Ireland, Italy and Corsica, Pyrenees, Western highlands, Western plains
BGR	Alpine Bio-geographical Region, Atlantic Bio-geographical Region, Boreal Bio-geographical Region, Continental Bio-geographical Region, Mediterranean Bio-geographical Region, Pannonian Bio-geographical Region

Table 3: Typical assemblages. Values give the proportion of sites of broad tiver type where the taxon is present. Combinations for which a taxon is found to be typical are marked with *.

taxon	RT1	RT2__3__8__9__12	RT4__5	RT14	RT15__16	RT18
Ancylus	0.62 (*)	0.634 (*)	0.502 (*)	0	0.424 (*)	0
Athericidae	0.217	0.555 (*)	0.454	0.631	0.661 (*)	0.517
Athripsodes	0.399 (*)	0.305	0.388 (*)	0.043	0.171	0.111
Baetidae	0.422	0.28	0.326	0.987 (*)	0.297	0.991 (*)
Baetis	0.556 (*)	0.809 (*)	0.713 (*)	0	0.84 (*)	0
Bithynia	0.476 (*)	0.138	0.379 (*)	0	0.055	0
Caenidae	0.158	0.074	0.112	0.599	0.149	0.877 (*)
Caenis	0.658 (*)	0.431 (*)	0.605 (*)	0	0.307	0
Calopteryx	0.452 (*)	0.464 (*)	0.494 (*)	0	0.172	0
Centroptilum	0.054	0.215	0.339 (*)	0	0.087	0
Chironomidae	0.982 (*)	0.892 (*)	0.858 (*)	0.95 (*)	0.928 (*)	0.968 (*)
Cloeon	0.37 (*)	0.099	0.222	0	0.031	0
Corbicula	0.745 (*)	0.116	0.235	0	0.053	0.021
Dikerogammarus	0.517 (*)	0.015	0.018	0	0	0
Dreissena	0.364 (*)	0.018	0.024	0	0.001	0.002
Dytiscidae	0.245	0.319	0.218	0.7 (*)	0.509	0.534
Ecdyonurus	0.151	0.513 (*)	0.197	0.3	0.647 (*)	0
Echinogammarus	0.247	0.117	0.43 (*)	0	0.143	0
Elmis	0.25	0.752 (*)	0.629 (*)	0.293	0.608 (*)	0.288
Empididae	0.294	0.519	0.392	0.587	0.756 (*)	0.678 (*)
Epeorus	0.005	0.245	0.017	0.222	0.461 (*)	0
Ephemera	0.336 (*)	0.52 (*)	0.52 (*)	0	0.24	0
Ephemerellidae	0.035	0.091	0.098	0.828 (*)	0.208	0.639
Esolus	0.441 (*)	0.546 (*)	0.497 (*)	0.257	0.531 (*)	0.281
Ferrissia	0.355 (*)	0.049	0.067	0	0.003	0
Gammaridae	0.345	0.298	0.358	0.306	0.403	0.725 (*)
Gammarus	0.498 (*)	0.718 (*)	0.776 (*)	0	0.285	0
Gerridae	0.146	0.028	0.022	0.385	0.128	0.679 (*)
Heptagenia	0.39 (*)	0.191	0.148	0.01	0.068	0
Heptageniidae	0.407	0.309	0.169	0.7 (*)	0.454	0.846 (*)
Hydraena	0.018	0.511 (*)	0.292	0	0.453 (*)	0
Hydraenidae	0.023	0.061	0.038	0.718 (*)	0.168	0.43
Hydropsyche	0.527 (*)	0.796 (*)	0.607 (*)	0	0.571 (*)	0
Hydropsychidae	0.288	0.253	0.21	0.891 (*)	0.45	0.954 (*)
Hydroptila	0.521 (*)	0.357 (*)	0.441 (*)	0	0.207	0
Hydroptilidae	0.245	0.107	0.14	0.268	0.18	0.746 (*)
Isoperla	0	0.19	0.028	0.15	0.339 (*)	0
Leuctra	0.133	0.689 (*)	0.293	0	0.791 (*)	0
Leuctridae	0.062	0.159	0.084	0.943 (*)	0.225	0.826 (*)
Limnephilidae	0.13	0.599	0.448	0.885 (*)	0.763 (*)	0.453

Table 3: Typical assemblages. Values give the proportion of sites of broad tiver type where the taxon is present. Combinations for which a taxon is found to be typical are marked with *. *(continued)*

taxon	RT1	RT2__3__8__9__10	RT4__5	RT14	RT15__16	RT18
Limnius	0.36 (*)	0.693 (*)	0.559 (*)	0.265	0.591 (*)	0.27
Limoniidae	0.352	0.655	0.395	0.84 (*)	0.904 (*)	0.681 (*)
Mystacides	0.401 (*)	0.379 (*)	0.432 (*)	0.119	0.185	0.145
Nemoura	0.012	0.259	0.061	0	0.367 (*)	0.055
Nemouridae	0.023	0.097	0.038	0.719 (*)	0.127	0.153
Oligochaeta	0.88 (*)	0.682 (*)	0.642	0.887 (*)	0.849 (*)	0.913 (*)
Oulimnius	0.267	0.537 (*)	0.602 (*)	0.157	0.267	0.191
Perlidae	0.023	0.087	0.015	0.716 (*)	0.309	0.339
Physella	0.488 (*)	0.147	0.287	0	0.115	0
Pisidium	0.515 (*)	0.509 (*)	0.683 (*)	0	0.204	0
Planorbidae	0.416	0.245	0.312	0.678 (*)	0.149	0.642
Platycnemis	0.34 (*)	0.182	0.335 (*)	0	0.049	0
Polycentropus	0.13	0.509 (*)	0.386 (*)	0	0.235	0
Potamopyrgus	0.593 (*)	0.423 (*)	0.628 (*)	0.022	0.225	0.196
Procloeon	0.455 (*)	0.19	0.24	0	0.134	0
Protonemura	0.005	0.347 (*)	0.029	0	0.541 (*)	0.102
Psychomyia	0.502 (*)	0.29	0.115	0	0.256	0
Radix	0.526 (*)	0.225	0.36 (*)	0	0.183	0
Rhithrogena	0.015	0.332 (*)	0.08	0.232	0.585 (*)	0
Rhyacophila	0.113	0.675 (*)	0.359 (*)	0	0.773 (*)	0
Rhyacophilidae	0.027	0.099	0.083	0.904 (*)	0.134	0.774 (*)
Sericostoma	0.018	0.395 (*)	0.224	0	0.37 (*)	0
Sericostomatidae	0.032	0.182	0.136	0.787 (*)	0.366	0.315
Serratella.ignita	0.096	0.321 (*)	0.299 (*)	0	0.309 (*)	0
Sialis	0.062	0.32	0.4 (*)	0	0.055	0
Simuliidae	0.521	0.771 (*)	0.581	0.94 (*)	0.953 (*)	0.916 (*)
Sphaerium	0.098	0.198	0.396 (*)	0	0.033	0
Trombidiformes	0.553	0.549	0.126	0.81 (*)	0.754 (*)	0.877 (*)

Table 4: Indicator scores for all taxon and stream type combination where at least one is statistically significant. Statistically significat entries are marked with *.

taxon	RT1	RT2	RT3	RT4	RT5	RT8	RT9	RT10	RT11	RT14	RT15	RT16	RT18
Ablabesmyia	0.01	0.05*	0.06*	0.14*	0.11*	0	0.01	0.01	0	0	0	0	0
Acentrella	0.04	0.01	0	0.01	0	0.01	0.01	0.03	0.01	0.01	0.14*	0.09*	0.09*
Acentria	0.1*	0.01	0.01	0.03	0.01	0	0	0.02	0.02	0	0	0	0
Acricotopus	0	0.01	0.03	0.05*	0.07*	0	0	0	0	0	0	0	0
Acroloxus	0.08	0.12*	0.04	0.18*	0.09*	0.02	0.02	0.07	0.07	0	0.04	0.03	0
Adicella	0.01	0.08	0.12*	0.04	0.06	0.15*	0.15*	0.02	0.03	0.06	0	0.1*	0.02
Aeshna	0.01	0.03	0.04	0.07*	0.08*	0.01	0.02	0.01	0.01	0	0	0	0
Agabus	0	0.03	0.07*	0.07*	0.13*	0.01	0.02	0	0.01	0	0	0	0
Agapetus	0.02	0.13*	0.17*	0.09	0.14*	0.09	0.1	0.04	0.04	0.06	0	0.19*	0.06
Agraylea	0.12*	0.05	0.01	0.07*	0.04	0.01	0.01	0.04	0.01	0	0.02	0.01	0.01
Agriotypus	0.01	0.02	0.08*	0.04	0.09*	0.03	0.07*	0.03	0.06	0.02	0	0.06	0
Agrypnia	0	0.03	0.05*	0.04*	0.04	0.01	0.01	0	0	0	0	0	0
Alainites	0	0.12*	0.16*	0.04	0.05	0.06	0.18*	0.01	0.08	0	0.01	0	0.01
Alboglossiphonia	0	0.07*	0.08*	0.12*	0.09*	0	0	0	0	0	0	0	0
Allogamus	0	0.02	0	0.01	0	0.04	0.03	0.08*	0.04	0	0.02	0.03	0
Allotrichia	0.03	0	0	0.01	0.01	0.01	0.01	0.04	0.04	0.01	0.03	0.07*	0.05
Ameletus	0	0.01	0.01	0	0	0.06*	0.12*	0	0.02	0.01	0	0	0
Amphinemura	0	0.08	0.11	0.03	0.04	0.09	0.14*	0.13*	0.1	0.03	0.18*	0.19*	0.01
Ampullaceana	0.05	0.04	0.05	0.05*	0.03	0.06	0.05	0.01	0.05	0	0	0	0
Anabolia	0.02	0.1*	0.1*	0.17*	0.1*	0.03	0.06	0.03	0.03	0	0	0.01	0
Anacaena	0.01	0.06*	0.08*	0.1*	0.11*	0	0.02	0	0.02	0	0	0.01	0
Anatopynia	0	0.04*	0	0.02	0.02	0	0	0	0	0	0	0	0
Anax	0.11*	0.03	0.02	0.06*	0.04	0	0	0.03	0	0	0	0.01	0
Ancylus	0.24*	0.24*	0.21	0.21*	0.18	0.32*	0.26*	0.2	0.21	0.09	0.03	0.25*	0.07
Anisus	0.01	0.09*	0.09*	0.19*	0.14*	0.03	0.01	0.01	0	0	0.02	0	0
Annitella	0	0	0.01	0	0	0.02	0.07*	0	0.02	0	0	0	0
Anodonta	0.04	0.08*	0.02	0.09*	0.05	0.02	0.02	0.05	0.03	0	0	0	0
Anomalopterygella	0	0.02	0.05	0.01	0	0.08*	0.15*	0.01	0.02	0.03	0	0.03	0.01
Anopheles	0.05	0.05*	0.03	0.1*	0.05*	0	0.02	0	0	0	0	0.01	0.01
Antocha	0.04	0.08	0.04	0.07	0.04	0.13*	0.06	0.09	0.1	0.06	0.07	0.21*	0.04
Aphelocheirus	0.18*	0.23*	0.1	0.19*	0.09	0.12*	0.11	0.14*	0.02	0.02	0	0.08	0.01
Apocorophium	0	0.02	0.06*	0	0	0	0	0	0	0	0	0	0
Apsectrotanypus	0	0.02	0.1*	0.07*	0.09*	0.01	0.01	0.01	0.01	0	0	0	0
Aquarius	0	0	0	0.08*	0.03	0	0	0	0	0	0	0	0
Armiger	0	0.06*	0.06*	0.1*	0.08*	0	0.02	0.01	0.02	0	0	0.04	0
Arrenurus	0	0	0	0.05*	0.03	0	0	0	0	0	0	0	0
Asellus	0.04	0.14*	0.14*	0.25*	0.2*	0.05	0.05	0.03	0.04	0	0.01	0	0.01
Atherix	0.02	0.15*	0.12*	0.09	0.06	0.15*	0.15*	0.07	0.1	0.04	0.04	0.17*	0.04
Athripsodes	0.21*	0.23*	0.15	0.23*	0.18*	0.16	0.12	0.19*	0.11	0.02	0.02	0.14	0.06
Atrichopogon	0.01	0.03	0.02	0.01	0.01	0.13*	0.05	0.06	0.03	0.05	0.02	0.08*	0.04
Atrichops	0.07	0.15*	0.11*	0.15*	0.1*	0.05	0.07	0.05	0.04	0	0	0.09	0.02
Atyaephyra	0.44*	0.05	0.01	0.06	0.02	0	0	0.03	0.01	0	0	0.02	0.01
Aulodrilus	0	0.05	0.13*	0.17*	0.13*	0.01	0	0.01	0	0	0	0	0
Baetis	0.18	0.25	0.25	0.23	0.24	0.31*	0.31*	0.29*	0.29*	0.12	0.18	0.32*	0.11
Baetopus	0.03	0.05*	0.01	0.01	0	0.01	0	0.02	0	0	0	0	0
Bathyomphalus	0	0.08*	0.09*	0.14*	0.1*	0	0.01	0	0.01	0	0	0	0
Bazarella	0	0.01	0.01	0.01	0.03	0	0	0	0.08*	0	0	0	0
Beraea	0	0.01	0.02	0	0.01	0.03	0.03	0.01	0.03	0.03	0.01	0.08*	0.05
Beraeamyia	0	0	0	0	0	0	0.01	0	0.02	0.01	0	0.01	0.07*
Beraeodes	0.01	0.06	0.1*	0.05	0.08*	0.04	0.04	0.05	0.04	0	0.01	0.02	0

Table 4: Indicator scores for all taxon and stream type combination where at least one is statistically significant. Statistically significat entries are marked with *. *(continued)*

taxon	RT1	RT2	RT3	RT4	RT5	RT8	RT9	RT10	RT11	RT14	RT15	RT16	RT18
Beraeodina	0	0	0	0	0	0	0	0	0	0.1*	0	0	0.01
Berosus	0	0	0	0.02	0.04*	0	0	0	0	0	0	0	0
Besdolus	0	0	0	0	0	0	0	0.01	0	0	0.07	0	0.06*
Bezzia	0.02	0	0.01	0.01	0.01	0.01	0.06*	0.06	0.05	0	0	0	0
Bithynia	0.31*	0.17*	0.1	0.29*	0.17*	0.02	0.02	0.18*	0.13	0	0.03	0.04	0.01
Blepharicera	0	0.03	0	0.01	0	0.1*	0.03	0.02	0.06	0.02	0.02	0.2*	0.04
Boyeria	0.01	0.12*	0.12*	0.14*	0.13*	0.11*	0.09	0.06	0.08	0.04	0	0.09	0.1
Brachycentrus	0.13	0.22*	0.11	0.1	0.03	0.17*	0.12	0.12	0.02	0.06	0	0.21*	0.03
Brachycercus	0	0.11*	0.14*	0.04	0.02	0.04	0.04	0	0.01	0	0	0	0
Brachyptera	0.01	0.05	0.08	0.01	0.03	0.06	0.11*	0.11*	0.05	0.02	0.1	0.05	0.01
Branchiobdella	0	0.01	0.01	0.01	0.01	0.09*	0.06*	0	0	0.01	0	0	0.01
Branchiura	0.04	0.02	0	0.06*	0.02	0	0	0.01	0	0	0	0.02	0
Brillia	0.01	0.1*	0.2*	0.07*	0.08*	0	0.03	0.02	0.04	0	0.01	0.01	0
Brychius	0.01	0.05	0.08*	0.09*	0.07	0.01	0.01	0.14*	0.03	0	0.08	0.03	0
Bythinella	0	0.02	0.02	0.03	0.03	0.12*	0.12*	0	0.03	0.07	0	0.17*	0.03
Bythiospeum	0	0.01	0.01	0.05*	0.07*	0	0	0	0.01	0	0	0.01	0
Caenis	0.28*	0.26*	0.14	0.28*	0.21*	0.21*	0.12	0.23*	0.13	0.09	0.06	0.19	0.12
Calamoceras	0	0.02	0.02	0.05*	0.05*	0	0	0	0	0	0	0.08*	0.01
Callicorixa	0	0.01	0.05*	0.03	0.03	0	0	0	0	0	0	0	0
Calopteryx	0.2*	0.2*	0.18	0.23*	0.22*	0.25*	0.22*	0.2*	0.21*	0.06	0.04	0.11	0.07
Cambarincola	0	0.01	0.01	0	0	0.06*	0.07*	0	0	0	0	0.01	0
Capnia	0.01	0	0	0	0	0.02	0	0.05	0.01	0.06	0.15*	0.12*	0
Capnioneura	0	0	0	0	0	0	0	0.04	0	0	0.19*	0.07	0
Cardiocladius	0.02	0.05*	0.01	0.02	0	0	0	0.01	0.01	0	0	0.01	0
Cataclysta	0.05	0.04*	0.04	0.08*	0.03	0	0	0.01	0	0	0	0.01	0
Centroptilum	0.03	0.16*	0.13	0.24*	0.19*	0.12	0.11	0.23*	0.12	0.03	0.02	0.08	0.06
Ceraclea	0.24*	0.15*	0.07	0.13*	0.05	0.09	0.04	0.18*	0.06	0	0	0.06	0.02
Ceratopsyche	0	0	0	0	0	0	0.12*	0	0	0	0	0	0
Chaetocladius	0.01	0.03	0.03	0.04*	0.05*	0	0.01	0	0.04	0	0.01	0	0
Chaetogaster	0.01	0.04*	0.03	0.06*	0.02	0	0.01	0	0	0	0	0	0
Chaetopterygopsis	0	0	0	0	0	0.06*	0.05	0.01	0	0.01	0	0	0
Chaetopteryx	0.01	0.05	0.09*	0.03	0.03	0.04	0.09*	0.01	0.06	0	0.01	0	0
Chalcolestes	0	0.04	0.05*	0.06*	0.06*	0.01	0.01	0.02	0.01	0.01	0	0	0.03
Chaoborus	0.01	0.05*	0.05*	0.06*	0.04	0	0	0	0	0	0	0.01	0
Chelicorophium	0.32*	0.04	0.02	0.04	0	0	0	0.03	0.02	0	0	0	0
Chelifera	0	0.07	0.11*	0.06	0.08*	0.07	0.09*	0.01	0.04	0.01	0	0.11*	0.01
Cheumatopsyche	0.15*	0.17*	0.04	0.11*	0.04	0.19*	0.11	0.16*	0.06	0.03	0	0.12	0.09
Chimarra	0.03	0.09*	0.04	0.03	0.03	0.12*	0.08*	0.05	0.01	0.02	0	0.04	0.08*
Chironomus	0.03	0.09*	0.13*	0.15*	0.14*	0	0.01	0	0	0	0	0	0
Chloroperla	0	0.05	0.04	0	0.01	0.07	0.08	0.05	0.06	0.04	0.07	0.17*	0
Choroterpes	0.19*	0.07	0	0.06	0	0.04	0	0.12*	0	0	0	0.04	0.07*
Chrysops	0.01	0.03	0.05*	0.07*	0.06*	0	0.01	0	0.02	0	0	0	0
Cladopelma	0.01	0.03	0.02	0.07*	0.06*	0	0	0	0	0	0	0	0
Cladotanytarsus	0.01	0.05	0.03	0.15*	0.13*	0	0	0	0	0	0	0	0
Clinocera	0	0.03	0.03	0.04*	0.03	0.01	0.01	0	0.01	0	0	0	0
Clinotanypus	0	0.02	0.04	0.18*	0.1*	0	0	0	0	0	0	0	0
Cloeon	0.3*	0.15*	0.08	0.21*	0.12*	0.05	0.04	0.11	0.05	0.01	0.02	0.03	0.04
Coenagrion	0.02	0.03	0.05*	0.11*	0.07*	0	0	0	0	0	0	0	0
Colymbetes	0	0.01	0.01	0.03	0.04*	0	0	0	0	0	0	0	0

Table 4: Indicator scores for all taxon and stream type combination where at least one is statistically significant. Statistically significat entries are marked with *. *(continued)*

taxon	RT1	RT2	RT3	RT4	RT5	RT8	RT9	RT10	RT11	RT14	RT15	RT16	RT18
Conchapelopia	0.03	0.03	0.03	0.06*	0.14*	0.01	0.01	0.03	0.02	0	0.01	0	0
Corbicula	0.54*	0.2*	0.04	0.22*	0.07	0.05	0.03	0.12	0.03	0	0	0.06	0.02
Cordulegaster	0	0.04	0.14*	0.06	0.11*	0.14*	0.19*	0.03	0.07	0.06	0.02	0.05	0.06
Corixa	0.01	0.05*	0.07*	0.05*	0.06*	0	0.01	0	0	0.01	0	0	0
Corophium	0.38*	0.02	0.02	0.03	0	0.01	0	0.04	0.02	0	0	0	0
Corynoneura	0	0.04	0.06*	0.09*	0.07*	0	0.01	0.02	0.02	0	0.03	0.01	0
Crangonyx	0.19*	0.11*	0.02	0.16*	0.07	0.06	0.02	0.03	0.01	0	0	0	0
Cricotopus	0.02	0.19*	0.2*	0.22*	0.16*	0.01	0.02	0.02	0.05	0	0.01	0	0
Crocothemis	0.07*	0	0.01	0.01	0	0	0	0.01	0	0	0	0.02	0
Crunoecia	0	0.01	0.02	0	0.01	0.02	0.05	0.01	0.01	0.01	0	0.07*	0.03
Cryptochironomus	0.03	0.04	0.04	0.16*	0.09*	0	0	0.01	0.01	0	0	0	0
Cryptotendipes	0	0.01	0	0.06*	0.03*	0	0	0	0	0	0	0	0
Culex	0	0.01	0	0.02	0.05*	0	0	0	0	0	0	0	0
Cybister	0	0.01	0.04*	0.02	0.01	0	0	0	0	0	0	0	0
Cymatia	0.01	0.01	0.05*	0.04*	0.06*	0	0.01	0	0	0	0	0	0
Cyrnus	0.06	0.17*	0.08	0.2*	0.13*	0.15*	0.08	0.17*	0.12	0.01	0	0.03	0.02
Dacnogenia	0.11*	0.01	0	0.01	0	0	0.02	0.01	0	0	0	0.02	0
Demicryptochironomus	0.01	0.05*	0.05*	0.07*	0.03	0.01	0	0	0	0	0	0	0
Dero	0.01	0.01	0.05*	0.09*	0.05*	0	0	0	0	0	0	0	0
Diamesa	0	0.05	0.08*	0.03	0.04	0	0.01	0.06	0.09*	0	0.03	0.01	0
Dicranomyia	0	0	0	0.03*	0.01	0	0	0	0	0	0	0	0
Dicranota	0.01	0.13*	0.22*	0.09	0.13*	0.13*	0.2*	0.05	0.14*	0.02	0.02	0.07	0
Dicrotendipes	0.01	0.06*	0.05*	0.16*	0.08*	0	0	0	0	0	0	0	0
Dictyogenus	0	0	0	0	0	0	0	0.04	0.06	0.03	0.04	0.11*	0.01
Dikerogammarus	0.63*	0.03	0	0.03	0	0	0	0.07	0.03	0	0	0	0
Dina	0.09*	0.03	0.02	0.01	0.02	0.01	0.02	0.04	0.01	0.01	0	0	0
Dinocras	0	0.06	0.03	0.01	0.01	0.17*	0.17*	0.07	0.06	0.11	0.08	0.28*	0.06
Diplectrona	0	0.01	0.01	0.04*	0.02	0.01	0.01	0	0	0	0	0	0
Diura	0	0.02	0.01	0	0	0.05*	0.2*	0	0.01	0.01	0	0	0
Dixa	0.01	0.03	0.07	0.07*	0.08*	0.04	0.07	0	0.06	0.03	0.01	0.06	0.02
Dixella	0	0.03	0.05*	0.05*	0.04*	0	0.01	0	0.01	0	0	0.01	0
Donacia	0.02	0.02	0.01	0.04*	0.01	0	0	0	0	0	0	0	0
Dreissena	0.5*	0.05	0.01	0.04	0.01	0	0	0.06	0.02	0	0	0	0.05
Drusus	0	0.03	0.08	0.02	0.05	0.05	0.08*	0.01	0.1*	0	0.05	0.01	0
Dryops	0.11*	0.08	0.09	0.11*	0.12*	0.08	0.09	0.05	0.06	0.02	0.01	0.08	0.11*
Dupophilus	0	0.14*	0.14*	0.04	0.03	0.35*	0.33*	0.04	0.05	0.13	0.01	0.15*	0.02
Dytiscus	0	0.03	0.06*	0.06*	0.05*	0	0.01	0	0.01	0	0	0	0
Ecclisopteryx	0	0.04	0.07*	0.01	0.02	0.03	0.08*	0.04	0.1*	0	0.01	0.01	0
Ecdyonurus	0.06	0.17	0.14	0.08	0.1	0.31*	0.28*	0.21*	0.19	0.14	0.11	0.36*	0.12
Echinogammarus	0.17*	0.21*	0.15*	0.31*	0.3*	0.01	0.02	0.02	0.03	0	0	0.15*	0.01
Ecnomus	0.39*	0.09*	0.01	0.1*	0.02	0.02	0	0.06	0.03	0	0	0.02	0.01
Einfeldia	0	0.01	0.03	0.04*	0.02	0	0	0	0	0	0	0	0
Eiseniella	0.01	0.1*	0.1*	0.05	0.06	0.07	0.09*	0.04	0.05	0	0.01	0	0
Electrogena	0.01	0.08	0.1*	0.04	0.05	0.07	0.09*	0.06	0.06	0.07	0.05	0.02	0.07
Elmis	0.09	0.23	0.23	0.22	0.24*	0.31*	0.3*	0.28*	0.29*	0.11	0.08	0.28*	0.11
Elodes	0.01	0.03	0.1*	0.04	0.09*	0.06	0.16*	0.04	0.13*	0.03	0.01	0.09	0.02
Eloeophila	0.01	0.05	0.16*	0.03	0.05	0.07	0.14*	0.01	0.08	0.01	0	0.02	0
Elophila	0.08*	0.03	0	0.09*	0.02	0	0	0.01	0	0	0	0	0
Embolocephalus	0	0	0.04	0.04*	0.01	0	0	0	0	0	0	0	0

Table 4: Indicator scores for all taxon and stream type combination where at least one is statistically significant. Statistically significat entries are marked with *. *(continued)*

taxon	RT1	RT2	RT3	RT4	RT5	RT8	RT9	RT10	RT11	RT14	RT15	RT16	RT18
Enallagma	0	0.01	0.01	0.02	0.05*	0	0.01	0	0	0	0	0	0
Enchytraeus	0	0.18*	0.17*	0.08*	0.05	0.02	0.02	0	0.05	0	0	0	0
Endochironomus	0	0.07*	0.1*	0.15*	0.09*	0	0	0	0	0	0	0	0
Enochrus	0.03	0.05*	0.05*	0.06*	0.04*	0	0	0	0	0	0	0	0
Epeorus	0	0.06	0.04	0.01	0.01	0.29*	0.27*	0.1	0.09	0.15	0.1	0.39*	0.06
Ephemera	0.14	0.19	0.18	0.23*	0.24*	0.26*	0.29*	0.24*	0.21	0.06	0.03	0.15	0.05
Ephemerella	0.02	0.1	0.1	0.08	0.1	0.25*	0.2*	0.14*	0.12	0.12	0.06	0.13	0.08
Ephoron	0.3*	0.05	0.01	0.12*	0.01	0.05	0	0.12*	0.01	0	0	0.06	0.01
Epoicocladius	0	0.02	0.05*	0.03	0.02	0	0	0	0.04	0	0	0	0
Erpobdella	0.03	0.14*	0.15*	0.23*	0.21*	0.08	0.07	0.04	0.06	0.04	0.03	0.01	0.01
Erythromma	0.2*	0.06	0.01	0.14*	0.03	0	0	0.03	0	0	0	0.03	0
Esolus	0.17	0.2	0.12	0.2	0.19	0.29*	0.2	0.29*	0.24*	0.11	0.07	0.28*	0.12
Euglesa	0	0.07*	0.14*	0.07*	0.05	0.01	0.01	0	0.02	0	0	0	0
Eukiefferiella	0	0.15*	0.18*	0.11*	0.09*	0.02	0.03	0.05	0.09	0	0.02	0.01	0
Eusimulium	0	0.01	0.04*	0.01	0.01	0	0	0	0	0	0	0	0
Faxonius	0.04	0.05*	0.02	0.04*	0.03	0.02	0.04	0.02	0	0.01	0	0.01	0.01
Ferrissia	0.4*	0.11*	0.03	0.1*	0.02	0.03	0.05	0.07	0.03	0	0	0	0
Forelia	0	0	0	0.04*	0.01	0	0	0	0	0	0	0	0
Galba	0.04	0.04	0.02	0.04	0.03	0.02	0.03	0.09*	0.05	0	0.02	0.1*	0.02
Gammarus	0.18	0.24*	0.25*	0.28*	0.29*	0.27*	0.25*	0.3*	0.29*	0.05	0.12	0.15	0.08
Gerris	0.11	0.12	0.13	0.17*	0.15*	0.12	0.15*	0.1	0.13	0.04	0.02	0.08	0.05
Glossiphonia	0.05	0.16*	0.2*	0.22*	0.25*	0.07	0.08	0.04	0.06	0.02	0.02	0.04	0.01
Glossosoma	0.02	0.11	0.09	0.03	0.02	0.22*	0.17*	0.06	0.08	0.09	0.03	0.28*	0.01
Glyphotaelius	0	0.02	0.04*	0.03*	0.03	0	0.01	0	0	0	0	0	0
Glyptotendipes	0	0.11*	0.12*	0.14*	0.05	0	0	0	0	0	0	0	0
Goera	0.06	0.13*	0.08	0.15*	0.11*	0.12*	0.09	0.11	0.12*	0.01	0.01	0.08	0.03
Gomphus	0.13	0.18*	0.09	0.18*	0.13*	0.17*	0.15*	0.12	0.04	0.02	0	0.05	0.06
Gordiacea	0	0.02	0.01	0.01	0	0.05	0.05	0.03	0.02	0.05	0.02	0.1*	0.01
Graphoderus	0	0.04*	0.02	0.01	0.01	0	0	0	0	0	0	0	0
Graptodytes	0.01	0.03	0.08*	0.1*	0.08*	0	0	0	0	0	0	0	0
Gyraulus	0.04	0.1*	0.11*	0.23*	0.16*	0.02	0.05	0.02	0.01	0	0	0.01	0
Gyrinus	0.01	0.09*	0.15*	0.1*	0.1*	0.01	0.03	0	0	0	0	0	0
Habroleptoides	0	0.04	0.03	0.02	0.02	0.18*	0.19*	0.08	0.15*	0.1	0.09	0.19*	0.05
Habrophlebia	0	0.06	0.1	0.05	0.09	0.23*	0.33*	0.09	0.17*	0.09	0.02	0.05	0.08
Haemopis	0.02	0.01	0.04	0.03	0.05*	0	0	0.01	0	0	0	0	0
Halesus	0.02	0.11*	0.16*	0.09*	0.08	0.07	0.11*	0.03	0.09	0.01	0.01	0.05	0.01
Haliplus	0.17*	0.11	0.1	0.22*	0.2*	0.02	0.02	0.16*	0.09	0.01	0.05	0.05	0.03
Halocladius	0	0	0.08*	0.01	0	0	0	0	0	0	0	0	0
Harnischia	0.03	0.01	0	0.09*	0.03	0	0	0	0	0	0	0	0
Hediste	0	0	0.06*	0	0	0	0	0	0	0	0	0	0
Helichus	0.03	0.04	0.03	0.06	0.06	0.04	0.03	0.07	0.03	0.02	0.06	0.08	0.12*
Helius	0	0.03	0.03	0.06*	0.05*	0	0	0	0	0	0	0	0
Helobdella	0.09	0.15*	0.11*	0.2*	0.17*	0.05	0.05	0.02	0.03	0.01	0.01	0.03	0.01
Helochares	0.03	0.04*	0.04	0.05*	0.06*	0	0.01	0	0	0	0	0.01	0
Helophorus	0.01	0.07	0.11*	0.09*	0.12*	0.06	0.07	0.07	0.07	0.02	0.02	0.01	0.01
Hemerodromia	0	0.08*	0.08	0.04	0.03	0.07	0.09*	0.08	0.05	0.04	0.07	0.07	0.03
Hemiclepsis	0.02	0.07*	0.07*	0.1*	0.05	0.01	0.01	0.03	0	0	0	0.01	0.01
Hemimysis	0.22*	0	0	0.01	0	0	0	0.03	0.03	0	0	0	0
Heptagenia	0.29*	0.22*	0.11	0.14*	0.04	0.14*	0.17*	0.08	0.02	0.01	0.01	0.07	0.02

Table 4: Indicator scores for all taxon and stream type combination where at least one is statistically significant. Statistically significat entries are marked with *. *(continued)*

taxon	RT1	RT2	RT3	RT4	RT5	RT8	RT9	RT10	RT11	RT14	RT15	RT16	RT18
Hesperocorixa	0.01	0.04	0.12*	0.06*	0.07*	0	0	0	0	0	0	0	0
Heterotrissocladius	0	0.03	0.08*	0.02	0.02	0.01	0.03	0.02	0	0	0	0.01	0
Hexatoma	0.05	0.1*	0.09*	0.03	0.01	0.04	0.05	0.05	0.04	0	0.03	0.14*	0
Hippeutis	0.03	0.08*	0.07*	0.12*	0.07*	0	0.01	0.01	0	0	0	0.01	0
Holocentropus	0.01	0.06	0.07*	0.08*	0.04	0.06	0.04	0.03	0	0.01	0.01	0.02	0.01
Hydraena	0.01	0.14	0.19	0.12	0.16	0.3*	0.31*	0.18	0.26*	0.12	0.11	0.3*	0.06
Hydrellia	0.04	0.03	0.04	0.06*	0.03	0.02	0.02	0	0.01	0.01	0	0.04	0
Hydrobius	0.01	0.03	0.04	0.04	0.07*	0	0	0	0	0	0	0	0
Hydrochus	0	0.05	0.06	0.03	0.05	0.03	0.05*	0.01	0.02	0.03	0	0.02	0.02
Hydrocyphon	0	0.04	0.05	0.01	0.04	0.11*	0.19*	0.07	0.12*	0.05	0	0.09	0.07
Hydrometra	0.02	0.07	0.06	0.07*	0.09*	0.09*	0.09*	0.05	0.07	0.02	0	0.02	0.04
Hydroporus	0	0.05	0.08*	0.07*	0.11*	0.01	0.01	0	0.01	0	0	0	0
Hydropsyche	0.18	0.25*	0.24*	0.21	0.21	0.32*	0.3*	0.27*	0.26*	0.11	0.12	0.29*	0.11
Hydroptila	0.24*	0.2*	0.12	0.22*	0.18*	0.17	0.09	0.28*	0.22*	0.05	0.07	0.14	0.11
Hydroscapha	0	0	0	0.01	0	0.01	0.01	0	0.02	0	0	0	0.05*
Hydrovatus	0	0.01	0.06*	0.01	0.03	0	0.01	0	0	0	0	0	0
Hygrobates	0	0	0	0.05*	0.01	0	0	0	0	0	0	0	0
Hygrotus	0	0.04	0.07*	0.11*	0.1*	0	0	0	0	0	0	0	0
Hyphydrus	0	0.03	0.09*	0.09*	0.08*	0	0	0	0	0	0	0	0
Ilybius	0.01	0.03	0.06	0.05*	0.04	0.04	0.07*	0.01	0.05	0.01	0.01	0.01	0
Ilyocoris	0.02	0.06*	0.05*	0.12*	0.08*	0	0	0	0	0	0	0	0
Ilyodrilus	0.01	0	0.01	0.11*	0.07*	0	0	0	0	0	0	0	0
Ironoquia	0	0.02	0.02	0.02	0.04*	0	0	0	0	0	0	0	0
Ischnura	0.09*	0.08*	0.06	0.2*	0.12*	0	0.01	0	0	0	0	0.01	0
Isoperla	0	0.1	0.14	0.03	0.06	0.16*	0.23*	0.13	0.1	0.1	0.17	0.25*	0.04
Ithytrichia	0.03	0.13*	0.16*	0.14*	0.14*	0.13*	0.14*	0.12*	0.06	0.02	0.01	0.04	0.01
Jaera	0.51*	0	0	0.02	0	0	0	0.03	0.04	0	0.01	0	0
Kiefferulus	0	0.02	0.03	0.06*	0.06*	0	0	0	0	0	0	0	0
Labiobaetis	0.01	0.03	0	0.03	0	0.01	0	0.03	0	0	0	0	0.04*
Laccobius	0.07*	0.03	0.06	0.08*	0.08*	0.01	0.03	0.01	0	0	0	0.01	0
Laccophilus	0.14*	0.06	0.06	0.14*	0.05	0.01	0.02	0.05	0.02	0	0	0.02	0.01
Lasiocephala	0	0.07	0.08	0.01	0.03	0.1*	0.07	0.07	0.06	0.03	0	0.2*	0
Lekanesphaera	0	0.01	0.07*	0	0	0	0	0	0	0	0	0	0
Lepidostoma	0.06	0.21*	0.21*	0.14*	0.11	0.17*	0.15*	0.14	0.09	0.04	0.03	0.13	0.02
Leptocerus	0.12*	0.07	0.02	0.14*	0.05	0.04	0.01	0.14*	0.04	0	0	0.04	0.03
Leptophlebia	0	0.04	0.09*	0.02	0.01	0.05	0.09*	0	0.02	0	0	0	0
Lestes	0.01	0.02	0.03	0.03	0.07*	0	0	0	0	0	0	0.01	0
Leuctra	0.05	0.21	0.2	0.13	0.12	0.33*	0.31*	0.27*	0.2	0.14	0.18	0.36*	0.12
Libellula	0.01	0.03	0.02	0.08*	0.06*	0.01	0.01	0.02	0	0	0	0.01	0
Limnebius	0	0.02	0.04	0.01	0.01	0.08*	0.1*	0	0.02	0.09*	0.01	0.01	0.01
Limnephilus	0.01	0.06	0.15*	0.14*	0.16*	0.01	0.02	0	0.02	0	0.01	0	0
Limnesia	0	0	0	0.05*	0.02	0	0	0	0	0	0	0	0
Limnius	0.13	0.23*	0.23*	0.2	0.22	0.28*	0.28*	0.27*	0.27*	0.1	0.08	0.29*	0.1
Limnodrilus	0.02	0.09*	0.12*	0.21*	0.16*	0.01	0.01	0.01	0.01	0	0	0	0
Limnomysis	0.46*	0.01	0	0	0	0	0	0	0	0	0	0	0
Limnophora	0.02	0.07	0.08*	0.06*	0.06	0.06	0.04	0.03	0.03	0.01	0.01	0.06	0.02
Limnophyes	0.01	0.02	0.04	0.06*	0.04*	0	0	0	0.02	0	0	0.01	0
Liponeura	0	0.01	0.02	0	0	0.03	0.08*	0.01	0.04	0.01	0.03	0.1*	0
Lithoglyphus	0.1*	0.03	0	0.02	0.04	0	0	0	0	0	0	0	0

Table 4: Indicator scores for all taxon and stream type combination where at least one is statistically significant. Statistically significat entries are marked with *. *(continued)*

taxon	RT1	RT2	RT3	RT4	RT5	RT8	RT9	RT10	RT11	RT14	RT15	RT16	RT18
Lophochaeta	0.01	0.06*	0.05*	0.06*	0.03	0	0.01	0	0.01	0	0	0	0
Lumbriculus	0.02	0.04	0.07*	0.09*	0.13*	0.02	0.04	0.01	0.03	0	0	0	0
Lumbricus	0	0.15*	0.2*	0.1*	0.06*	0.01	0.01	0	0.01	0	0	0	0
Lymnaea	0.03	0.07*	0.05	0.15*	0.08*	0.02	0.04	0.01	0	0	0.01	0.01	0
Lype	0.07	0.13*	0.16*	0.18*	0.19*	0.12	0.11	0.13*	0.12	0.01	0	0.03	0.02
Macronychus	0.11*	0.17*	0.06	0.16*	0.04	0.04	0.03	0.05	0.01	0	0	0.08	0.01
Macropelopia	0	0.04	0.13*	0.07*	0.11*	0	0.01	0.01	0.01	0	0.01	0.01	0
Margaritifera	0	0.01	0	0	0	0.01	0.08*	0	0	0	0	0	0
Marstoniopsis	0	0.03*	0.01	0.05*	0.01	0	0	0	0	0	0	0	0
Melampophylax	0.01	0	0.01	0.02	0.05	0.01	0.02	0	0.07*	0.01	0	0	0
Menetus	0.21*	0.09*	0.02	0.1*	0.03	0.04	0.04	0.03	0	0	0	0.05	0
Metalype	0	0.01	0.01	0.02	0.03	0.02	0.01	0.06*	0.01	0	0.01	0.02	0.06*
Metriocnemus	0	0.04*	0.07*	0.05*	0.05*	0	0	0	0.01	0	0	0	0
Micrasema	0	0.07	0.06	0.01	0	0.33*	0.28*	0.05	0.05	0.16*	0	0.33*	0.06
Micronecta	0.29*	0.14*	0.08	0.18*	0.13	0.15*	0.1	0.16*	0.13	0.05	0.01	0.08	0.09
Micropsectra	0.02	0.12*	0.17*	0.14*	0.15*	0.01	0.03	0.03	0.08	0	0.01	0.01	0
Microtendipes	0.01	0.14*	0.08*	0.19*	0.14*	0.01	0.01	0.02	0.02	0	0	0	0
Microvelia	0.01	0.02	0.04	0.06*	0.02	0.02	0.01	0	0.01	0.04	0.02	0.02	0.01
Mideopsis	0	0	0	0.06*	0.01	0	0	0	0	0	0	0	0
Molanna	0.01	0.07*	0.06	0.15*	0.11*	0.01	0	0.05	0.03	0	0.01	0	0
Musculium	0.01	0.08*	0.06*	0.12*	0.05*	0	0.01	0.01	0.01	0	0	0	0
Mystacides	0.19*	0.2*	0.12	0.22*	0.19*	0.25*	0.16	0.21*	0.17	0.06	0.02	0.13	0.07
Myxas	0.01	0.03	0	0.01	0.01	0.03	0.01	0.1*	0.05	0.02	0.08	0.03	0.03
Nais	0.01	0.13*	0.18*	0.11*	0.08*	0.02	0.02	0.03	0.07	0	0.01	0	0
Nanocladius	0.01	0.07*	0.03	0.08*	0.04	0	0.01	0.01	0.01	0	0	0	0
Natarsia	0	0.01	0.05*	0.03	0.04	0	0	0.01	0	0	0	0	0
Naucoris	0.06*	0.02	0	0.05*	0.01	0.01	0	0	0.02	0	0	0	0
Nebrioporus	0	0.06*	0.07*	0.15*	0.05	0.01	0.01	0	0.03	0	0	0.04	0
Nemoura	0.01	0.08	0.14	0.04	0.05	0.21*	0.29*	0.12	0.11	0.08	0.15	0.27*	0.04
Nemurella	0	0.02	0.02	0.01	0.03	0.04	0.05*	0.02	0.02	0.01	0	0	0
Neoephemera	0	0.1*	0	0	0	0	0	0	0	0	0	0	0
Nepa	0.01	0.04	0.05	0.06*	0.11*	0.03	0.04	0.02	0.04	0	0.03	0.01	0.03
Neureclipsis	0.05	0.1*	0.06	0.09*	0.05	0.04	0.04	0.06	0.02	0	0.01	0	0
Nevrorthus	0	0	0	0	0	0.01	0	0	0	0.08*	0	0	0
Nigrobaetis	0	0.04	0.08*	0.02	0.04	0.05	0.19*	0	0.02	0	0	0	0
Niphargus	0.01	0.05	0.07*	0.05	0.09*	0.05	0.05	0.01	0.02	0.01	0	0	0.01
Normandia	0.09	0.06	0.01	0.14*	0.06	0.03	0.01	0.15*	0.06	0.02	0.04	0.04	0.06
Noterus	0.02	0.08*	0.08*	0.12*	0.08*	0	0	0	0	0	0	0	0
Notidobia	0.01	0.06	0.08*	0.05	0.09*	0.04	0.07*	0.09*	0.04	0	0.02	0	0
Notiphila	0	0	0.01	0.03*	0.03	0	0	0	0	0	0	0	0
Notonecta	0.01	0.06	0.11*	0.14*	0.17*	0.02	0.03	0	0.02	0	0	0	0
Nymphula	0	0.02	0.03	0.04*	0.03	0	0.01	0	0	0	0	0	0
Obesogammarus	0.06*	0	0	0	0	0	0.01	0	0	0	0	0	0
Ochthebius	0.01	0.01	0.04	0.04	0.04	0.02	0.03	0.03	0.02	0.01	0.02	0.07*	0.03
Odhneripisidium	0	0.03*	0	0.04*	0	0	0	0	0	0	0	0	0
Odontocerum	0.01	0.03	0.07	0.02	0.04	0.16*	0.19*	0.17*	0.17*	0.13	0.05	0.24*	0.05
Odontomesa	0	0.01	0.03	0.02	0.05*	0	0.01	0.02	0.01	0	0	0.01	0
Odontomyia	0	0.02	0.04*	0.02	0.01	0	0	0	0	0	0	0	0
Oecetis	0.21*	0.16*	0.1	0.16*	0.09	0.2*	0.14*	0.14	0.06	0.03	0.01	0.12	0.05

Table 4: Indicator scores for all taxon and stream type combination where at least one is statistically significant. Statistically significat entries are marked with *. *(continued)*

taxon	RT1	RT2	RT3	RT4	RT5	RT8	RT9	RT10	RT11	RT14	RT15	RT16	RT18
Oecismus	0	0.03	0.03	0	0.01	0.03	0.06*	0.01	0.01	0	0	0	0
Oligoneuriella	0.01	0.07*	0.02	0.01	0	0.09*	0.04	0.08*	0.01	0	0.04	0.09*	0.11*
Omphiscola	0	0	0	0.02	0.05*	0	0	0	0	0	0	0	0
Onychogomphus	0.08	0.17*	0.08	0.18*	0.15*	0.2*	0.13	0.14*	0.07	0.03	0.03	0.08	0.14*
Ophidonais	0.02	0.04	0.04	0.11*	0.08*	0	0.01	0.01	0.01	0	0	0	0
Oplodontha	0	0.01	0.03	0.03*	0.02	0	0	0	0	0	0	0	0
Orchestia	0.03	0.05*	0.01	0.01	0	0	0	0	0	0	0	0	0
Orconectes	0.18*	0.12*	0.03	0.12*	0.04	0.04	0.07	0.07	0.07	0	0	0.01	0.01
Orectochilus	0.03	0.17*	0.16*	0.1	0.08	0.22*	0.17*	0.13	0.11	0.05	0.04	0.18*	0.07
Oreodytes	0	0.11*	0.13*	0.03	0.05	0.07	0.08*	0.02	0.09	0.02	0.01	0.05	0
Orthetrum	0.1*	0.04	0.03	0.04	0.04	0	0.01	0.03	0.01	0	0	0.03	0.01
Orthocladius	0.01	0.03	0.04	0.07*	0.11*	0.01	0.02	0	0.02	0	0	0	0
Orthotrichia	0.3*	0.08	0.01	0.11*	0.01	0.03	0	0.13*	0.01	0	0.01	0.05	0.07
Oulimnius	0.11	0.25*	0.22*	0.27*	0.24*	0.24*	0.22*	0.23*	0.21*	0.07	0.04	0.15	0.08
Oxyethira	0.03	0.06*	0.07*	0.04	0.03	0.04	0.08*	0.02	0.01	0.01	0	0	0.01
Oxygastra	0.06*	0.04	0	0.09*	0.03	0.04	0	0.04	0.01	0	0	0.03	0.02
Pachyleuctra	0	0	0	0	0	0	0.01	0	0	0	0	0.16*	0
Pacifastacus	0.01	0.04	0.04	0.01	0.03	0.23*	0.19*	0.1	0.06	0.04	0.03	0.02	0.16*
Paduniella	0.24*	0.02	0	0.03	0.01	0	0	0.01	0	0	0	0.01	0
Palaemonetes	0	0.03	0.09*	0	0	0	0	0	0	0	0	0	0
Parachiona	0	0	0	0.07*	0.01	0	0	0	0	0	0	0	0
Parachironomus	0.02	0.06*	0.07*	0.12*	0.07*	0	0	0	0	0	0	0	0
Paracladius	0	0	0.01	0.04*	0.07*	0	0	0.02	0	0	0	0	0
Paracladopelma	0.01	0.01	0.04	0.06*	0.1*	0	0	0.01	0	0	0.02	0	0
Paracymus	0	0	0.05*	0	0.01	0	0	0	0	0	0	0	0
Paralauterborniella	0	0	0	0.03*	0.04*	0	0	0	0	0	0	0	0
Paraleptophlebia	0.01	0.13*	0.14*	0.08	0.1	0.24*	0.26*	0.1	0.11	0.04	0.01	0.06	0.02
Parapoynx	0.21*	0.03	0	0.09*	0.01	0	0	0.03	0	0	0	0.03	0
Paratanytarsus	0.01	0.12*	0.12*	0.18*	0.13*	0.01	0.01	0.01	0.02	0	0	0	0
Paratendipes	0.02	0.02	0.04	0.11*	0.17*	0	0	0.01	0.01	0	0	0	0
Paratrichocladius	0.03	0.05	0.03	0.02	0.02	0	0.01	0.08*	0.03	0	0.04	0.01	0
Paratrissocladius	0	0.01	0.11*	0.03	0.04	0	0	0	0.02	0	0	0	0
Pedicia	0	0.02	0.04	0.01	0.02	0.04	0.05*	0.01	0.02	0.01	0	0.01	0
Peltodytes	0.1*	0.02	0.03	0.06*	0.03	0.01	0	0.02	0.01	0	0.01	0.02	0.04
Peregriana	0	0.01	0.01	0.02	0.06*	0	0	0	0.03	0	0	0	0
Pericoma	0	0.04	0.05	0.04	0.05*	0	0.01	0	0.07*	0	0	0	0
Perla	0	0.08	0.05	0.01	0.01	0.28*	0.21*	0.08	0.11	0.13	0.1	0.33*	0.09
Perlodes	0	0.08	0.07	0.01	0.01	0.18*	0.17*	0.06	0.05	0.13	0.08	0.33*	0.02
Phaenopsectra	0.03	0.03	0.03	0.14*	0.15*	0	0.01	0	0	0	0	0	0
Philopotamus	0	0.03	0.05	0.01	0.01	0.14*	0.21*	0.02	0.08	0.06	0.01	0.17*	0.03
Phryganea	0.01	0.04	0.04	0.08*	0.06*	0.01	0	0.03	0	0	0	0	0
Physa	0.02	0.08*	0.12*	0.19*	0.1*	0.01	0.02	0.01	0	0	0	0.03	0
Physella	0.32*	0.17*	0.06	0.21*	0.16*	0.07	0.06	0.14	0.08	0	0.03	0.11	0.06
Pilaria	0.01	0.01	0.07*	0.06*	0.07*	0	0.01	0	0	0.01	0	0.01	0
Piona	0	0	0	0.04*	0.01	0	0	0	0	0	0	0	0
Piscicola	0.22*	0.11*	0.09	0.17*	0.1*	0.03	0.01	0.09	0.04	0	0.01	0.02	0
Pisidium	0.21*	0.23*	0.23*	0.29*	0.3*	0.19	0.21*	0.22*	0.23*	0.05	0.04	0.13	0.05
Planorbarius	0.01	0.06*	0.07*	0.1*	0.09*	0	0	0	0	0	0	0	0
Planorbis	0.01	0.09*	0.1*	0.16*	0.13*	0	0	0	0	0	0	0	0

Table 4: Indicator scores for all taxon and stream type combination where at least one is statistically significant. Statistically significat entries are marked with *. *(continued)*

taxon	RT1	RT2	RT3	RT4	RT5	RT8	RT9	RT10	RT11	RT14	RT15	RT16	RT18
Platambus	0.02	0.06	0.07	0.09*	0.07	0.09*	0.1*	0.03	0.06	0.02	0	0.08	0.01
Platycnemis	0.22*	0.18*	0.06	0.25*	0.18*	0.11	0.08	0.18*	0.12	0.01	0.01	0.05	0.04
Plea	0.01	0.05*	0.08*	0.11*	0.09*	0	0	0	0	0	0	0	0
Plectrocnemia	0.01	0.03	0.08	0.03	0.08	0.08*	0.15*	0.03	0.11*	0.01	0	0.03	0.02
Polycentropus	0.06	0.24*	0.21*	0.19*	0.15	0.29*	0.27*	0.19*	0.14	0.09	0.04	0.16	0.08
Polypedilum	0.02	0.17*	0.19*	0.2*	0.16*	0.01	0.02	0.02	0.04	0	0.01	0	0
Pomatinus	0.07	0.04	0.01	0.05	0.03	0.03	0.02	0.05	0.06	0	0	0.24*	0.03
Potamanthus	0.32*	0.08	0	0.07	0	0.07	0	0.1*	0	0	0	0.11*	0.03
Potamophilus	0.21*	0.06	0	0.1*	0.01	0.03	0	0.03	0.01	0	0	0.06	0
Potamophylax	0.01	0.09*	0.18*	0.06	0.07	0.06	0.1*	0.03	0.1*	0	0.01	0	0
Potamopyrgus	0.26*	0.25*	0.23*	0.28*	0.28*	0.15	0.11	0.21*	0.23*	0.01	0.02	0.14	0.09
Potamothrix	0	0.03	0.06*	0.16*	0.08*	0	0	0.02	0.01	0	0	0	0
Potomida	0.01	0.01	0.01	0.05*	0	0.01	0.01	0.02	0	0	0	0	0
Potthastia	0.01	0.14*	0.15*	0.11*	0.07*	0.02	0.02	0.02	0.04	0	0.01	0	0
Prionocera	0	0	0	0	0	0.03	0.11*	0	0.01	0	0	0	0
Proasellus	0.01	0.08*	0.11*	0.1*	0.18*	0	0.02	0	0.01	0	0	0	0
Procambarus	0.09*	0.03	0.02	0.06	0.07*	0	0.01	0.01	0	0.01	0.07	0.01	0.14*
Procladius	0.02	0.08*	0.08*	0.2*	0.18*	0	0	0	0	0	0	0	0
Procloeon	0.28*	0.15*	0.07	0.18*	0.1	0.14*	0.08	0.2*	0.09	0.04	0.03	0.11	0.09
Prodiamesa	0.02	0.05	0.14*	0.12*	0.14*	0.02	0.04	0.02	0.02	0	0	0	0
Propappus	0.02	0	0	0	0	0.01	0.01	0.09*	0.03	0	0.04	0.01	0
Prosimulium	0.01	0.03	0.05	0	0.02	0.07*	0.12*	0.03	0.07	0	0.03	0.01	0
Protonemura	0	0.09	0.13	0.01	0.02	0.27*	0.32*	0.14	0.14	0.15	0.15	0.36*	0.06
Psammoryctides	0	0.05*	0.03	0.07*	0.03	0	0	0	0	0	0	0	0
Psectrocladius	0.01	0.04	0.07*	0.07*	0.08*	0	0	0	0	0	0	0	0
Psectrotanypus	0	0.05*	0.06*	0.07*	0.11*	0	0	0	0	0	0	0	0
Pseudocentroptilum	0.05	0.04	0.02	0.03	0.03	0.12*	0.05	0.02	0.02	0.06	0.01	0.06	0.04
Pseudochironomus	0	0	0	0.01	0.06*	0	0	0	0	0	0	0	0
Psychomyia	0.28*	0.17*	0.05	0.09	0.02	0.28*	0.15	0.21*	0.08	0.06	0.03	0.22*	0.08
Ptilocolepus	0	0	0	0.01	0	0.01	0	0	0	0	0	0.08*	0.01
Ptychoptera	0	0.02	0.09*	0.02	0.04	0.01	0.05	0.01	0.04	0	0.01	0.01	0
Pyrrhosoma	0.01	0.03	0.08*	0.07*	0.08*	0	0.01	0	0	0	0	0	0
Quistadrilus	0	0.03	0.05*	0.12*	0.03	0	0	0	0	0	0	0	0
Radix	0.29*	0.18*	0.13	0.22*	0.17*	0.07	0.05	0.22*	0.18*	0.02	0.04	0.15	0.04
Ranatra	0	0.04	0.02	0.05*	0.04	0.01	0.01	0.01	0.02	0	0	0	0
Raptobaetopus	0.24*	0.02	0	0.03	0	0.02	0	0.02	0	0	0	0	0
Rhabdiopteryx	0	0	0	0	0	0.03	0.01	0.07	0.04	0.07	0.16*	0.13*	0
Rhantus	0	0.01	0.06*	0.05*	0.08*	0	0	0	0	0	0	0	0
Rheocricotopus	0.01	0.08*	0.09*	0.07*	0.06*	0.01	0.02	0.04	0.05	0	0.03	0.01	0
Rheotanytarsus	0.02	0.1*	0.12*	0.05	0.08*	0.01	0.04	0.03	0.05	0	0.01	0	0
Rhithrogena	0.01	0.13	0.12	0.04	0.05	0.23*	0.23*	0.19*	0.15	0.13	0.16	0.38*	0.06
Rhyacodrilus	0.01	0.11*	0.12*	0.11*	0.09*	0	0.01	0	0.02	0	0	0	0
Rhyacophila	0.04	0.18	0.18	0.12	0.17	0.33*	0.31*	0.26*	0.29*	0.13	0.18	0.35*	0.11
Rhynchelmis	0	0.01	0.01	0.02	0	0	0	0.07*	0.04	0	0	0	0
Riolus	0.05	0.03	0.02	0.18*	0.22*	0.06	0.02	0.36*	0.29*	0	0.14	0.13	0.09
Ripistes	0	0	0	0.06*	0	0	0.01	0	0	0	0	0	0
Satchelliella	0	0.02	0.05*	0.04*	0.03	0	0	0	0	0	0	0	0
Schoenobius	0	0.01	0.01	0.04*	0.03	0	0	0	0	0	0	0	0
Segmentina	0	0.04	0.05*	0.02	0.06*	0	0	0	0	0	0	0	0

Table 4: Indicator scores for all taxon and stream type combination where at least one is statistically significant. Statistically significat entries are marked with *. *(continued)*

taxon	RT1	RT2	RT3	RT4	RT5	RT8	RT9	RT10	RT11	RT14	RT15	RT16	RT18
Semblis	0	0	0	0	0	0	0.08*	0	0	0	0	0	0
Septaria	0	0	0	0	0	0.06*	0	0	0	0	0	0	0
Sericostoma	0.01	0.13	0.19*	0.1	0.15	0.22*	0.26*	0.18	0.22*	0.14	0.08	0.27*	0.06
Serratella	0.05	0.19*	0.19*	0.18*	0.17	0.19*	0.2*	0.21*	0.21*	0.06	0.06	0.25*	0.07
Setacera	0	0	0	0.04*	0	0	0	0	0	0	0	0	0
Setodes	0.26*	0.05	0.01	0.03	0.01	0.06	0.01	0.07	0.01	0.03	0	0.04	0.1*
Sialis	0.03	0.18*	0.2*	0.23*	0.23*	0.19*	0.19*	0.17*	0.16	0.05	0.03	0.05	0.02
Sigara	0.04	0.08*	0.12*	0.2*	0.14*	0	0.01	0	0	0	0	0.01	0
Silo	0.02	0.1	0.15*	0.08	0.14	0.25*	0.26*	0.1	0.1	0.1	0.01	0.2*	0.04
Silonella	0	0	0	0	0	0	0	0	0	0.05	0	0	0.12*
Simulium	0.03	0.19*	0.23*	0.13*	0.13	0.15*	0.15*	0.08	0.14	0.04	0.05	0.08	0.02
Siphonoperla	0	0.09	0.12*	0.01	0.03	0.14*	0.23*	0.02	0.04	0.08	0.03	0.11*	0.02
Sisyra	0.22*	0.14*	0.05	0.13*	0.04	0.03	0.01	0.08	0.04	0	0	0.01	0
Slavina	0.01	0.04*	0.06*	0.06*	0.02	0	0	0	0	0	0	0	0
Somatochlora	0	0.06*	0.06*	0.05*	0.09*	0.01	0.02	0.02	0	0	0	0	0
Spercheus	0	0.06*	0.03	0.01	0	0	0	0	0	0	0	0	0.01
Sphaerium	0.06	0.17*	0.18*	0.28*	0.24*	0.1	0.08	0.16*	0.12	0.02	0.04	0.03	0.01
Spirosperma	0	0.1*	0.13*	0.04	0.03	0.01	0.01	0	0.02	0	0	0	0
Stagnicola	0.03	0.07*	0.05	0.09*	0.11*	0.01	0.01	0.05	0.02	0	0	0.01	0
Stempellina	0	0.01	0.01	0.07*	0.01	0	0	0	0	0	0	0	0
Stempellinella	0.01	0.03	0.07*	0.03	0.02	0	0.04	0	0.01	0	0.01	0	0
Stenelmis	0.16*	0.17*	0.05	0.2*	0.12	0.1	0.06	0.13*	0.06	0.03	0	0.13	0.1
Stenophylax	0	0.02	0.08*	0.02	0.03	0.01	0.02	0	0	0	0	0	0
Stictochironomus	0	0.06*	0.05*	0.06*	0.04	0	0	0.01	0	0	0	0	0
Stictonectes	0	0.03	0.07*	0	0	0	0.01	0	0	0	0	0	0
Stictotarsus	0	0.03	0.06*	0.07*	0.04	0	0.01	0	0.02	0	0	0.03	0
Stylaria	0.02	0.08*	0.1*	0.19*	0.11*	0	0.01	0.01	0.01	0	0	0.01	0
Stylodrilus	0.03	0.16*	0.16*	0.13*	0.11*	0.04	0.06	0.04	0.08	0	0.01	0.01	0
Succinea	0	0.03	0.07*	0.05*	0.05*	0	0	0	0.01	0	0	0	0
Sympetrum	0.02	0.03	0.03	0.05*	0.07*	0	0.01	0	0.01	0	0	0.01	0.01
Synorthocladius	0	0.07*	0.03	0.06*	0.03	0.01	0.02	0.03	0.03	0	0.02	0	0
Synurella	0	0.02	0	0.02	0.07*	0	0	0.01	0	0	0	0	0
Tabanus	0	0.06*	0.03	0.02	0.03	0	0	0	0.04	0	0	0	0
Taeniopteryx	0.01	0.05	0.03	0.03	0.01	0.11*	0.12*	0.03	0.06	0.07	0.06	0.11*	0.01
Tanypus	0	0.07*	0.06*	0.06*	0.03	0	0	0	0	0	0	0	0
Tanytarsus	0.02	0.08*	0.09*	0.14*	0.18*	0	0.01	0	0.02	0	0	0	0
Theodoxus	0.18*	0.11*	0.03	0.25*	0.11*	0.01	0.01	0.15*	0.01	0	0	0.15*	0.03
Theromyzon	0.01	0.05*	0.06*	0.12*	0.11*	0	0	0.01	0	0	0	0	0
Thienemanniella	0	0.07*	0.1*	0.05*	0.04	0	0.03	0.01	0.03	0	0.02	0.01	0
Thienemannimyia	0	0.13*	0.17*	0.12*	0.08*	0.02	0.02	0.02	0.06	0	0.01	0	0
Thraulus	0.01	0.02	0	0.01	0	0.03	0.05*	0	0	0.01	0	0	0.03
Thremma	0	0	0	0	0	0.02	0.06*	0	0.01	0.03	0	0.09*	0.05
Tinodes	0.06	0.09	0.06	0.14*	0.14*	0.1	0.07	0.14*	0.23*	0.03	0	0.03	0.07
Tipula	0.02	0.11*	0.11*	0.09*	0.08*	0.02	0.04	0.02	0.08	0	0	0	0
Torleya	0	0.03	0.01	0.01	0.01	0.22*	0.11*	0.17*	0.12*	0.09	0	0.11*	0.02
Triaenodes	0.05	0.05	0.05	0.17*	0.06	0.03	0.01	0.03	0.02	0	0	0.03	0.05
Trichostegia	0	0	0	0.04*	0	0	0	0	0	0	0	0	0
Trissopelopia	0	0.02	0.07*	0.01	0.03	0	0.01	0	0.02	0	0	0	0
Trithemis	0.06*	0	0	0	0	0	0	0	0	0	0	0	0

Table 4: Indicator scores for all taxon and stream type combination where at least one is statistically significant. Statistically significat entries are marked with *. *(continued)*

taxon	RT1	RT2	RT3	RT4	RT5	RT8	RT9	RT10	RT11	RT14	RT15	RT16	RT18
Trocheta	0	0.04*	0.04	0.04*	0.02	0.01	0.01	0	0	0	0	0.01	0
Tubifex	0.03	0.02	0.07*	0.09*	0.07*	0.01	0.01	0.01	0.01	0	0	0	0
Tvetenia	0.01	0.13*	0.15*	0.07*	0.08*	0	0.03	0.05	0.06	0	0.02	0.01	0
Uncinais	0	0.03	0.01	0.05*	0.01	0	0	0	0	0	0	0	0
Unio	0.05	0.08*	0.03	0.09*	0.07*	0.01	0.02	0.11*	0.03	0	0	0.01	0
Valvata	0.27*	0.1	0.05	0.19*	0.12*	0.03	0.03	0.11*	0.07	0	0.01	0.03	0.02
Velia	0.01	0.03	0.11*	0.06*	0.12*	0.03	0.07*	0.01	0.04	0.02	0	0	0
Virgatanytarsus	0	0.06*	0.04	0	0.03	0	0	0	0	0	0	0	0
Viviparus	0.13*	0.11*	0.02	0.11*	0.03	0	0	0.04	0	0	0	0	0
Wiedemannia	0	0.09*	0.11*	0.05	0.05	0.01	0.02	0.03	0.07	0	0.01	0	0
Wormaldia	0	0.03	0.05	0.01	0.03	0.07*	0.1*	0.03	0.05	0.04	0	0.04	0.04
Xanthoperla	0.13*	0	0	0	0	0	0	0	0	0.02	0	0	0
Xenochironomus	0	0.05*	0.02	0.04*	0	0	0	0	0	0	0	0	0
Xenopelopia	0.01	0.02	0.04	0.04*	0.03	0	0	0	0	0	0	0	0
Xironogiton	0	0.02	0.03	0	0	0.1*	0.12*	0.02	0.01	0	0	0.04	0
Ylodes	0.01	0.02	0	0.05*	0.01	0.03	0.01	0.03	0.01	0	0	0.01	0.02
Zavreliella	0	0	0.02	0.05*	0.02	0	0	0	0	0	0	0	0
Zavrelimyia	0.01	0.05*	0.07*	0.03	0.05	0.01	0.01	0.01	0.01	0	0	0	0
Zonitoides	0	0	0.06*	0.01	0.01	0	0	0	0.02	0	0	0	0
Zygoptera	0	0.02	0.02	0.07*	0.08*	0	0	0	0	0	0	0	0

References

Abrego, N., Roslin, T., Huotari, T., Ji, Y., Schmidt, N.M., Wang, J., *et al.* (2021). Accounting for species interactions is necessary for predicting how arctic arthropod communities respond to climate change. *Ecography*, 1–12.

Adams, H.E., Crump, B.C. & Kling, G.W. (2014). Metacommunity dynamics of bacteria in an arctic lake: The impact of species sorting and mass effects on bacterial production and biogeography. *Frontiers in Microbiology*, 5, 82.

Alric, B., Dézerald, O., Meyer, A., Billoir, E., Coulaud, R., Larras, F., *et al.* (2021). How diatom-, invertebrate- and fish-based diagnostic tools can support the ecological assessment of rivers in a multi-pressure context: Temporal trends over the past two decades in France. *Science of the Total Environment*, 762, 143915.

Alvarez-Cabria, M., Barquin, J. & Juanes, J.A. (2010). Spatial and seasonal variability of macroinvertebrate metrics: Do macroinvertebrate communities track river health? *Ecological Indicators*, 10, 370–379.

Alvarez-Cabria, M., Barquin, J. & Juanes, J.A. (2011). Macroinvertebrate community dynamics in a temperate european atlantic river. Do they conform to general ecological theory? *Hydrobiologia*, 658, 277–291.

Astorga, A., Oksanen, J., Luoto, M., Soininen, J., Virtanen, R. & Muotka, T. (2012). Distance decay of similarity in freshwater communities: Do macro-and microorganisms follow the same rules? *Global Ecology and Biogeography*, 21, 365–375.

Baranov, V., Jourdan, J., Pilotto, F., Wagner, R. & Haase, P. (2020). Complex and nonlinear climate-driven changes in freshwater insect communities over 42 years. *Conservation Biology*, cobi.13477.

Belletti, B., Garcia de Leaniz, C., Jones, J., Bizzi, S., Börger, L., Segura, G., *et al.* (2020). More than one million barriers fragment Europe's rivers. *Nature*, 588, 436–441.

Berger, E., Haase, P., Schäfer, R.B. & Sundermann, A. (2018). Towards stressor-specific macroinvertebrate indices: Which traits and taxonomic groups are associated with vulnerable and tolerant taxa? *Science of the Total Environment*, 619, 144–154.

Béné, C., Arthur, R., Norbury, H., Allison, E.H., Beveridge, M., Bush, S., *et al.* (2016). Contribution of fisheries and aquaculture to food security and poverty reduction: Assessing the current evidence. *World Development*, 79, 177–196.

Bhowmik, A.K. & Schaefer, R.B. (2015). Large scale relationship between aquatic insect traits and climate. *PLOs one*, 10, e0130025.

Birk, S., Bonne, W., Borja, A., Brucet, S., Courrat, A., Poikane, S., *et al.* (2012). Three hundred ways to assess Europe's surface waters: An almost complete overview of biological methods to implement the Water Framework Directive. *Ecological Indicators*, 18, 31–41.

Birk, S., Chapman, D., Carvalho, L., Spears, B.M., Andersen, H.E., Argillier, C., *et al.* (2020). Impacts of multiple stressors on freshwater biota across spatial scales and ecosystems. *Nature Ecology & Evolution*.

Birk, S., Willby, N.J., Kelly, M.G., Bonne, W., Borja, A., Poikane, S., *et al.* (2013). Intercalibrating classifications of ecological status: Europe's quest for common management objectives for aquatic ecosystems. *Science of the Total Environment*, 454-455, 490–499.

Bonferroni, C.E. (1935). Il calcolo delle assicurazioni su gruppi di teste. *Studi in onore del professore salvatore ortu carboni*, 13–60.

Borgwardt, F., Leitner, P., Graf, W. & Birk, S. (2019). Ex uno plures – defining different types of very large rivers in Europe to foster solid aquatic bio-assessment. *Ecological Indicators*, 107, 105599.

Börger, T., Campbell, D., White, M.P., Elliott, L.R., Fleming, L.E., Garrett, J.K., *et al.* (2021). The value of blue-space recreation and perceived water quality across europe: A contingent behaviour study. *Science of The Total Environment*, 145597.

Caceres, M.D. & Legendre, P. (2009). Associations between species and groups of sites: inindices and statistical inference. *Ecology*, 90, 3566–3574.

Caliński, T. & Harabasz, J. (1974). A dendrite method for cluster analysis. *Communications in Statistics-theory and Methods*, 3, 1–27.

Cardinale, B.J. (2011). Biodiversity improves water quality through niche partitioning. *Nature*, 472, 86–89.

Carvalho, L., Mackay, E.B., Cardoso, A.C., Baattrup-Pedersen, A., Birk, S., Blackstock, K.L., *et al.* (2019). Protecting and restoring Europe's waters: An analysis of the future development needs of the Water Framework Directive. *Science of the Total Environment*, 658, 1228–1238.

Chamberlain, S., Szoecs, E., Foster, Z., Arendsee, Z., Boettiger, C., Ram, K., *et al.* (2020). *Taxize: Taxonomic information from around the web*.

Chytry, M., Tichy, L., Holt, J. & Botta-Dukat, Z. (2002). Determination of diagnostic species with statistical fidelity measures. *Journal of Vegetation science*, 13, 79–90.

Clarke, R.T., Wright, J.F. & Furse, M.T. (2003). RIVPACS models for predicting the

expected macroinvertebrate fauna and assessing the ecological quality of rivers. *Ecological modelling*, 160, 219–233.

CLC. (2018). CORINE land cover. *https://land.copernicus.eu/pan-european/corine-land-cover*.

Comte, L., Grantham, T. & Ruhi, A. (2021). Human stabilization of river flows is linked with fish invasions across the USA. *Global Ecology and Biogeography*, 725–737.

Connor, E.F. & Simberloff, D. (1983). Interspecific competition and species co-occurrence patterns on islands: Null models and the evaluation of evidence. *Oikos*, 455–465.

Costanza, R., De Groot, R., Sutton, P., Van der Ploeg, S., Anderson, S.J., Kubiszewski, I., *et al.* (2014). Changes in the global value of ecosystem services. *Global environmental change*, 26, 152–158.

Cumberlidge, N., Ng, P.K., Yeo, D.C., Magalhães, C., Campos, M.R., Alvarez, F., *et al.* (2009). Freshwater crabs and the biodiversity crisis: Importance, threats, status, and conservation challenges. *Biological Conservation*, 142, 1665–1673.

Darwall, W., Bremerich, V., De Wever, A., Dell, A.I., Freyhof, J., Gessner, M.O., *et al.* (2018). The Alliance for Freshwater Life: A global call to unite efforts for freshwater biodiversity science and conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 28, 1015–1022.

Diamond, J.M. (1975). Ecology and evolution of communities. In: *Ecology and evolution of communities* (ed. Cody, J.M., M. L. & Diamond). Harvard University Press, pp. 342–444.

Dimitriadou, E., Barth, M., Windischberger, C., Hornik, K. & Moser, E. (2004). A quantitative comparison of functional MRI cluster analysis. *Artificial Intelligence in Medicine*, 31, 57–71.

Dodkins, I., Rippey, B., Harrington, T.J., Bradley, C., Chathain, B.N., Kelly-Quinn, M., *et al.* (2005). Developing an optimal river typology for biological elements within the Water Framework Directive. *Water Research*, 39, 3479–3486.

Dowle, M. & Srinivasan, A. (2021). *Data.table: Extension of 'data.frame'*.

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.I., Knowler, D.J., Lévêque, C., *et al.* (2006). Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews*, 81, 163–182.

Duffy, J.E., Godwin, C.M. & Cardinale, B.J. (2017). Biodiversity effects in the wild are common and as strong as key drivers of productivity. *Nature*, 549, 261–264.

Dufrêne, M. & Legendre, P. (1997). Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological monographs*, 67, 345–366.

EEA. (2016). Biogeographical Regions.

EEA. (2018). European waters assessment of status and pressures 2018. *EEA Report*.

Elo, M., Jyrkänkallio-Mikkola, J., Ovaskainen, O., Soininen, J., Tolonen, K.T. & Heino, J. (2021). Does trait-based joint species distribution modelling reveal the signature of competition in stream macroinvertebrate communities? *Journal of Animal Ecology*.

Epele, L.B., Dos Santos, D.A., Sarremejane, R., Grech, M.G., Macchi, P.A., Manzo, L.M., *et al.* (2021). Blowin' in the wind: Wind directionality affects wetland invertebrate metacommunities in Patagonia. *Global Ecology and Biogeography*, 1–13.

Escribano, N., Oscoz, J., Galicia, D., Cancellario, T., Durán, C., Navarro, P., *et al.* (2018). Freshwater macroinvertebrate samples from a water quality monitoring network in the iberian peninsula. *Scientific data*, 5, 1–6.

European Commission. (2000). DIRECTIVE 2000/60/EC OF THE EUROPEAN PARLIAMENT AND OF THE COUNCIL of 23 October 2000 establishing a framework for Community action in the field of water policy. *Official Journal of the European Union*, L327.

European Commission. (2019). European overview – river basin management plans. Report from the commission to the european parliament and the council on the implementation of the water framework directive (2000/60/EC) and the floods directive (2007/60/EC): Second river basin management plans and first flood risk manage- ment plans. *SWD*, 296.

Floury, M., Usseglio-Polatera, P., Ferreol, M., Delattre, C. & Souchon, Y. (2013). Global climate change in large European rivers: Long-term effects on macroinvertebrate communities and potential local confounding factors. *Global Change Biology*, 19, 1085–1099.

García, L.V. (2004). Escaping the Bonferroni iron claw in ecological studies. *Oikos*, 105, 657–663.

Gerritsen, J., Barbour, M.T. & King, K. (2000). Apples, oranges, and ecoregions: On determining pattern in aquatic assemblages. *Journal of the North American Benthological Society*, 19, 487–496.

Gilbert, B. & Bennett, J.R. (2010). Partitioning variation in ecological communities: Do the numbers add up? *Journal of Applied Ecology*, 47, 1071–1082.

Globevnik, L. (2019). Broad typology for rivers and lakes in Europe for large scale analysis.

Goodwin, C.N. (1999). Fluvial classification: Neanderthal necessity or needless normalcy. *Wildland Hydroloy*, 5230, 229–236.

Graco-Roza, C., Aarnio, S., Abrego, N., Acosta, A.T., Alahuhta, J., Altman, J., *et al.* (2021). Distance decay 2.0–a global synthesis of taxonomic and functional turnover in ecological communities. *bioRxiv*.

Grizzetti, B., Liquete, C., Pistocchi, A., Vigiak, O., Zulian, G., Bouraoui, F., *et al.* (2019). Relationship between ecological condition and ecosystem services in European rivers , lakes and coastal waters. *Science of the Total Environment*, 671, 452–465.

Haegeman, B. & Loreau, M. (2015). A graphical-mechanistic approach to spatial resource competition. *The American Naturalist*, 185, E1–E13.

Haubrock, P.J., Pilotto, F. & Haase, P. (2020). Do changes in temperature affect EU Water Framework Directive compliant assessment results of central European streams? *Environmental Sciences Europe*, 32.

Hawkins, C.P., Norris, R.H., Gerritsen, J., Hughes, R.M., Jackson, S.K., Johnson, R.K., *et al.* (2000). Evaluation of the Use of Landscape Classifications for the Prediction of Freshwater Biota : Synthesis and Recommendations. *Journal of the North American Benthological Society*, 19, 541–556.

He, F., Zarfl, C., Bremerich, V., David, J.N.W., Hogan, Z., Kalinkat, G., *et al.* (2019). The global decline of freshwater megafauna. *Global Change Biology*, 25, 3883–3892.

Heino, J., Grönroos, M., Soininen, J., Virtanen, R. & Muotka, T. (2012). Context dependency and metacommunity structuring in boreal headwater streams. *Oikos*, 121, 537–544.

Heino, J., Melo, A.S., Siqueira, T., Soininen, J., Valanko, S. & Bini, L.M. (2015). Metacommunity organisation, spatial extent and dispersal in aquatic systems: Patterns, processes and prospects. *Freshwater Biology*, 60, 845–869.

Heino, J. & Mykrä, H. (2006). Assessing physical surrogates for biodiversity: Do tributary and stream type classifications reflect macroinvertebrate assemblage diversity in running waters? *Biological Conservation*, 129, 418–426.

Hennig, C. (2020). *Fpc: Flexible procedures for clustering*.

Huttunen, K.-L., Mykrä, H., Oksanen, J., Astorga, A., Paavola, R. & Muotka, T. (2017). Habitat connectivity and in-stream vegetation control temporal variability of benthic invertebrate communities. *Scientific Reports*, 7, 1–9.

Illies, J. (1978). *Limnofauna europaea*. Fischer Stuttgart.

Irving, K., Kuemmerlen, M., Kiesel, J., Kakouei, K., Domisch, S. & Jähnig, S.C. (2018). A high-resolution streamflow and hydrological metrics dataset for ecological modeling using a regression model. *Scientific data*, 5, 1–14.

Johnson, R.K., Furse, M.T., Hering, D. & Sandin, L. (2007). Ecological relationships between stream communities and spatial scale: Implications for designing catchment-level monitoring programmes. *Freshwater Biology*, 52, 939–958.

Johnson, R.K., Goedkoop, W. & Sandin, L. (2004). Spatial scale and ecological relationships between the macroinvertebrate communities of stony habitats of streams and lakes. *Freshwater Biology*, 49, 1179–1194.

Jourdan, J., O'Hara, R.B., Bottarin, R., Huttunen, K.L., Kuemmerlen, M., Monteith, D., *et al.* (2018). Effects of changing climate on European stream invertebrate communities: A long-term data analysis. *Science of the Total Environment*, 621, 588–599.

Kaufmann, L. & Rousseeuw, P. (1990). *Finding Groups in Data: An Introduction to Cluster Analysis*. John Wiley&Sons.

Lance, G.N. & Williams, W.T. (1967). A general theory of classificatory sorting strategies: 1. Hierarchical systems. *The computer journal*, 9, 373–380.

Landeiro, V.L., Bini, L.M., Melo, A.S., Pes, A.M.O. & Magnusson, W.E. (2012). The roles of dispersal limitation and environmental conditions in controlling caddisfly (trichoptera) assemblages. *Freshwater Biology*, 57, 1554–1564.

Le, T.D.H., Schreiner, V.C., Kattwinkel, M. & Schäfer, R.B. (2021). Invertebrate turnover along gradients of anthropogenic salinisation in rivers of two German regions. *Science of the Total Environment*, 753, 141986.

Leboucher, T., Tison-Rosebery, J., Budnick, W.R., Jamoneau, A., Vyverman, W., Soininen, J., *et al.* (2020). A metacommunity approach for detecting species influenced by mass effect. *Journal of Applied Ecology*, 57, 2031–2040.

Leibold, M.A., Economo, E.P. & Peres-Neto, P. (2010). Metacommunity phylogenetics: Separating the roles of environmental filters and historical biogeography. *Ecology letters*, 13, 1290–1299.

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., *et al.* (2004). The metacommunity concept: A framework for multi-scale community ecology. *Ecology letters*, 7, 601–613.

Leitner, P., Borgwardt, F., Birk, S. & Graf, W. (2020). Multiple stressor effects on benthic macroinvertebrates in very large European rivers – A typology-based evaluation of faunal responses as a basis for future bioassessment. *Science of The Total Environment*, 143472.

Lengyel, A. & Botta-Dukát, Z. (2019). Silhouette width using generalized mean—A flexible method for assessing clustering efficiency. *Ecology and Evolution*, 9, 13231–13243.

Lenoir, A. & Coste, M. (1996). Development of a practical diatom index of overall water quality applicable to the french national water board network. In: *International symposium, volksbildungsheim grilhof vill, AUT, 17-19 september 1995*. Universität Innsbruck, pp. 29–43.

Leunda, P.M., Oscoz, J., Miranda, R. & Ariño, A.H. (2009). Longitudinal and seasonal variation of the benthic macroinvertebrate community and biotic indices in an undisturbed Pyrenean river. *Ecological Indicators*, 9, 52–63.

Leung, B., Hargreaves, A.L., Greenberg, D.A., McGill, B., Dornelas, M. & Freeman, R. (2020). Clustered versus catastrophic global vertebrate declines. *Nature*.

Lin, P., Pan, M., Wood, E.F., Yamazaki, D. & Allen, G.H. (2021). A new vector-based global river network dataset accounting for variable drainage density. *Scientific Data*, 1–9.

Lindström, E.S. & Langenheder, S. (2012). Local and regional factors influencing bacterial community assembly. *Environmental Microbiology Reports*, 4, 1–9.

Lindström, E.S. & Östman, Ö. (2011). The importance of dispersal for bacterial community composition and functioning. *PloS one*, 6, e25883.

Logue, J.B. & Lindström, E.S. (2010). Species sorting affects bacterioplankton community composition as determined by 16S rDNA and 16S rRNA fingerprints. *The ISME journal*, 4, 729–738.

Lorenz, A., Feld, C.K. & Hering, D. (2004). Typology of streams in Germany based on benthic invertebrates: Ecoregions, zonation, geology and substrate. *Limnologica*, 34, 379–389.

Lorenz, A., Feld, C.K. & Hering, D. (2004). Typology of streams in Germany based on benthic invertebrates: Ecoregions, zonation, geology and substrate. *Limnologica*, 34, 379–389.

Loveland, T.R. & Merchant, J.M. (2004). Ecoregions and ecoregionalization: geographical and ecological perspectives. *Environmental management*, 34 Suppl 1, 1–13.

Lyche Solheim, A., Austnes, K., Globevnik, L., Kristensen, P., Moe, J., Persson, J., *et al.* (2019). A new broad typology for rivers and lakes in Europe: Development and application for large-scale environmental assessments. *Science of the Total Environment*, 697, 134043.

Lyche-Solheim, A., Feld, C.K., Birk, S., Phillips, G., Carvalho, L., Morabito, G., *et al.* (2013). Ecological status assessment of european lakes: A comparison of metrics for phytoplankton, macrophytes, benthic invertebrates and fish. *Hydrobiologia*, 704, 57–74.

McGeoch, M.A., Van Rensburg, B.J. & Botes, A. (2002). The verification and application of bioindicators: A case study of dung beetles in a savanna ecosystem. *Journal of Applied Ecology*, 39, 661–672.

Melles, S.J., Jones, N.E. & Schmidt, B.J. (2014). Evaluation of current approaches to stream classification and a heuristic guide to developing classifications of integrated aquatic networks. *Environmental Management*, 53, 549–566.

Mondy, C.P. & Usseglio-Polatera, P. (2013). Using conditional tree forests and life history traits to assess specific risks of stream degradation under multiple pressure scenario. *Science of the Total Environment*, 461-462, 750–760.

Moog, O., Schwalb, A.N., Ofenböck, T. & Gerritsen, J. (2004). Does the ecoregion approach support the typological demands of the EU 'Water Framework Directive'? *Hydrobiologia*, 516, 21–33.

Morlon, H., Chuyong, G., Condit, R., Hubbell, S., Kenfack, D., Thomas, D., *et al.* (2008). A general framework for the distance–decay of similarity in ecological communities. *Ecology letters*, 11, 904–917.

Mouquet, N. & Loreau, M. (2003). Community patterns in source-sink metacommunities. *The american naturalist*, 162, 544–557.

Mouton, T.L., Tonkin, J.D., Stephenson, F., Verburg, P. & Floury, M. (2020). Increasing climate-driven taxonomic homogenization but functional differentiation among river macroinvertebrate assemblages. *Global Change Biology*, 0–3.

Munné, A. & Prat, N. (2009). Use of macroinvertebrate-based multimetric indices for water quality evaluation in Spanish Mediterranean rivers: An intercalibration approach with the IBMWP index. *Hydrobiologia*, 628, 203–225.

Mykrä, H., Aroviita, J., Hämäläinen, H., Karjalainen, S.M., Visuri, M., Riihimäki, J., *et al.* (2009). Utility of a single a priori river typology for reference conditions of boreal macroinvertebrates and diatoms. *Fundamental and Applied Limnology*, 175, 269–280.

Mykrä, H., Heino, J. & Muotka, T. (2007). Scale-related patterns in the spatial and environmental components of stream macroinvertebrate assemblage variation. *Global Ecology and Biogeography*, 16, 149–159.

Nakagawa, S. (2004). A farewell to Bonferroni: The problems of low statistical power and publication bias. *Behavioral Ecology*, 15, 1044–1045.

Nekola, J.C. & White, P.S. (1999). The distance decay of similarity in biogeography and ecology. *Journal of biogeography*, 26, 867–878.

Ng, I.S., Carr, C.M. & Cottenie, K. (2009). Hierarchical zooplankton metacommunities: Distinguishing between high and limiting dispersal mechanisms. *Hydrobiologia*, 619, 133–143.

Ouellet Dallaire, C., Lehner, B., Sayre, R. & Thieme, M. (2019). A multidisciplinary framework to derive global river reach classifications at high spatial resolution. *Environmental Research Letters*, 14, 024003.

Outhwaite, C.L., Gregory, R.D., Chandler, R.E., Collen, B. & Isaac, N.J.B. (2020). Complex long-term biodiversity change among invertebrates, bryophytes and lichens. *Nature Ecology & Evolution*, 4, 384–392.

Ovaskainen, O. & Abrego, N. (2020). *Joint species distribution modelling: With applications in r*. Cambridge University Press.

Pearson, R.G. & Dawson, T.P. (2003). Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Global ecology and biogeography*, 12, 361–371.

Pebesma, E. (2018). Simple Features for R: Standardized Support for Spatial Vector Data. *The R Journal*, 10, 439–446.

Peeters, E.T.M., Zuidam, J.P. van, Zuidam, B.G. van, Van Nes, E.H., Kosten, S., Heuts, P.G., *et al.* (2013). Changing weather conditions and floating plants in temperate drainage ditches. *Journal of Applied Ecology*, 50, 585–593.

Podani, J. & Csányi, B. (2010). Detecting indicator species: Some extensions of the IndVal measure. *Ecological Indicators*, 10, 1119–1124.

Poikane, S., Kelly, M.G., Salas Herrero, F., Pitt, J.A., Jarvie, H.P., Claussen, U., *et al.* (2019). Nutrient criteria for surface waters under the European Water Framework Directive: Current state-of-the-art, challenges and future outlook. *Science of the Total Environment*, 695, 133888.

Poikane, S., Zampoukas, N., Borja, A., Davies, S.P., Bund, W. van de & Birk, S. (2014). Intercalibration of aquatic ecological assessment methods in the european union: Lessons learned and way forward. *Environmental Science & Policy*, 44, 237–246.

Popovic, G.C., Warton, D.I., Thomson, F.J., Hui, F.K.C. & Moles, A.T. (2019). Untangling direct species associations from indirect mediator species effects with graphical models. *Methods in Ecology and Evolution*, 2019, 1571–1583.

Posthuma, L., Zijp, M.C., De Zwart, D., Van de Meent, D., Globevnik, L., Koprivsek, M., *et al.* (2020). Chemical pollution imposes limitations to the ecological status of European surface waters. *Scientific Reports*, 1–20.

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rees, C.B. van, Waylen, K.A., Schmidt-Kloiber, A., Thackeray, S.J., Kalinkat, G., Martens, K., *et al.* (2020). Safeguarding Freshwater Life Beyond 2020: Recommendations for the New Global Biodiversity Framework from the European Experience. *Conservation Letters*, preprints202001.0212.v1.

Reid, A.J., Carlson, A.K., Creed, I.F., Eliason, E.J., Gell, P.A., Johnson, P.T., *et al.* (2018). Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews*.

Resetarits, W.J. & Binckley, C.A. (2013). Patch quality and context, but not patch number, drive multi-scale colonization dynamics in experimental aquatic landscapes. *Oecologia*, 173, 933–946.

Resh, V.H. & Rosenberg, D.M. (1993). *Freshwater biomonitoring and benthic macroinvertebrates*. Chapman & Hall New York, NY, USA:

Reyjol, Y., Argillier, C., Bonne, W., Borja, A., Buijse, A.D., Cardoso, A.C., *et al.* (2014). Assessing the ecological status in the context of the european water framework directive: Where do we go now? *Science of the Total Environment*, 497, 332–344.

Roberts, D.W. (2019). *Labdsv: Ordination and multivariate analysis for ecology*.

Roberts, D.W. (2020). *Optpart: Optimal partitioning of similarity relations*.

Ryabov, A.B. & Blasius, B. (2011). A graphical theory of competition on spatial resource gradients. *Ecology Letters*, 14, 220–228.

Schinegger, R., Trautwein, C., Melcher, A. & Schmutz, S. (2012). Multiple human pressures and their spatial patterns in European running waters. *Water and Environment Journal*, 26, 261–273.

Schmera, D. & Baur, B. (2011). Testing a typology system of running waters for conservation planning in Hungary. *Hydrobiologia*, 665, 183–194.

Schmera, D., Baur, B. & Erős, T. (2012). Does functional redundancy of communities provide insurance against human disturbances? An analysis using regional-scale stream invertebrate data. *Hydrobiologia*, 693, 183–194.

Scott Chamberlain & Eduard Szocs. (2013). Taxize - taxonomic search and retrieval in r. *F1000Research*.

Smith, T.W. & Lundholm, J.T. (2010). Variation partitioning as a tool to distinguish between niche and neutral processes. *Ecography*, 33, 648–655.

Snelder, T.H., Cattanéo, F., Suren, A.M. & Biggs, B.J.F. (2004). Is the River Environment Classification an improved landscape-scale classification of rivers? *Journal of the North American Benthological Society*, 23, 580–598.

Soininen, J. (2012). Macroecology of unicellular organisms–patterns and processes. *Environmental microbiology reports*, 4, 10–22.

Statzner, B., Bis, B., Dolédec, S. & Usseglio-Polatera, P. (2001). Perspectives for biomonitoring at large spatial scales: A unified measure for the functional composition of invertebrate communities in European running waters. *Basic and Applied Ecology*, 2, 73–85.

Telford, R.J., Vandvik, V. & Birks, H.J.B. (2006). Dispersal limitations matter for microbial morphospecies. *Science*, 312, 1015.

Tennekes, M. (2018). tmap: Thematic maps in R. *Journal of Statistical Software*, 84, 1–39.

Tichy, L. & Chytry, M. (2006). Statistical determination of diagnostic species for site groups of unequal size. *Journal of Vegetation Science*, 17, 809–818.

Tickner, D., Opperman, J.J., Abell, R., Acreman, M., Arthington, A.H., Bunn, S.E., *et al.* (2020). Bending the Curve of Global Freshwater Biodiversity Loss: An Emergency Recovery Plan. *BioScience*, XX, 1–13.

Tuomisto, H., Ruokolainen, L. & Ruokolainen, K. (2012). Modelling niche and neutral dynamics: On the ecological interpretation of variation partitioning results. *Ecography*, 35, 961–971.

Turley, M.D., Bilotta, G.S., Extence, C.A. & Brazier, R.E. (2014). Evaluation of a fine sediment biomonitoring tool across a wide range of temperate rivers and streams. *Freshwater Biology*, 59, 2268–2277.

van Klink, R., Bowler, D.E., Gongalsky, K.B., Swengel, A.B., Gentile, A. & Chase, J.M. (2020). Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science*, 368, 417–420.

Van Sickle, J. (1997). Using Mean Similarity Dendrograms to Evaluate Classifications. *Journal of Agricultural, Biological and Environmental Statistics*, 2, 370–388.

Van Sickle, J. & Hughes, R.M. (2000). Classification strengths of ecoregions, catchments, and geographic clusters for aquatic vertebrates in Oregon. *Journal of the North American*

Benthological Society, 19, 370–384.

Vasconcelos, M.C., Melo, A.S. & Schwarzbold, A. (2013). Comparing the performance of different stream classification systems using aquatic macroinvertebrates. *Acta Limnologica Brasiliensia*, 25, 406–417.

Vellend, M. (2016). *The theory of ecological communities (MPB-57)*. Princeton University Press.

Verdonschot, P.F.M. (2006a). Data composition and taxonomic resolution in macroinvertebrate stream typology. *Hydrobiologia*, 566, 59–74.

Verdonschot, P.F.M. (2006b). Evaluation of the use of Water Framework Directive typology descriptors, reference sites and spatial scale in macroinvertebrate stream typology. *Hydrobiologia*, 566, 39–58.

Verdonschot, P.F.M. & Nijboer, R.C. (2004). Testing the European stream typology of the Water Framework Directive for macroinvertebrates. *Hydrobiologia*, 516, 35–54.

Vilmi, A., Gibert, C., Escarguel, G., Happonen, K., Heino, J., Jamoneau, A., *et al.* (2020). Dispersal–niche continuum index: a new quantitative metric for assessing the relative importance of dispersal versus niche processes in community assembly. *Ecography*, 1–10.

Vogt, J., Soille, P., De Jager, A., Rimavičiūtė, E., Mehl, W., Foisneau, S., *et al.* (2007). *A pan-European river and catchment database*.

Vörösmarty, C.J., Mcintyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green, P., *et al.* (2010). Global threats to human water security and river biodiversity. *Nature*, 467, 555.

Vörösmarty, C.J., Mcintyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green, P., *et al.* (2010). Global threats to human water security and river biodiversity. *Nature*, 467, 555.

Wagner, H.H. & Edwards, P.J. (2001). Quantifying habitat specificity to assess the contribution of a patch to species richness at a landscape scale. *Landscape Ecology*, 16, 121–131.

Whittaker, R.H. & others. (1970). Communities and ecosystems. *Communities and ecosystems.*

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag New York.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R., *et al.* (2019). Welcome to the tidyverse. *Journal of Open Source Software*, 4, 1686.

Wilson, M.V. & Shmida, A. (1984). Measuring beta diversity with presence-absence data. *The Journal of Ecology*, 1055–1064.

Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., *et al.* (2013). The role of biotic interactions in shaping distributions and realised assemblages of species: Implications for species distribution modelling. *Biological Reviews*, 88, 15–30.

World Bank. (2021). https://data.worldbank.org/indicator/ny.gdp.mktp.cd.

Wright, J.F., Sutcliffe, D.W. & Furse, M.T. (2000). Assessing the biological quality of fresh waters. *RIVPACS and other techniques. Freshwater Biological Association, Ambleside, England*.

WWF. (2020). *Living planet report 2020-bending the curve of biodiversity loss*. World Wildlife Fund.

Youn, S.-J., Taylor, W.W., Lynch, A.J., Cowx, I.G., Beard Jr, T.D., Bartley, D., *et al.* (2014). Inland capture fishery contributions to global food security and threats to their future. *Global Food Security*, 3, 142–148.