The capacity of broad-scale aquatic typology systems to capture differences in composition and chemical sensitivity of biological assemblages

by

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Accepted Dissertation thesis for the partial fulfilment of the requirements for Doctor of Natural Sciences
Fachbereich 7: Natur- und Umweltwissenschaften
Rhineland Palatinate Technical University

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Date of the oral examination: 2nd February 2024

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Acknowledgements

I am deeply thankful to all who contributed to this thesis. Most directly, that is, of course, Ralf Schäfer, who conceived of the project and got it funded. The things I learned under his mentorship have impacted my understanding of the scientific process and profession in profound ways that elude neat listing. Beyond his mentorship, he also hosted the wonderful working group in which I had the pleasure to work these last years. The enduring camaraderie and cooperation made the time much more enjoyable and productive. Further, I want to thank all the other scientists who walked parts of this way with me. Starting from the GETREAL project team and advisory group and extending to my numerous co-authors, most specifically Sebastian Birk, Christian K. Feld, Jukka Aroviita, Núria Bonada, Miguel Cañedo-Argüelles, Edwin T.H.M. Peeters, and Maria Kahlert. They all contributed critical thoughts and unmistakably helped shape the final papers.

Finally, and most importantly, I want to thank Nora, Isabel, and my mother. Without your love and support, this would have been impossible.

List of Abbreviations

Abbreviation	Full description
$US	United states dollar
AGS	Agri-environmental schemes
ANOSIM	Analysis of similarities
AQEM	Assessment system for the ecological quality of streams and rivers throughout Europe using benthic macroinvertebrates
ATS	Aquatic typology system
AUC	Area under the zeta diversity decline curve
BGR	Biogeographic regions
CS	Classification strength
e-DNA	Environmental DNA
EC	European Commission
EC50	Effective concentration 50
ECA	European court of auditors
EEA	European environmental agency
EFSA	European food safety authority
EN	European norm
EnZ	Environmental zones
ERA	Ecological risk assessment

Abbreviation	Full description
EU	European union
EUNIS	European nature information system
FCM	Fuzzy C-means
FEoW	Freshwater ecoregions of the world
fMRI	Functional magnetic resonance imaging
FPZ	Functional process zones
GDM	Generalized dissimilarity models
HC5	Hazard concentration 5
HDI	Highest density interval
hSSD	Hierarchical species sensitivity model
IFE	Illie's freshwater ecoregions
IPBES	International panel on biodiversity and ecosystem services
IPCC	International panel on climate change
IRES	Intermittent rivers and ephemeral streams
JRC	Joint research center
LC50	Lethal concentration 50
MCMC	Markov chain monte carlo
Ncut	normalized cut cost
PEC	Predicted exposure concentration
PNEC	Predicted no effect concentration
RAC	Regulatory accepted concentration
RBMP	River basin management plan
RES	Riverine ecosystem synthesis
RT	River type
SA	Spatial autocorrelation
SDG	Sustainable development goal
SSD	Species sensitivity distribution
STAR	Standardization of river classifications
TSA	Typical species analysis
US EPA	United states environmental protection agency
WFD	Water framework directive
WWTP	Waste water treatment directive

Summary

Pervasive human impacts rapidly change freshwater biodiversity. Frequently recorded exceedances of regulatory acceptable thresholds by pesticide concentrations suggest that pesticide pollution is a relevant contributor to broad-scale trends in freshwater biodiversity. A more precise pre-release Ecological Risk Assessment (ERA) might increase its protectiveness, consequently reducing the likelihood of unacceptable effects on the environment. European ERA currently neglects possible differences in sensitivity between exposed ecosystems. If the taxonomic composition of assemblages would differ systematically among certain types of ecosystems, so might their sensitivity toward pesticides. In that case, a single regulatory threshold would be over- or underprotective.

In this thesis, we evaluate (1) whether the assemblage composition of macroinvertebrates, diatoms, fishes, and aquatic macrophytes differs systematically between the types of a European river typology system, and (2) whether these taxonomical differences engender differences in sensitivity toward pesticides. While a selection of ecoregions is available for Europe, only a single typology system that classifies individual river segments is available at this spatial scale - the Broad River Types (BRT).

In the first two papers of this thesis, we compiled and prepared large databases of macroinvertebrate (paper one), diatom, fish, and aquatic macrophyte (paper two) occurrences throughout Europe to evaluate whether assemblages are more similar within than among BRT types. Additionally, we compared its performance to that of different ecoregion systems. We employed multiple tests to evaluate the performances, two of which were also designed in the studies. All typology systems failed to reach common quality thresholds for the evaluated metrics for most taxa. Nonetheless, performance differed markedly between typology systems and taxa, with the BRT often performing worst. We showed that currently available, European

freshwater typology systems are not well suited to capture differences in biotic communities and suggest several possible amelioration.

In the third study, we evaluated whether ecologically meaningful differences in sensitivity exist between BRT types. To this end, we predicted the sensitivity of macroinvertebrate assemblages across Europe toward Atrazine, copper, and Imidacloprid using a hierarchical species sensitivity distribution model. The predicted assemblage sensitives differed only marginally between BRT types. The largest difference between median river type sensitivities was a factor of 2.6, which is far below the assessment factor suggested for such models (6), as well as the factor of variation commonly observed between toxicity tests of the same species-compound pair (7.5 for copper). Our results don't support the notion that a type-specific ERA might improve the accuracy of thresholds. However, in addition to the taxonomic composition the bioavailability of chemicals, the interaction with other stressors, and the sensitivity of a given species might differ between river types.

Zusammenfassung

Der allgegenwärtige Einfluss des Menschen beeinflusst die biologische Vielfalt in Süßwassersystemen stark. Die häufig festgestellten Überschreitungen der zulässigen Schwellenwerte für Pestizidkonzentrationen deuten darauf hin, dass die Belastung mit Pestiziden die großräumigen Trends in der biologischen Vielfalt von Süßwassern beeinflusst. Eine präzisere ökologische Risikobewertung (ÖRB) könnte dessen Schutzwirkung erhöhen und damit die Wahrscheinlichkeit unannehmbarer Auswirkungen auf die Umwelt verringern. Die europäische ÖRB vernachlässigt derzeit mögliche Unterschiede in der Empfindlichkeit der exponierten Ökosysteme. Wenn sich die taxonomische Zusammensetzung von Lebensgemeinschaften zwischen bestimmten Arten von Ökosystemen systematisch unterscheidet, könnte auch ihre Sensitivität gegenüber Pestiziden unterschiedlich sein. In diesem Fall wäre ein einziger gesetzlicher Schwellenwert über- oder unterprotektiv.

In dieser Arbeit untersuchen wir, (1) ob sich die Zusammensetzung der Gemeinschaften von Makroinvertebraten, Diatomeen, Fischen und aquatischen Makrophyten systematisch zwischen den Typen eines europäischen Flusstypologiesystems unterscheidet und (2) ob diese taxonomischen Unterschiede zu einer unterschiedlichen Sensitivität gegenüber Pestiziden führen. Während für Europa eine Auswahl von Ökoregionen verfügbar ist, gibt es auf dieser räumlichen Ebene nur ein einziges Typologiesystem, das einzelne Flussabschnitte klassifiziert - die Broad River Types (BRT).

In den ersten beiden Artikeln dieser Arbeit haben wir umfangreiche Datenbanken über das Vorkommen von Makroinvertebraten (Artikel 1), Diatomeen, Fischen und aquatischen Makrophyten (Artikel 2) in ganz Europa zusammengestellt und aufbereitet, um zu bewerten, ob die Lebensgemeinschaften innerhalb der BRT-Typen ähnlicher sind als zwischen ihnen. Darüber hinaus haben wir die Leistung der BRT mit der verschiedener Ökoregionssysteme verglichen. Zur Bewertung der Leistungen haben wir mehrere Tests

durchgeführt, von denen zwei neu entwickelt wurden. Für die meisten Taxa erreichte kein Typologiesystem allgmeine Qualitätsschwellen für die bewerteten Metriken. Dennoch gab es deutliche Leistungsunterschiede zwischen den einzelnen Typologiesystemen und Taxa, wobei die BRT häufig am schlechtesten abschnitten. Wir zeigen, dass aktuell verfügbare, europaweite Süßwassertypologiesysteme sind nicht gut geeginet um Unterschiede in Lebensgemeinschaften abzubilden und zeigen verschiedene Möglichekiten zur Verbesserung auf.

In der dritten Studie untersuchten wir, ob es ökologisch relevante Unterschiede in der Empfindlichkeit zwischen verschiedenen BRT Typen gibt. Zu diesem Zweck haben wir die Empfindlichkeit von Makroinvertebratengemeinschaften in ganz Europa gegenüber Atrazin, Kupfer und Imidacloprid mit Hilfe eines *hierarchical Species Sensitivity Distribution* Modells vorhergesagt. Die vorhergesagten Sensitivitäten der Gemeinschaften unterschieden sich nur geringfügig zwischen den BRT-Typen. Der größte Unterschied zwischen den Mediansensitivitäten der Flusstypen lag bei einem Faktor von 2,6, was sowohl weit unter dem für solche Modelle vorgeschlagenen Bewertungsfaktor (6) als auch dem Variationsfaktor liegt, der üblicherweise zwischen Toxizitätstests desselben Taxon-Chemikalienpaares beobachtet wird (7,5 für Kupfer). Unsere Ergebnisse unterstützen nicht daher nicht, dass eine typ-spezifische ÖRB die Genauigkeit der Konezntrationsschwellenwerte verbessern könnte. Neben der taxonomischen Zusammensetzung könnten jedoch auch die Bioverfügbarkeit von Chemikalien, die Interaktion mit anderen Stressoren und die Empfindlichkeit einer bestimmten Art zwischen den Flusstypen variieren.

CHAPTER 1

Introduction

Research Aims

We are experiencing a rapid decline in biodiversity, most dramatically in freshwater ecosystems. Pesticide pollution likely contributes to this loss. One of the most effective mechanisms to reduce the burden of pesticide pollution is improving the mandatory pesticide risk assessment each compound undergoes before entering the market. However, current risk assessment fails to protect populations of non-target taxa. Its precision and protectiveness might be improved if it explicitly considered the type of exposed ecosystem. If the taxonomic composition of assemblages differs systematically among ecosystem types, so might assemblage sensitivity to pesticides. In that case, using a single regulatory accepted concentration across broad scales (e.g., Europe) would be imprecise, resulting in over- and underprotection. Therefore, we tested whether taxonomic assemblage compositions of aquatic macroinvertebrates, diatoms, fishes, and aquatic macrophytes and assemblage sensitivities of aquatic macroinvertebrates differed systematically among European river types.

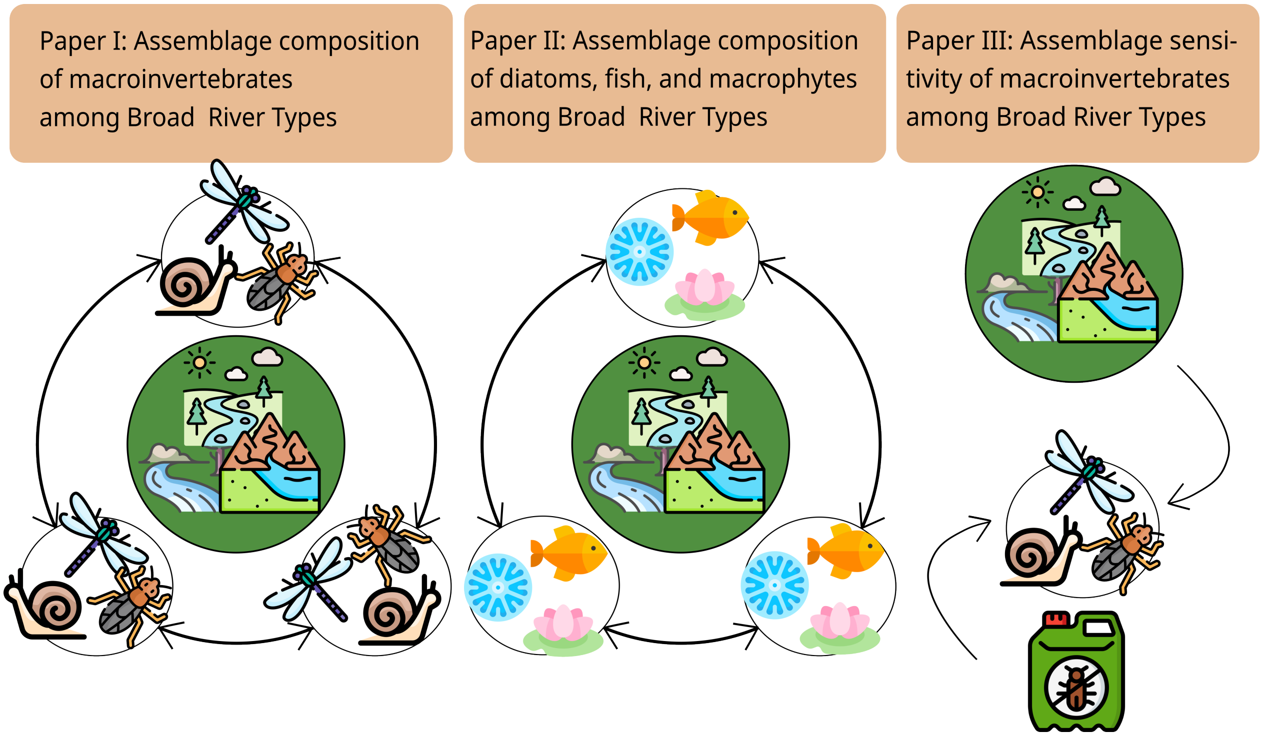

Figure 1.1: Overview of studies the thesis reports on. This thesis consists of three research papers. The first paper evaluates the similarity of macroinvertebrate assemblages within and among the Broad River Types. The second paper does the same for assemblages of diatoms, fishes, and aquatic macrophytes. The third paper evaluates whether the assemblage sensitivity of macroinvertebrates to three pesticides differs between these river types.

1.1 The freshwater biodiversity crisis

Freshwater ecosystems harbor an immense diversity of organisms and are crucial to human flourishing and survival. Within only $\sim 0.8\,\%$ of the globe's surface area, rivers, lakes, and wetlands are home to $10\,\%$ of all described animal species and contribute even more to the diversity of vertebrates ($20\,\%$) and fishes ($40\,\%$) (Balian, 2008). Relative to their area, fresh waters are the most species-rich realm, surpassing terrestrial or marine ecosystems (Román-Palacios, Moraga-López & Wiens, 2022). Partly by dint of this richness, they provide clean drinking water (JRC *et al.*, 2015; B-Béres *et al.*, 2023; Thomaz, 2023), as well as subsistence and income to millions of people globally (Welcomme *et al.*, 2010; FAO, 2014; Lynch *et al.*, 2016). They are pivotal for transport, energy generation, recreation, and irrigation (Gleick, 2003; IPBES, 2019). These services are estimated to be worth $\$US_{2007}$ 28.5 trillion, approximately $38\,\%$ of all non-marine ecosystem services (Costanza *et al.*, 2014). This number omits all non-material, spiritual, or religious valuations of fresh waters that elude precise quantification (Loreau, 2014; Choné, 2017; Díaz *et al.*, 2020). However, the capacity of fresh waters to provide these services is endangered by our interventions in their hydromorphology, ecology, and chemistry (Hooper *et al.*, 2005; Cardinale, 2011; Grizzetti *et al.*, 2019; Leenhardt *et al.*, 2023).

Due to human actions, global biodiversity is steeply declining (Pereira *et al.*, 2010; Ceballos, Ehrlich & Dirzo, 2017; Cowie, Bouchet & Fontaine, 2022), especially in freshwater systems. The Living Planet Index (LPI) indicates an $84\,\%$ decline in the abundance of monitored freshwater vertebrate populations around the globe between 1970 and 2016 (Almond, Grooten & Petersen, 2020). The validity of the LPI has been questioned (Leung *et al.*, 2020; Buschke *et al.*, 2021; Puurtinen, Elo & Kotiaho, 2022; Talis & Lynch, 2023), but it seems to be robust to at least some of the proposed changes (Almond *et al.*, 2020). Populations of megafauna ($> 30\,\text{kg}$) even declined by $88\,\%$. Fish populations in this size category declined by $94\,\%$ (He *et al.*, 2019). Almost a third of freshwater species globally face the threat of extinction (Collen *et al.*, 2014). While ecosystems in all realms experience heightened extinction rates (Pimm *et al.*, 2014; Pereira *et al.*, 2020; Ceballos, Ehrlich & Raven, 2020), biodiversity in freshwater ecosystems decreases faster than in terrestrial or marine ones (Ricciardi & Rasmussen, 1999; Collen *et al.*, 2014; Almond *et al.*, 2020).

These consistent global trends mask a considerable amount of local variation. Trends vary between different river types (Powell *et al.*, 2022) and ecoregions (Pilotto *et al.*, 2020) but also within similar ecosystems (Galewski *et al.*, 2011). Indeed, several studies have reported increasing invertebrate species richness in freshwater systems in Germany (Baker *et al.*, 2021; Manfrin *et al.*, 2023), the United Kingdom (Vaughan & Gotelli, 2019; Powell *et al.*, 2022; Pharaoh *et al.*, 2023), France (Tison-Rosebery *et al.*, 2022), Switzerland (Gebert *et al.*, 2022), Europe (Pilotto *et al.*, 2020; Haase *et al.*, 2023), the United States of America (Rumschlag *et al.*, 2023), and at the global scale (van Klink *et al.*, 2022). These findings might indicate the success of protection and restoration schemes (Haase *et al.*, 2023), but they are no unconditional endorsement for the current state of affairs.

Positive trends in species richness can result from geographic biases or shifted baselines if time series are too short (Gonzalez *et al.*, 2016). Some studies concentrate on sites with limited human impact (e.g., Pilotto *et al.*, 2020) or specific river types (Manfrin *et al.*, 2023). On further inspection, these trends often show diverging patterns between functional and taxonomic groups (Gebert *et al.*, 2022; Powell *et al.*, 2022; Rumschlag *et al.*, 2023; Manfrin *et al.*, 2023) or cessation of positive trends (Haase *et al.*, 2023). Sensitive taxa, like ephemeropterans, plecopterans, and trichopterans, are often displaced by more tolerant taxa (Baker *et al.*, 2021) or native taxa by alien and invasive ones (Haase *et al.*, 2023). Lastly, there might be a considerable and unrealized extinction debt (Tilman & Lehman, 1994; Kuussaari *et al.*, 2009), as extinctions are typically not immediate when environmental conditions shift outside of a species' niche. Models suggest that species richness increases temporarily in constantly changing environments as colonizations outpace extinctions (Kuczynski, Ontiveros & Hillebrand, 2023).

Given the alarming rate of human-caused freshwater biodiversity decline, concerted policy and action are urgently needed (Darwall *et al.*, 2018; Harrison *et al.*, 2018; Tickner *et al.*, 2020; Albert *et al.*, 2021; van Rees *et al.*, 2021; Arthington, 2021; Maasri *et al.*, 2021a). Despite their ecological, economic, and cultural importance, freshwater ecosystems are underrepresented in conservation efforts, research, and funding (Darwall *et al.*, 2011; Mazor *et al.*, 2018; Tydecks *et al.*, 2018). Nonetheless, we know the factors that drive the observed declines (Dudgeon *et al.*, 2006; Strayer & Dudgeon, 2010; Vörösmarty *et al.*, 2010; Reid *et al.*, 2019; Jaureguiberry *et al.*, 2022).

1.2 Drivers of the Freshwater Biodiversity Decline

A multitude of drivers have contributed to the current decline of freshwater biodiversity. We can divide them into hydromorphological alterations, species invasions, and pollution. The hydromorphology of a river determines the availability of habitats and the interaction between different parts of the riverine landscape. Interactions between the main stem, the flood plain, and the hyporheic zone are vital to biological communities (Junk, Bayley & Sparks, 1989; Schiemer *et al.*, 2001) but require connectivity between the parts. In rivers monitored for the European Water Framework Directive (WFD), hydromorphological alterations are the most common stressor in reports from the second river basin management plans (RBMP), occurring in 34 % of rivers (EEA, 2021). Grill *et al.* (2019) estimate that humans critically impact two-thirds of very long rivers (> 1000km) along the longitudinal, latitudinal, vertical, or temporal direction. However, Grill *et al.* (2019) also show that 95% of short rivers (10 – 100 km) remain free-flowing. However, small barriers are sufficient to impact longitudinal connectivity (Fencl *et al.*, 2015) and are more common than most broad-scale databases report (Jones *et al.*, 2019; Belletti *et al.*, 2020). Further, 60 % of all rivers globally cease to flow for at least one day per year on a multi-year average (Messager *et al.*, 2021). Economic development and climate change will likely increase the proportion (Alcamo, Flörke & Märker, 2007; Jaeger, Olden & Pelland, 2014; Pumo *et al.*, 2016; Zipper *et al.*, 2021). Small rivers are more likely to run episodically dry than larger rivers and are thus more strongly affected by these developments (Benstead & Leigh, 2012). Together, these factors suggest that Grill *et al.* (2019) overestimate the connectivity of small rivers and that these systems suffer from reduced connectivity and altered flow regimes.

Non-native species overcome natural dispersal barriers through human intervention (Russell & Blackburn, 2017). The subset of non-native species that causes substantial negative impacts on the recipient ecosystem is called invasive species. Their effects depend on the invasive species' identity and the recipient ecosystem's properties. The direct impacts can be species-specific, as in the case of the signal crayfish *Pacifastacus leniusculus*, which was introduced to Europe from North America and acted as a vector for the crayfish plague agent *Aphanomyces astaci* (Unestam, 1969; Unestam & Weiss, 1970). European crayfish infected with *A. astaci* have high mortality, while *P. leniusculus* is mostly tolerant (Unestam & Weiss, 1970). Hence, *A. astaci* only affects European crayfish species directly. However, their demise entails ecosystem-wide effects (Matthews & Reynolds, 1992). Two examples of invasive species that directly impact the whole ecosystem are the water hyacinth *Eichhornia crassipes*, which builds dense mats of interlocking leaves on the water surface, thereby lowering phytoplankton productivity and oxygen saturation (Rommens *et al.*, 2003; Mangas-Ramírez & Elías-Gutiérrez, 2004; Perna & Burrows, 2005) and the quagga mussel *Dreissena rostriformis bugensis*, which is now the primary regulator of phosphorus cycling in the lower four Great Laurentian lakes (Li *et al.*, 2021). More generally, invasions decrease β-diversity between regions and contribute to taxonomic homogenization (Rahel, 2000; Petsch, 2016). Such homogenization can propagate through food webs (e.g., Beisner, Ives & Carpenter, 2003; Douda *et al.*, 2013), increase population and community synchrony (Olden *et al.*, 2004), and reduce community stability (Erős *et al.*, 2020; Wang *et al.*, 2021; Walter *et al.*, 2021). Management and damage costs of invasive species are estimated to lie at $US 26.8 billion per year on a multi-year average between 1970 and 2017 (Diagne *et al.*, 2021). A more recent analysis estimates the global costs in 2019 were $US 423 billion and qualifies this estimate as "*likely a gross underestimation*" (IPBES, 2023). The costs and number of invasive species are predicted to increase in the future (Seebens *et al.*, 2021; Diagne *et al.*, 2021; IPBES, 2023).

Pollution is the introduction of harmful or undesirable substances or energy into a medium. In fresh waters, pollution typically refers to the introduction of chemicals. While other forms of pollution (heat, light, or noise pollution, Reid *et al.*, 2019; Jägerbrand & Spoelstra, 2023) garner increased interest, this thesis focuses on chemical pollution. Chemical pollution has been recognized as one of the primary drivers of global biodiversity decline (Díaz *et al.*, 2020) and is widespread in Europe (Malaj *et al.*, 2014), where it is a limiting factor for the ecological state of water bodies (Posthuma *et al.*, 2020). The increases in production and diversification of synthetic chemicals outpace most other agents of global change (Bernhardt, Rosi &

Gessner, 2017). The reduction of pollution is enshrined in political frameworks like the Aichi Biodiversity Targets (Target 8), Sustainable Development Goals (e.g., SDG 3 and 6, UN, 2015), and multiple parts of the European Green Deal (Farm to Fork Strategy (EC, 2020a), Biodiversity Strategy, (EC, 2020b), and zero pollution action plan (EC, 2020c)) and encompasses four of ten key challenges for European water management identified by EEA (2021). After air pollution, water pollution has the highest burden of disease among all forms of pollution, with an estimated 1.8 million deaths per year (Landrigan *et al.*, 2018).

There are two types of water pollution: point source and diffuse. Point source pollution has a distinct spatio-temporal entry pathway and mainly stems from wastewater treatment plants (WWTPs) for industrial, urban, and mining wastewater (EEA *et al.*, 2018). According to the second RBMP, 15 % of surface water bodies are affected by point source pollution (EEA, 2021). Point source pollution is relatively easy to mitigate, as we can identify distinct entry pathways and responsible stakeholders. Relevant regulations (e.g., the Urban Wastewater Treatment Directive (EC, 1991), the Industrial Emissions Directive (EC, 2010), and the European Pollutant Release and Transfer Register (EC, 2006)) have successfully reduced this pollution pathway (EEA, 2018; Haase *et al.*, 2023). While the overall pollution from WWTPs seems to be declining, the focus is shifting toward those chemicals current WWTPs cannot remove: pharmaceuticals, personal care products, and microplastics (Margot *et al.*, 2015), collectively known as novel entities, micropollutants, or emerging contaminants. Their combined impact in WWTP effluents has been evaluated in numerous studies showing reductions in species richness and in the occurrence of sensitive taxa (Ortiz & Puig, 2007; Peschke *et al.*, 2014; Berger *et al.*, 2017; Peschke *et al.*, 2019; Enns *et al.*, 2023). In a global study, pharmaceutical concentrations exceeded risk thresholds in 25.7 % of sites (Wilkinson *et al.*, 2022). We might expect ecological effects at even more sites due to additive mixture effects and chronic effects at below-threshold concentrations (e.g., Cleuvers, 2003, 2004). In Europe, pharmaceuticals are the most often detected group of chemicals, occurring in 58.3 % of routine water monitoring samples (Wolfram *et al.*, 2021) and in more than 90 % of samples from four European river basins (Von Der Ohe *et al.*, 2011). Despite their commonly low concentrations, pharmaceuticals affect community composition (Bácsi *et al.*, 2016), reproduction (Jobling *et al.*, 2002), genetic diversity (Hamilton *et al.*, 2016), ecosystem function (Richmond *et al.*, 2016), and phenology (Richmond *et al.*, 2016; Richmond *et al.*, 2019). Given the rapid growth in production and diversification of novel entities (Bernhardt *et al.*, 2017) and the relative scarcity of toxicity data, Persson *et al.* (2022) argue that we have left the safe operating space for novel entities. While pesticides can dominate the toxic effects exerted by WWTP effluents (Munz *et al.*, 2017), WWTP effluents are not the dominant entry pathways for pesticides. Those are rather diffuse pathways, such as run-off, leaching, and spray drift (e.g., Le *et al.*, 2017).

Diffuse source pollution is more difficult to regulate since interventions must address many decentralized emission sources. Diffuse pollution affects 33 % of surface water bodies, according to the second RBMP (EEA, 2021). This pollution is attributable to agrochemicals at two-thirds of affected sites (EEA, 2021).

Wolfram *et al.* (2021) found that pesticides exceed risk thresholds in 32.4 % of waterbodies and cause 85 % of threshold exceedances by organic chemicals in Europe. While these data suggest that pesticides frequently occur in freshwater bodies at ecologically relevant concentrations, they likely underestimate the true broad-scale risk. The estimates of EEA (2021) and Wolfram *et al.* (2021) build upon WFD monitoring data. The routine monitoring of the WFD considers priority substances and, locally, river-basin-specific pollutants. The list of priority substances originally encompassed 45 substances (20 pesticides) and was recently expanded by another 47 compounds (EC, 2022). Hence, most pesticides are not monitored under the WFD (Weisner *et al.*, 2022). The selection of chemicals is inadequate to capture risk through chemicals and has recently been described as arbitrary (Brack *et al.*, 2017). The recent fitness check of the WFD identified insufficient monitoring as one of the WFD's most significant weaknesses (EC, 2019a, 2022).

Further, WFD monitoring fails to capture the actual risk for the monitored chemicals, as it uses grab samples and neglects mixture toxicity and small water bodies. Grab samples are taken irrespective of conditions and underestimate the peak concentrations of temporally highly variable chemicals, such as pesticides, by several orders of magnitude (Xing *et al.*, 2013). Weisner *et al.* (2022) showed that using event-driven passive samplers and extending the spectrum of analyzed chemicals increased the fraction of sites with threshold exceedances from 35 % to 85 %. Chemicals typically occur in mixtures (Gillom *et al.*, 1999; Schreiner *et al.*, 2016; Neale *et al.*, 2020; Liess *et al.*, 2021), and considering each substance individually or only a subset of the chemicals can underestimate toxicity (Moschet *et al.*, 2014; Posthuma *et al.*, 2020; Weisner *et al.*, 2021). Lastly, most member countries only consider waterbodies with a catchment size $>10\,km^2$ in their monitoring (Kristensen & Globevnik, 2014), which is likely less than half of all waterbodies (Horton, 1945; Hughes, Kaufmann & Weber, 2011; Kristensen & Globevnik, 2014). Several studies demonstrate the high risk pesticide exposure poses to small water bodies (Stehle & Schulz, 2015b; Szöcs *et al.*, 2017; Betz-Koch *et al.*, 2023). A recent country-wide monitoring study of small streams in Germany found that at least one regulatory threshold exceedance of pesticides in 81 % of streams and pesticide toxic pressure explained more variation in macroinvertebrate community composition than all other explanatory variables (Liess *et al.*, 2021).

Hence, pesticide pollution at ecologically relevant concentrations likely occurs in more than a quarter of European water bodies. Field studies have repeatedly shown the adverse effects of pesticides at environmentally relevant concentrations on species' abundance (Schäfer *et al.*, 2012; Bereswill, Streloke & Schulz, 2013), ecosystem functions (Schäfer *et al.*, 2007; Schäfer *et al.*, 2012; Münze *et al.*, 2017), species richness (Liess & von der Ohe, 2005), and the occurrence of sensitive taxa (Liess & von der Ohe, 2005; Schäfer *et al.*, 2007; Schäfer *et al.*, 2012; Bereswill *et al.*, 2013; Münze *et al.*, 2017; Liess *et al.*, 2021). Notably, several studies have observed adverse effects at concentrations below thresholds deemed safe (e.g., Schäfer *et al.*, 2007; Schäfer *et al.*, 2012), further pointing to the fact that the estimates above, which use such thresholds, likely underestimate the true extent of pesticide pollution. Van Dijk, Van Staalduinen & Van der Sluijs

(2013) further corroborate these findings by showing a significant relationship between macroinvertebrate abundances and the concentration of neonicotinoids in Dutch monitoring data.

1.3 Pesticides as agents of global change

Pesticides likely play an essential role in the observed declines of freshwater biodiversity. Broad-scale studies linking chemical pollution in general or pesticides more specifically to the current decline in biodiversity are scarce (Groh *et al.*, 2022; Sigmund *et al.*, 2023; Sylvester *et al.*, 2023), particularly with regards to its predicted impacts (Mazor *et al.*, 2018). The absence of broad-scale emission and exposure data (but see Pistocchi *et al.*, 2023) and a spatio-temporal mismatch between biological and chemical monitoring (Schulz et al., in preparation) impede such studies. Meanwhile, despite ongoing efforts (e.g., Guichard *et al.*, 2017), pesticide sales, measured environmental concentration, and the risk posed to biodiversity have remained stable or increased over the last ten years (EEA, 2021; Schulz *et al.*, 2021; Wolfram *et al.*, 2021; EEA, 2023; Bub *et al.*, 2023). While the harmonized risk indicators (HRI1 and 2) developed by the European Environmental Agency and implemented in an amendment to the sustainable use directive (EC, 2019b) indicate a slightly declining risk over the last few years, the European Court of Auditors (ECA, 2020) and the German Environmental Agency (Bär *et al.*, 2022) have criticized these metrics as they use arbitrary weightings and do not consider measured environmental concentrations.

1.3.1 How can we reduce the impact of pesticides on biodiversity?

Reducing chemical pollution is one of the most pressing problems in freshwater conservation (Harper *et al.*, 2021). While the political will to do so has been reaffirmed again through the Green New Deal (e.g., EC, 2020c), the risk has not receded considerably in the recent past. Meaningful efforts must not stop at reducing the use of and risk through current pesticides but must prevent new risks and regrettable substitutions through improved mechanisms of assessment and authorization (Blum *et al.*, 2019; Schäfer *et al.*, 2019; Siviter & Muth, 2020). The prospective environmental risk assessment (ERA) of pesticides currently used in the European Union has been repeatedly criticized (e.g., SAPEA, 2018; Schäffer *et al.*, 2018; Schäfer *et al.*, 2019; Sousa *et al.*, 2022). Common points of contention are its focus on substance-by-substance evaluations, which neglects mixture toxicity (e.g., Backhaus & Faust, 2012; Bopp *et al.*, 2019), the absence of retrospective monitoring and validation of laboratory results with field data or demonstration farm networks (Milner & Boyd, 2017; Schäfer *et al.*, 2019), and the neglect of landscape-scale effects such as source-sink dynamics or ecological traps (Topping *et al.*, 2015; Hale & Swearer, 2016). These shortcomings result in exceedances of predicted environmental concentrations (Szöcs *et al.*, 2017; Liess *et al.*, 2021) and ecological effects at ostensibly safe concentrations (Liess & von der Ohe, 2005; Schäfer *et *al.*, 2007; Schäfer *et al.*, 2012; Beketov *et al.*, 2013). In short, the current ERA practices are not protective of freshwater biodiversity.

One of the conceptual problems of ERA is the prohibitively large number of compounds and potentially affected species. Based on ethical grounds as well as monetary and time constraints, testing all combinations of species and chemicals is impossible. Therefore, we need to resort to models *in vivo* (model organisms), *in silico* (computer model predicting sensitivities), and *in vitro* (bioassays). All models are reductionist, representing a complex reality with a simpler substitute. Reductions require general patterns that allow us to map the former on the latter and vice versa. Therefore, it is of great interest for ERA to identify general patterns (spatial, taxonomical, functional) in the sensitivity of organisms toward pesticides. One such pattern could be the spatial arrangement of assemblage sensitivities. Are assemblages, i.e., populations that co-occur in space and time, typical for some places or types of ecosystems, systematically more or less sensitive toward specific chemicals, modes of action, or compound classes than in other places? If so, we might improve ERA by identifying the relevant ecosystem types and their typical assemblages, selecting representative test organisms or assemblages for mesocosms, and deriving bespoke exposure estimates and effect thresholds.

Beyond the applied interest in this question, it corresponds to one of the shortfalls of biodiversity knowledge: the Hutchinsonian shortfall (Cardoso *et al.*, 2011; Hortal *et al.*, 2015). The Hutchinsonian Shortfall describes our ignorance of species tolerances to abiotic conditions. In its original definition by Cardoso *et al.* (2011), this shortfall corresponded only to the scenopoetic variables (the Grinellian niche *sensu* Soberón (2007)), i.e., environmental conditions that are not impacted by other organisms. However, including anthropogenic or anthropologically modified variables in its definition is helpful, as they often restrict realized niches (Vitousek *et al.*, 1997; Albert *et al.*, 2023; Sigmund *et al.*, 2023). Accurate estimates of a species' niche help us anticipate how that species might react to environmental changes and what management actions to take (Peterson *et al.*, 2011; Guisan, Thuiller & Zimmermann, 2017). They are also required to understand patterns in abundance and occurrence (Elith & Leathwick, 2009; Slatyer, Hirst & Sexton, 2013; Murphy & Smith, 2021). Estimating niches typically involves a mix of estimates based on physiological considerations, performance curves along gradients, and occurrence data (Peterson *et al.*, 2011). While species distribution models extensively use the latter (e.g., Ovaskainen & Abrego, 2020; Pichler & Hartig, 2021; Adde *et al.*, 2023), we rely on the former two to infer tolerance to pesticides, as no natural gradients in chemical pollution exist, and establishing them would be unethical.

Only a few studies have searched for broad-scale patterns in assemblage pesticide sensitivity. Most broad-scale ecotoxicological studies assess the prevalence of threshold exceedances without explicitly considering differences in the exposed assemblages (e.g., Malaj *et al.*, 2014; Morrissey *et al.*, 2015; Stehle & Schulz, 2015a). A notable exception is Van den Berg *et al.* (2020), who compared the predicted relative sensitivity of typical and observed macroinvertebrate assemblages among European ecoregions (Illies' Freshwater Ecoregions, Illies, 1978) and among British river types (super groups in Davy-Bowker *et al.*, 2008). They found considerable differences in the occurrence of sensitive macroinvertebrate taxa among the ecoregions and river types, though the magnitude of these differences varied between the pesticides' modes of action. Their analysis has multiple drawbacks. The analysis of ecoregions compared lists of typical species determined by expert knowledge rather than observational data (Illies, 1978). Thus, these results rely on the initial validity, i.e., representativeness, of the species lists, the biological validity of the ecoregions, and the assumption that these lists still correspond to the existing ecological communities over 40 years after their compilation. The comparison of British river types only covers the area of the United Kingdom, a single ecoregion. It is not at a broad scale in this context. Lastly, the metric they use to quantify and compare sensitivities relies on a dichotomization of a relative sensitivity metric (mode-specific sensitivity, Rubach, Baird & Van den Brink, 2010), which depends on the included taxa and their taxonomic resolution. Maltby *et al.* (2005) constructed species sensitivity distributions for 16 insecticides with species from the Nearctic and Palaearctic regions and found no significant differences between the derived hazard concentration five values (HC_5), i.e., the concentration that would affect five percent of taxa. The spatial scale considered in their study is broader than relevant for any single risk assessment scheme, and data availability rather than representativeness drove the selection of test species. Field studies conducted in different regions typically find minor differences between the sensitivities of assemblages from different ecoregions (e.g., Schäfer *et al.*, 2007; Schäfer *et al.*, 2012). Biggs *et al.* (2007) found considerable variation in sensitivity among different kinds of water bodies (i.e., rivers, ponds, ditches, streams) within a region but did not evaluate differences among different types within these kinds (e.g., lowland rivers and highland rivers). Together, these studies do not conclusively suggest the existence nor the absence of broad-scale patterns in sensitivity.

Instead of studies on sensitivity, we can consider related properties of the species and their distribution in space. Multiple studies have shown that functional traits, such as voltinism, body size, and feeding mode, can partly explain the interspecific variation in sensitivity (Rubach *et al.*, 2010; Rico & Van den Brink, 2015; Van den Berg *et al.*, 2019), especially when considered in trait profile groups (Pilière *et al.*, 2016), and when complemented with phylogenetic or taxonomic information (Guénard *et al.*, 2014; Poteat, Jacobus & Buchwalter, 2015; Malaj *et al.*, 2016). Thus, spatial patterns in the functional trait composition of ecological communities can inform our expectations about spatial patterns in sensitivity. Multiple studies have considered such patterns and have generally found a dominance of fine-scale over broad-scale variation (e.g., Statzner *et al.*, 2001; Bonada, Dolédec & Statzner, 2007; Dolédec & Statzner, 2008). The functional composition of biological assemblages tends to vary more strongly between river types within regions than among the regions. We might, therefore, expect that sensitivity to pesticides also varies at a small spatial scale, which would be in line with the observed differences among British river types (Van den Berg *et al.*, 2020) or kinds of water bodies (Biggs *et al.*, 2007) and the absence of such differences between the Nearctic and the Paleartic (Maltby *et al.*, 2005).

1.4 The unit of comparison: ecosystem types

The studies discussed above compare discrete representations of ecosystems or space. They study ecoregions, river types, kinds of water bodies, and biogeographic realms (Figure 1.2). An alternative approach would have been to examine assemblage sensitivities along continuous gradients in, for example, elevation, temperature, or space. Discrete classes are appealing as they integrate multiple variables simultaneously and are assumed to capture breaks in diverse biotic and abiotic properties. This conception might be accurate for biogeographic boundaries, such as the Wallace line, which separates Asian and Australian faunas (Wallace, 1863; Rueda, Rodríguez & Hawkins, 2013). However, such rigid boundaries are less common at finer spatial scales, i.e., within biogeographic realms. Even if they do not represent the ground truth, they can be valuable instruments to identify patterns and implement policy. The following section will shortly introduce the idea behind classification, which underpins this thesis, discuss the role of classification in ecology and limnology, and lastly, identify and present an appropriate classification for our purpose.

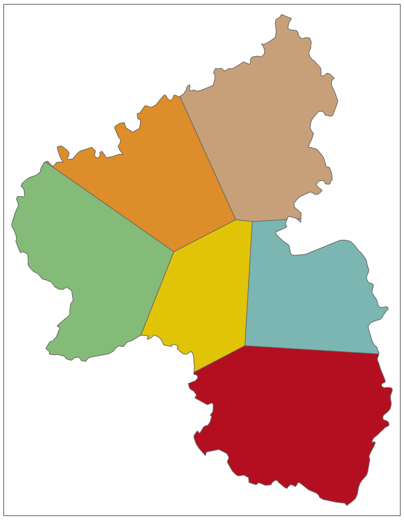

Figure 1.2: Example of a discrete classification of an area. Each colored subarea represents a distinct type.

1.4.1 Classification: A primer

Classification arranges objects into classes based on the properties of these objects. We commonly encounter the term typology system for ecosystems instead of classification or classification system (e.g., Verdonschot

& Nijboer, 2004; Harrison & Whitfield, 2006; Powell *et al.*, 2022). Following Hoehne (1980), we define a typology system as a partitioning of objects into types based on multiple properties of these objects instead of just one. It is synonymous with the term polythetic classification. Further, following Sokal (1974), the term *typology system* denotes the final set of types, *classification* consists of defining types, and *identification* is the assignment of objects to types. Using multiple variables prevents the essentialist fallacy, i.e., the notion that the objects in any of our types hold some intrinsic essence that is necessary and sufficient to render them instances of one type (Sokal, 1974; Marradi, 1990). Here, no specific values of any variables must be sufficient or necessary to assign an object to any type. Therefore, the discussed types are *nominal*, human constructs defined for a given purpose rather than *natural*, representing true ontological groupings (Mill, 1856). Even in the classifications of natural properties, the selection of properties is artificial; hence, the types are (Cohen & Nagel, 1993). Further, each object can represent its type to different degrees (Rosch, 1978; Smith & Medin, 1981). Later, this perspective will allow us to consider approaches using fuzzy or possibilistic set theory (Zadeh, 1965; Zadeh, 1978), in which objects are part of multiple types. Such typology systems are uncommon in ecology (but see Feoli, 2018; Jena *et al.*, 2022; Lusiana, 2023) and will only be addressed in the outlook. Until then, the term typology system always refers to crisp classification systems with non-overlapping types.

Typology systems are models, purposeful representations of reality (Goodwin, 1999; Loveland & Merchant, 2004). Like all models, they are wrong - they do not directly and completely correspond to or depict reality, but they can be useful (Box, 1976). Indeed, classification might be a fundamental feature of human cognition - a prerequisite of language and understanding (Hegel, 1807; Sokal, 1974; Estes, 1994; Lakoff, 2008; Harnad, 2017). In employing a typology system, we assume that objects of one type behave in the same or a similar way. At least, objects should be more similar to other objects of their type than to objects of another. If this assumption holds, we can generalize from observations made on a set of objects to others of the same type (Marradi, 1990). Hence, typology systems can facilitate generalization, which is fundamental to all sciences (Riggs, 2013; Spake *et al.*, 2022), a possible obstacle in the replication crisis (Yarkoni, 2020), and, historically, a problem in ecology (e.g., Peters, 1991; Lawton, 1999; Vellend, 2016), given a high degree of context-dependence (Catford *et al.*, 2022; Liu & Gaines, 2022; Spake *et al.*, 2023).

In ecology, typology systems are ubiquitous and range from classifications of functional traits into trait syndromes (Sih *et al.*, 2004; Meyer *et al.*, 2022), species into life forms (Raunkiaer, 1905), functional feeding groups (Clausen, 1940), or archetypes (Dunstan, Foster & Darnell, 2011); ecological assemblages into associations (Humboldt & Bonplan, 1807); and ecosystems into ecosystem types (e.g., Wallace, 1876; Wasson *et al.*, 2007; Lyche Solheim *et al.*, 2019) or successional stages (Clements, 1916; Odum, 1969). The concept of associations from plant sociology (reviewed in Whittaker, 1962) nicely portrays the valuable role that these systems can play in theory generation. It motivated the works of Clements (1916) and, in turn, Tansley (1935), which resulted in the now central concept of ecosystems.

1.4.2 Typology systems in limnology

The typology systems we are concerned with here are aquatic typology systems (ATS). Though ATS can encompass all kinds of water bodies, we only consider rivers. Here, *river* refers to all lotic water bodies rather than a specific size class (Czuba & Allen, 2023), and hence, ATS are typology systems that group lotic water bodies into nominal types. Such ATS have a long history in limnology. Melles, Jones & Schmidt (2012) consider the cyclic theory of Davis (1899) to be the foundation of the modern ATS. Davis (1899) proposed the temporal succession of rivers through degrees of maturity towards a stable base grade. Before Clements (1916) popularized the idea of temporal ecological succession, Shelford (1911) identified a spatial succession of fish communities along the courses of rivers. This finding started a wave of longitudinal river zonations based on the community composition of fishes (e.g., Thienemann, 1912; Steinmann, Siegrist & Gams, 1915; Carpenter, 1928; Huet, 1954, 1959; Illies, 1961; McGarvey & Hughes, 2008). Later, limnologists developed ATS based on hydrogeomorphic factors. Leopold & Wolman (1957) divided rivers into braided, meandering, and straight, while Kellerhals, Church & Bray (1976) devised types based on channel patterns, islands, channel bars, and major bedforms. Rosgen (1994) identified river types that differ in the number of channel threads, the entrenchment ratio, the width-depth ratio, and sinuosity. Following the seminal work of Hynes (1975), the role of the catchments surrounding the rivers received more focus. Subsequently, researchers tried to adapt terrestrial ecosystem typology systems to represent the catchment's impact on rivers (e.g., Lotspeich & Platts, 1982; Omernik, 1987; Wasson *et al.*, 2007)

With the advent of computer-based classification, the number of ATS notably increased (Sokal, 1974; Melles *et al.*, 2012). The number of currently available ATS is too high to recount or mention them all explicitly. A review included 81 ATS (Melles *et al.*, 2013), and notable systems are continuously published (e.g., Ouellet Dallaire *et al.*, 2019; McManamay & DeRolph, 2019; Lyche Solheim *et al.*, 2019). We can group ATS into place-independent, regional, and mixed (Figure 1.3)(Melles, Jones & Schmidt, 2014). Place-independent approaches classify river reaches or segments based on selected properties without considering their spatial position or optimizing for spatial contiguity. Regional approaches classify large continuous regions. Catchments, basins, or political borders can determine their boundaries (e.g., Economou *et al.*, 2004; Abell *et al.*, 2008). Mixed approaches combine place-independent and regional approaches. They are often hierarchical, having multiple nested levels. The higher levels are usually regional, and the lower levels are place-independent within the spatial constraints of their region (e.g., Seelbach, 2006).

1.4.3 Using Aquatic Typology Systems

First and foremost, ATS are designed for ecosystem management (Melles *et al.*, 2013). They are applied there to plan water quality monitoring or designate protected areas. They help to determine what types

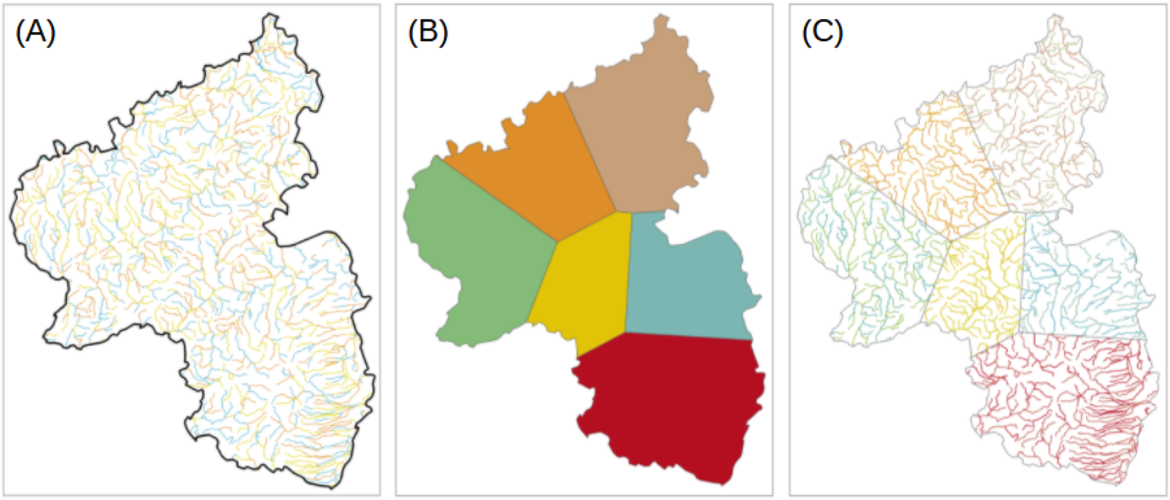

Figure 1.3: Three types of typology systems: (A) place-independent, (B) region-based, and (C) mixed.

of ecosystems need more protection (Mackey *et al.*, 1988), what a desired ecosystem state after successful restoration or protection should be (Vynne *et al.*, 2022), and more generally, they can help to implement type-specific protection or management goals (Keith *et al.*, 2015; Bordt & Saner, 2019). The distribution of sites in networks of protected areas is, therefore, often influenced by ATS, for example, in the Ramsar Convention (Ramsar Convention on Wetlands, 2018) and the Natura 2000 network (Evans, 2012). Different stressors afflict different river types (Leitner *et al.*, 2021), and the responses of the local biota to the same stressor can differ between them (Alahuhta *et al.*, 2017; Pajunen, Kahlert & Soininen, 2020; Denison *et al.*, 2021). Therefore, managers must consider the recipient ecosystem type when planning preventative or restorative measures. The limited niche conservatism of aquatic organisms further makes it necessary to calibrate and validate biotic indices for different ecosystem types (e.g., Szoszkiewicz *et al.*, 2019). Under the assumption that relatively stable equilibrium states exist, typology systems can delineate areas or systems with similar stable states. Historically, this has been used to anticipate the composition of climax communities, which were assumed to be uniform within climatic regions (Clements, 1916; Phillips, 1934). More recently, this idea has formed the bedrock of water quality assessment within the WFD. In the WFD, quality assessments use the concept of reference conditions, i.e., a hypothetical state (biological, chemical, hydromorphological) a river is assumed to be in, barring human intervention (Reynoldson *et al.*, 1997). As pristine states vary between rivers, a single set of reference conditions would be overly simplistic, but because we usually lack data on a river's past and pristine state, we need to refer to similar rivers that still are in such a state. Similar is defined as belonging to the same river type, and all rivers of the same type have the same set of reference conditions. Determining reference conditions with river types is an instance of space-for-time substitution, i.e., inferring a temporal trend at single sites from contemporary observations of spatially distinct sites (Pickett, 1989). While the approach makes strong and potentially unrealistic assumptions (Damgaard, 2019), it is often the only way to estimate past or least impacted states on a broad spatial scale and in a standardized manner. Therefore, further management or study approaches that use space-for-time substitution can benefit from typology systems.

Outside the management context, researchers stratify sampling and analyses with typology systems. Studies might try to sample only one or a predetermined selection of types (e.g., Manfrin *et al.*, 2023) or to sample all types equally or proportionally to their prevalence. Many broad-scale studies stratify their analyses by ecosystem type to identify diverging trends (Pilotto *et al.*, 2020; Posthuma *et al.*, 2020; Lemm *et al.*, 2021; Powell *et al.*, 2022; Schürings *et al.*, 2022; Bogotá-Gregory *et al.*, 2023).

1.4.4 The Broad River Types

To analyze spatial variation in assemblage pesticide sensitivity, we required an ATS covering Europe whose types capture patterns in biotic community composition. For our purposes, we consider place-independent ATS as superior to regional ATS. The former can integrate rivers' dendritic and directed network structure (Benda *et al.*, 2004; Campbell Grant, Lowe & Fagan, 2007; Melles *et al.*, 2014), and their fine spatial scale will be required to capture spatial patterns in sensitivity if fine-scale variation in sensitivity exceeds broad-scale variation, as we argued before. Most place-independent ATS cover comparatively small areas, such as federal- or nation-states (e.g., Mandrak, 1999; Snelder & Biggs, 2002; Briem, 2003; Seelbach, 2006), or are global but have a low resolution (Rosgen, 1994; Ouellet Dallaire *et al.*, 2019). The WFD stimulated a proliferation of national ATS in Europe, requiring member states to devise ATS for the determination of reference conditions (EC, 2000). The WFD is implemented separately by each member state, and while guidance existed (Annex II, EC, 2000), the national ATS differ markedly between member states (Lyche Solheim *et al.*, 2019). While Italy uses 367 classes, Lithuania has five. Lyche Solheim *et al.* (2019) harmonized these disparate ATS into the Broad River Types (BRT). They identified the most common type descriptors and mapped each national type to one of 20 broad types. These types differentiate between catchment size, bedrock geology, altitude, region (Mediterranean or non-Mediterranean), and flow regime (only in the Mediterranean region). Eight rare types were aggregated with the respectively most similar type, leaving twelve broad types. The BRT are the first and currently only pan-European place-independent ATS. Despite the region variable, we categorize the BRT as place-independent rather than mixed because of the simplistic nature of this regionalization (Mediterranean vs. non-Mediterranean). The fast adaptation of the BRT by the research community might be taken as a sign of the high interest in or need for such a system (e.g., Borgwardt *et al.*, 2019; Poikane *et al.*, 2019; Birk *et al.*, 2020; Posthuma *et al.*, 2020; Gerke *et al.*, 2021; Leitner *et al.*, 2021; Lemm *et al.*, 2021; Büttner *et al.*, 2022).

Each classification should be designed for a specific purpose (Loveland & Merchant, 2004; Soranno *et al.*, 2010; Melles *et al.*, 2014). The BRT aim to summarize European water body status trends (Lyche Solheim *et al.*, 2019). They were not primarily intended to capture patterns in the community composition of different biota. However, since they are proposed as a new ATS for the European Nature Information System (EUNIS) inland water typology system (Watson, Arts & Lyche Solheim, 2021), where this assumption is crucial, it might be assumed to hold. Indeed, Lyche Solheim *et al.* implicitly made this assumption during the construction of the BRT (Lyche-Solheim, personal communication), but never tested it formally. Our intended application builds upon this assumption: if different broad river types do not contain different assemblages, differences in sensitivity due to different assemblage compositions are less likely. Therefore, we needed to evaluate the BRT for our purposes. Thus, the contents of the three following papers are twofold: (i) evaluate whether assemblage composition differs between different broad river types, and (ii) evaluate whether the pesticide sensitivity of assemblages differs between broad river types.

1.5 Conducted studies

The research presented in this thesis aims to advance our knowledge of the spatial distribution of assemblage sensitivities of macroinvertebrates towards pesticides at the European scale. Such insights are of interest to basic and applied research, helping to narrow fundamental knowledge gaps (Hutchinsonian Shortfall) and to improve the specificity of ecological risk assessment. The work is divided into three papers. The first two papers, Jupke *et al.* (2022) and Jupke *et al.* (2023), evaluate whether the BRT capture compositional patterns in assemblages of macroinvertebrates, diatoms, fishes, and aquatic macrophytes. In the third paper (Jupke *et al.*, in preparation), we evaluated whether the assemblage sensitivity of macroinvertebrates to pesticides varies among the broad river types. To this end, we predict the concentration that would be hazardous to 5 % of taxa in a community (HC_5) with a hierarchical Species Sensitivity Distribution model.

CHAPTER 2

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

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Published in:
Science of The Total Environment 842 156689.
http://dx.doi.org/10.1016/j.scitotenv.2022.156689

Abstract

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

2.1 Introduction

The European Water Framework Directive (WFD, EC, 2000) is intended to protect and restore freshwater ecosystems in the European Union (EU). Within the WFD each water body is assigned an ecological status class, spanning from high to bad status. The assignment is based on the deviation between the observed conditions and the reference conditions, which are the conditions assumed to prevail under no or minimal disturbance. Due to the large natural variation in physical, chemical, and biological conditions between rivers, reference conditions vary between rivers and between different segments of the same river (Verdonschot, 2000). Typology systems are a method to accommodate this variability. The individual river segments are assigned to river types based on selected abiotic conditions (Pennak, 1971; Melles *et al.*, 2014) The WFD requires that type-specific reference conditions are defined for hydromorphological, physical, chemical, and biological variables, either using a spatially-based reference site network from each river type, hindcasting (e.g., Launois *et al.*, 2011), paleoecology (e.g., Andersen, Conley & Hedal, 2004), or expert judgment (e.g., Poikane *et al.*, 2019). Typology systems commonly apply one of two spatial approaches to allocate rivers to types: regional or segmental. Regional typology systems define large, spatially contiguous areas as types, which are also known as ecoregions (e.g., Abell *et al.*, 2008). This approach is typical for terrestrial typology systems, for example, the Biogeographic Regions (EEA, 2016) are used within the Habitats (92/43/EEC) and the Birds Directive (79/ 409/EEC 1979). When used for lotic freshwater systems, ecoregions fail to account for changes along a river's course (Vannote *et al.*, 1980) or its position within the dendritic river network (Campbell Grant *et al.*, 2007). Nonetheless, regional typology systems have been proposed (Abell *et al.*, 2008; Omernik & Griffith, 2014) and endorsed (e.g., Stoddard, 2004) for freshwater systems. Within the WFD, Illies' Freshwater Ecoregions (Illies, 1978) are used alongside catchment size, altitude, and geology, as a minimum set of criteria to define segmental river types. Segmental typology systems consider individual river segments, which commonly stretch between tributary junctions or confluences. These typologies are more commonly used for freshwater systems since they can account for longitudinal patterns and network position. Recent examples include a global typology system (Ouellet Dallaire *et al.*, 2019), one for the conterminous United States (McManamay & DeRolph, 2019), and one for Europe (Lyche Solheim *et al.*, 2019). To establish reliable biological reference conditions for bioassessment, the variables used to define the types should also influence biotic community composition (Verdonschot & Nijboer, 2004). When this is the case, the relative homogeneity of environmental variables, such as climate, geology, and geomorphology, that exist within each type can engender correspondingly homogeneous biocenoses. The degree to which any typology system meets this expectation can be evaluated by comparing the similarity of biotic communities from the same type (within-type similarity) to that of communities from different types (between-type similarity). For large-scale assessments of biodiversity trends and anthropogenic pressures (henceforth biodiversity monitoring), a typology system is useful if the between-type similarity is low and exceeded by the within-type similarity. For bioassessment, however, the within-type similarity must be high, irrespective of between-type similarity. If the within-type similarity is low, no reliable type-specific conditions can be established and the type must be excluded from the status assessment (EC, 2000). An evaluation of coherence between typology systems and biotic communities is known as biological validation and is a necessary consideration in the construction of a typology system (Melles *et al.*, 2014). Biological validations that compare the variation of biological communities within types to that among types and is common practice for national WFD typology systems (Lorenz, Feld & Hering, 2004; Zahrádková *et al.*, 2005; Sánchez-Montoya *et al.*, 2007; Aroviita *et al.*, 2008; Chaves *et al.*, 2011; Lazaridou *et al.*, 2013), but also regional typology systems (Feminella, 2000) and typology systems outside of Europe (Hawkins *et al.*, 2000; Pero *et al.*, 2019; Ferronato *et al.*, 2021). The national typology systems used in the WFD vary widely among EU countries in the number of river types they discern (between 1 and 367) and the features that are used to define their types (Lyche Solheim *et al.*, 2019). Lyche Solheim *et al.* (2019) combined >$,$1000 national WFD river types into twelve Broad River Types in an attempt to define a generic pan-European river typology system. The aim was to create a typology system that can aggregate type-specific data on ecological status across Europe. Furthermore, the Broad River Types were proposed and quickly adopted as a means for large scale assessments of nutrient thresholds (Poikane *et al.*, 2019; Nikolaidis *et al.*, 2021) and anthropogenic stressors (Birk *et al.*, 2020; Posthuma *et al.*, 2020; Lemm *et al.*, 2021) and are currently being discussed as the basis of the revised European Nature Information System freshwater classification (Watson *et al.*, 2021). However, until now, the Broad River Types have not been biologically validated. In this paper, we evaluated the biological validity of the Broad River Types typology of European freshwater systems and thus whether they are appropriate for bioassessment and biodiversity monitoring. To contextualize the results, we compared the results to those of two other pan-European typology systems that are currently used within the EU legislature: The Biogeographic Regions and Illies' Freshwater Ecoregions. We evaluated the three typology systems by analyzing the within- and between-type similarities of riverine macroinvertebrate communities and determining whether we can derive distinct typical communities for the respective types. Specifically, we aim to answer four research questions:

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

2.2 Methods

2.2.1 Typology Systems

2.2.1.1 Broad River Types

Lyche Solheim *et al.* (2019) derived 20 pan-European river types from the five descriptors catchment size, altitude, geology, region, and flow. As some of the initial 20 types were rare or deemed redundant, they aggregated them into 12 types (see Table 2.1). The first three descriptors are part of the System A approach outlined in Annex II of the WFD and Lyche Solheim *et al.* (2019) largely followed the class thresholds proposed there. While System A includes a region descriptor that recognizes 25 distinct regions throughout Europe, the region descriptor used by Lyche Solheim *et al.* (2019) only separates the Mediterranean and the rest of Europe. Flow is also treated as a binary variable (perennial or temporary/intermittent) and was only applied to rivers in the Mediterranean region. A digital representation of the Broad River Types was published by Globevnik (2019).

Table 2.1: Codes and names of the twelve Broad River Types proposed by Lyche Solheim et al. (2019). The sizes refer to catchment area: very small-small <100 km2, mediumlarge 100–10.000 km2 and very large >10.000 km2. Lowland denotes river segments <200 meters above sea level (m.a.s.l.), mid-altitude 200–800 m.a.s.l. and highland >1.000 m.a.s.l. The geologies describe the prevailing lithological or pedological conditions in the catchments. Catchments are calcareous or siliceous if the respective soil types or minerals cover >50 % of the catchments area. If coverage is between 40 % and 50 % it is classified as mixed. Catchments with >20 % of their area covered by histosols are classified as organic.

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

2.2.1.2 Biogeographic Regions

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

2.2.1.3 Illies' Freshwater Ecoregions

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

2.2.2 Macroinvertebrate data

To evaluate the three typologies, we compiled a database of macroinvertebrate samples from lotic freshwater systems (e.g., rivers, streams, and brooks) throughout Europe (Fig. 2.1). The database consisted of 21 datasets (Appendix, Table 6.1) and included 49.220 distinct sampling sites at which 163.114 samples have been collected. All samples were obtained by fully or partially proportional multihabitat sampling (Appendix, Table 6.1) similar to the AQEM/STAR sampling method (Consortium, 2003). Most samples originate from regional or national biomonitoring campaigns. Despite extensive harmonization efforts, sampling strategies for biomonitoring differ between European countries in terms of sampling effort, sampling device, and habitat selection (Larras & Usseglio-Polatera, 2020). Even though differences between years or streams are commonly larger than between sampling methods (Borisko *et al.*, 2007; Brua, Culp & Benoy, 2011), the differences can bias the samples. We undertook three steps to reduce this bias. First, we removed samples from monitoring data sets that were taken before 2005. Many countries implemented the AQEM/STAR sampling method in 2005, which is deemed to significantly reduce the differences between data sets. Second, all comparisons were conducted at the family level. This was done to reduce differences between sampling schemes (Brua *et al.*, 2011) but also because the evaluation of similarities requires the same taxonomic resolution (Cao & Hawkins, 2011). The family level was the highest taxonomic resolution for which we could achieve broad spatial coverage. However, this taxonomic harmonization likely increased the similarity between samples from the same as well as from different types (Vasconcelos, Melo & Schwarzbold, 2013; Heino, 2014). A higher taxonomic resolution (i.e., genus- or species-level data) could only reduce the similarities but not increase them, since members of the same family can be from different genera or species but the same species cannot be part of multiple families. Lastly, we omitted abundance information and transformed all data to presence-absence. This removed differences that arise from different counting efforts or procedures and is common in analyses of data from different sampling schemes (e.g., de Vries, Kraak & Verdonschot, 2020a). Finding a common transformation was necessary for comparisons (Heino, 2008) and choosing presence-absence maximized the number of samples included. It should be noted that this is not consistent with the requirements of the WFD, which requires abundance data (EC, 2000) and several studies have found a considerable loss of information through the transformation from abundance to presence-absence (e.g., Melo, 2005; Marshall, Steward & Harch, 2006; Vasconcelos *et al.*, 2013). However, different streams (Melo, 2005) and catchments (Heino, 2014) could still be discerned with presence-absence data in previous studies. We conducted two analyses to evaluate the effect of taxonomic and numeric resolutions on the similarities. First, we conducted Mantel tests (Mantel, 1967) for all data sets. In data sets with most observations at the species level and abundance data, we compared the distance matrices of (i) species-level abundance data to genus-level and family-level abundance data as well as genus-level data to family-level abundance data, (ii) abundance to presence-absence at species, genus and family levels and lastly (iii) species abundance to genus and family occurrences as well as genus abundances to family occurrences. We used the Bray-Curtis distance to compute distance matrices for abundance data and Jaccard for presence absence data. For a data set with data from three seasons with species level abundances, we thus conducted 27 Mantel tests. In total, we ran 366 of 594 theoretically possible tests, as many data sets did not have sufficient species-level data or only provided presence-absence data. These tests indicated that little information was lost in the transformations to family level and presence-absence. The distance matrices of different taxonomic levels or numerical resolutions were statistically significantly correlated ($p < 0.05$ for 362 of 366 Mantel tests). A more detailed description of these results is presented in the supplementary materials (see Appendix, section 6.1.4). Second, we repeated the main analyses described below for genus-level data with relative abundances. Like the Mantel tests, they indicated only minor differences between the different resolutions (see Appendix, section 6.1.5). To avoid seasonal trends from affecting the community compositions (Reece *et al.*, 2001; Lorenz & Clarke, 2006; Huttunen *et al.*, 2022), we stratified the samples by season and conducted each analysis for each season separately. We define spring as covering the months March to May, summer covering the months June to August, and autumn covering the months September to November. We did not analyze winter samples (December to February) as there were only few in the data set. Some of the sites were sampled repeatedly over the years. Samples from the same site and season are often very similar (Lorenz & Clarke, 2006; Huttunen *et al.*, 2022), so we only used the most recent sample from each site for every season. Removing samples from before 2005, samples taken in winter, and only using the most recent sample for each site reduced the number of sites and samples to 39.252 (79.7 % remaining) and 56.894 (34.9 % remaining), respectively. We used the Global Biodiversity Information Facility (www.gbif.org) to replace taxon synonyms with accepted names and to assign a taxonomic level to each observation. We restricted observations to the invertebrate classes Insecta, Gastropoda, Bivalvia, Malacostraca, and Arachnida which were observed in all data sets. Oligochaetes were observed in most data sets but rarely determined beyond the class level and thus removed. Within these classes, we further reduced the data to the orders Trombidiformes, Megaloptera, Isopoda, Littorinimorpha, Odonata, Sphaeriida, Hemiptera, Amphipoda, Coleoptera, Trichoptera, Diptera, Ephemeroptera, and Plecoptera. We included families that belong to the polyphyletic taxon Pulmonata (i.e., Acroloxidae, Lymnaeidae, Physidae, Planorbidae) as well as the gastropod family of Valvatidae. Lastly, we removed families that occurred in < 1 % of samples. This was done separately for each season. The final data set contained 95, 104, and 97 families for spring, summer, and autumn, respectively.

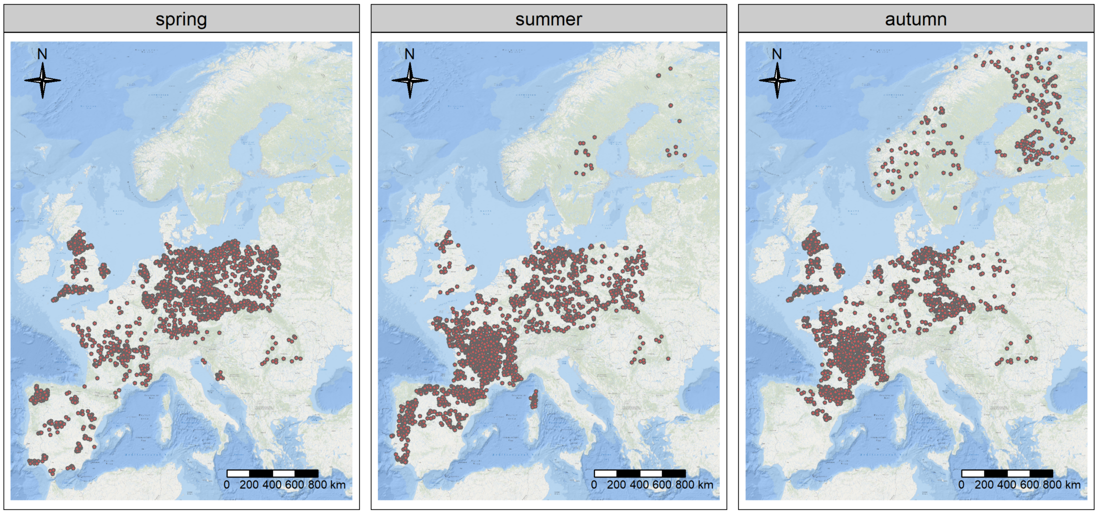

Figure 2.1: The locations of macroinvertebrate sampling sites for each season. All sites shown are least disturbed sites (see text), sampled after 2005, and could be assigned a Broad River Type (see text).

2.2.3 Selection of Sampling Sites

Broad River Types were assigned to macroinvertebrate samples digitally by matching each sampling site with the next river reach in the digital representation of the Broad River Types (Globevnik, 2019). We retained only sites that we could unambiguously assign to a specific river reach. All sites with a distance >500 m to the nearest river reach were omitted from further analyses. These sites were likely located at river reaches that were missing from the digital river network provided by Globevnik (2019). This occurs with very small or intermittent rivers and in flat areas such as coastal plains, where the derivation of river networks from digital elevation models is most error-prone. Removing sites with a distance $> 500\,\mathrm{m}$ to the nearest river reach reduced the number of sites and samples to 25.334 (51.5 % remaining) and 36.694 (22.5 % remaining), respectively. Anthropogenic stressors are suspected to harmonize communities (Petsch, 2016; but see Petsch *et al.*, 2021) and might thus increase the similarity among communities of different types. Therefore, we identified the least disturbed sites (sensu Stoddard *et al.*, 2006) based on the pan-European stressor database created by Lemm *et al.* (2021). The database contains information on seven anthropogenic stressors (extent of urban and agricultural land use in the riparian zone, alteration of mean annual flow and baseflow index, total phosphorus and nitrogen load, and mixture toxic pressure) for over 50.000 sub-catchment units across Europe. We scaled each variable:

$$x_i' = \frac{x_i - min(x)}{max(x) - min(x)}$$

, where x_i' is the scaled variable, x_i the unscaled variable, $min(x)$ the minimum of the unscaled variable, and $max(x)$ the maximum of the unscaled variable. We considered all sub-catchment units as least disturbed that had scores below 0.24 for all seven stressors. The rationale for a threshold of 0.24 as well as summary statistics of least disturbed sites (Appendix, Table 6.2) are provided in the supplementary materials (see Appendix, section 6.1.2). Only least disturbed sites were retained. Sampling sites that were located outside the area covered by Lemm *et al.* (2021) were removed, except for data set 21 (Appendix, Table 6.1) which only consisted of samples from least disturbed sites. The final selection included 6.965 sites (14.1 % remaining) and 9.976 samples (6.1 % remaining).

2.2.4 Evaluation of Typologies

We only included those types in the analyses, for which we had at least 15 samples from least disturbed sites (Appendix, Fig. 6.3 and 6.4). Following this criterion, all twelve Broad River Types were covered with spring and summer samples and only RT12 was omitted for autumn samples, four of eleven Biogeographic Regions were covered for all seasons, and one for two seasons. We included ten of twenty-five Illies' Freshwater Ecoregions for all seasons, two for two seasons, and three for one season. After removing samples from types that we did not analyze, 6890 sites and 9850 samples remained. The distribution of samples between seasons and types is shown in Tables 6.3 to 6.5 (Appendix).

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

2.2.5 Software

All computations were conducted in the R Statistical Environment v.4.0.3 (R Core Team, 2023). Data were prepared using data.table 1.14.0 (Dowle & Srinivasan, 2023), tidyverse packages (Wickham *et al.*, 2019), taxize 0.9.98 (Chamberlain & Szöcs, 2013; Chamberlain *et al.*, 2020) and parallelDist (Eckert, 2022). Geospatial analyses were conducted using sf (Pebesma, 2018). ANOSIMs were computed with the vegan R package (Oksanen *et al.*, 2022). The CS was computed with an R-function that is available as supplementary material (Appendix, section 6.1.8). Indicator and typical communities were derived with indicspecies (Cáceres & Legendre, 2009). Figures and maps were created with ggplot2 (Wickham, 2016), ggdist (Kay, 2023), colorspace (Zeileis *et al.*, 2020), and tmap (Tennekes, 2018). All R scripts are available in the github repository https://github.com/ JonJup/freshwater-typologies-mzb.

2.3 Results

All three typology systems delineated distinguishable biotic communities that were more similar within than between types (for all ANOSIM and CS: $p < 0.05$; Fig. 2.2). However, within-type similarities were often only marginally higher than between-type similarities (Appendix, Fig. 6.11). The difference was most pronounced in Illies' Freshwater Ecoregions ($\overline{R_{ANOSIM}} = 0.27$; $\overline{CS} = 0.08$), followed by the Broad River Types ($\overline{R_{ANOSIM}} = 0.19$; $\overline{CS} = 0.05$) and the Biogeographic Regions ($\overline{R_{ANOSIM}} = 0.07$; $\overline{CS} = 0.03$). The performance varied across seasons. The Broad River Types were a better classification of the summer samples than of the spring or autumn samples, and Illies' Freshwater Ecoregions performed worse in spring than in summer and autumn (Fig. 2.2).

The within-type similarity varied considerably between the Broad River types (Fig. 2.3). As a general trend, we observed that mid- and high-altitude river types (RT6–10) have higher within-type similarity than low-altitude river types (RT1–5). Similarities also varied across seasons but without a general pattern.

We were able to derive distinct indicator taxa and typical communities for the individual types of all three typologies. On average, the indicator taxa were more indicative (higher mean IndVal) than those derived from random site combinations (Fig. 2.4A) and the number of indicator taxa was larger (Fig. 2.4B). The

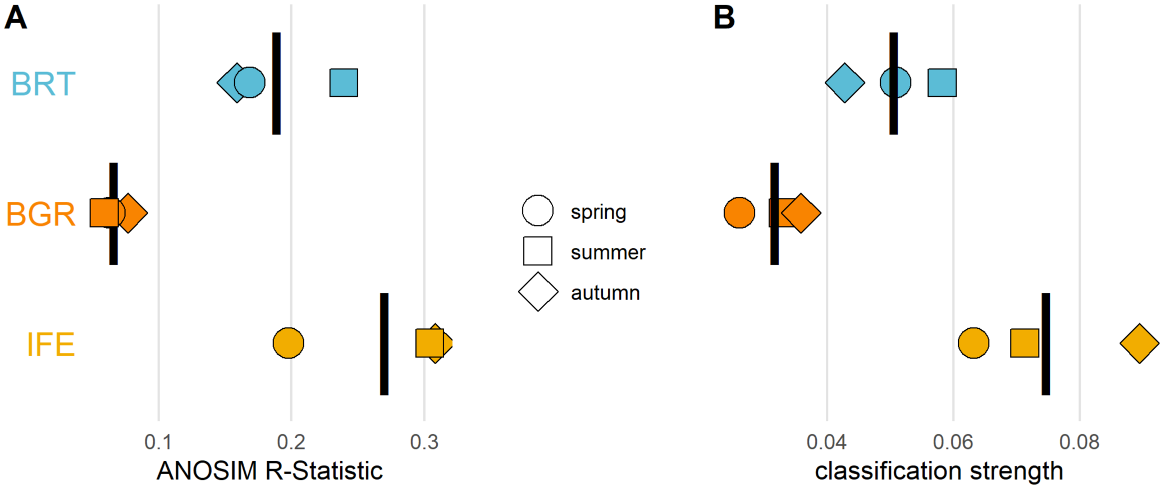

Figure 2.2: Comparison of within-type and between-type. In both panels, larger values imply a larger difference between within-type and between-type similarity and hence a better classification performance. Y-axis and colors indicate the typology system: the Broad River Types (BRT), Biogeographic Regions (BGR), and Illies' Freshwater Ecoregions (IFE). The shapes indicate the season (circle = spring, square = summer, and diamond = autumn). The vertical black lines are mean values across seasons. (A) Results of the ANOSIM; (B) results of classification strength analysis.

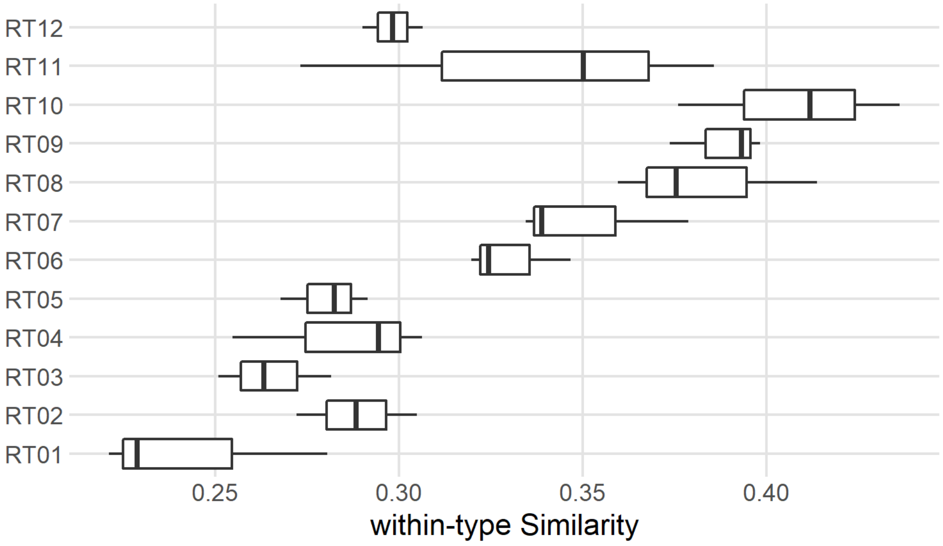

Figure 2.3: The within-type similarity of Broad River Types. Each boxplot summarizes the values for the three seasons (except for RT12 where only spring and summer were analyzed). See Lyche Solheim et al. (2019) or Table 2.1 for a description of the types.

indicator families of Biogeographic Regions and Illies' Freshwater had similar indication power (mean InDVal ($\overline{Indval} = 0.49$ for both). The indicator families of the Biogeographic regions were slightly more indicative in spring and autumn whereas Illies' Freshwater Ecoregions' indicator families were more indicative in summer. Indicator values for the Broad River Types were lower in every season ($\overline{Indval} = 0.38$). However, the number of families that were statistically significant indicators was consistently higher in the Broad River Types than in the other two typology systems. For all three typology systems, the number of indicators was highest in autumn. Lists of indicator taxa for each season and typology system are available in the supplementary materials.

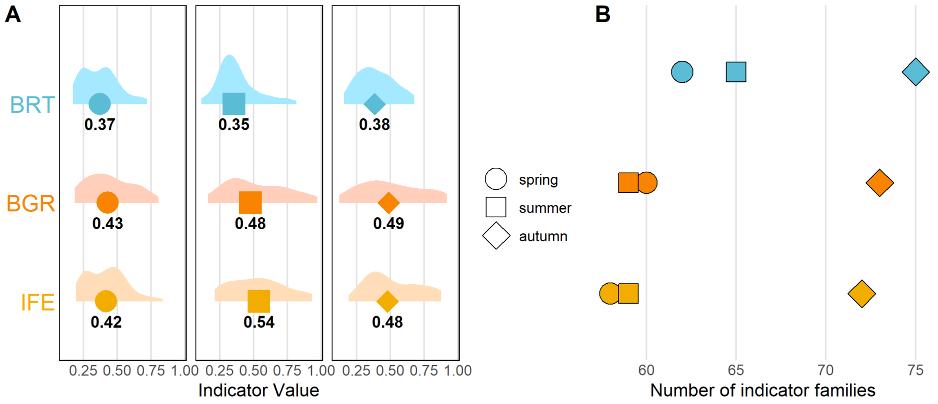

Figure 2.4: Indicator taxa for the Broad River Types (BRT), the Biogeographic Regions (BGR), and Illies' Freshwater Ecoregions (IFE). (A) Distribution of indicator values. Values can range between 0 and 1, where 1 indicates a perfect indicator taxon. The points within the density curves highlight the median, which is also provided as a number. Three panels show the three different seasons (spring, summer, and autumn), which are also highlighted by the symbol of the median. (B) The number of indicator families. Point shapes indicate seasons and point colors the typology systems.

All typical communities were more distinct from each other than for random combinations of sites ($p < 0.01$). The typical communities did not show strong seasonal trends. The mean similarity was always lowest in Illies' Freshwater Ecoregions (mean similarity of 0.40), followed by the Broad River Types (0.48) and the Biogeographic regions (0.50) (Fig. 2.5). Lists of the typical communities are available as supplementary material (Appendix, section 6.1.7) and in Appendix Figures 6.12 to 6.14.

2.4 Discussion

2.4.1 Coherence of biological communities

The three pan-European freshwater typology systems considered here did delineate more distinguishable biotic communities than random partitions of the samples. Within-type similarity always exceeded between-type similarity, but only by a small margin. The between-type similarities of all typology systems indicate

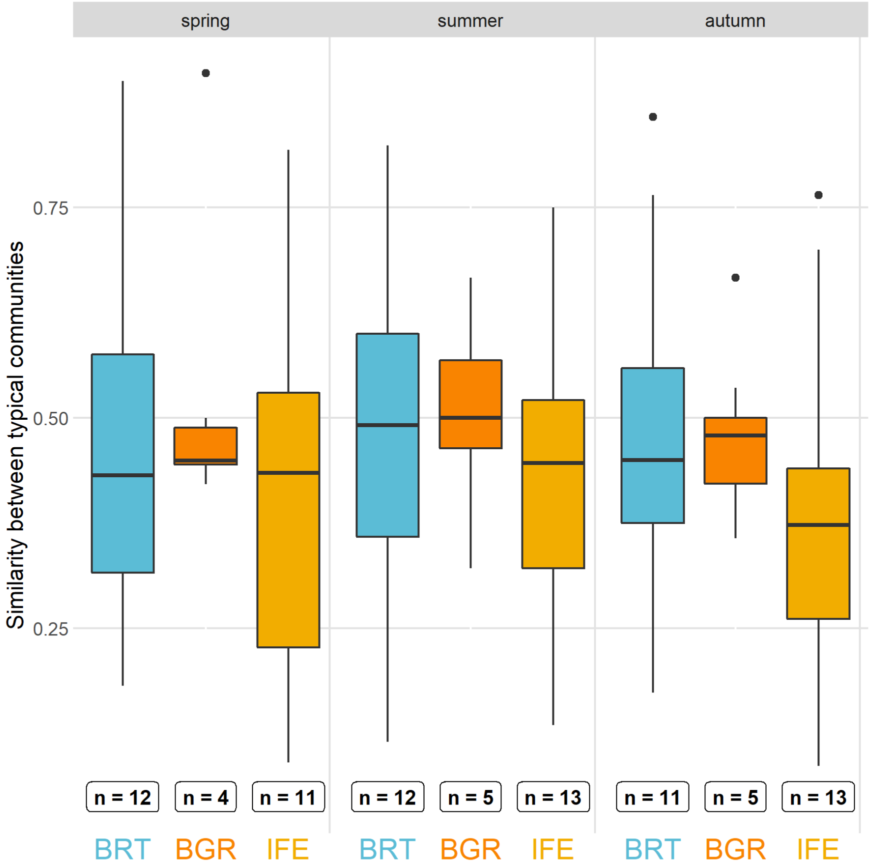

Figure 2.5: Jaccard similarities between typical communities for the Broad River Types (BRT), Biogeographic Regions (BGR), and Illies Freshwater Ecoregions (IFE). A similarity of 1 implies an identical community, while a similarity of 0 implies no shared taxa. The three horizontally ordered panels show different seasons (spring, summer, and autumn). The n below the boxplots is the number of individual types in the comparison.

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

Our third question was whether the Broad River Types are better suited for bioassessment and biodiversity monitoring than Illies' Freshwater Ecoregions or the Biogeographic Regions. Even though we regard all typologies as suitable for biodiversity monitoring and none as suitable for bioassessment, there were noticeable differences between them. In a direct comparison, the Broad River Types performed better (higher CS and ANOSIM R) than the Biogeographic Regions but both performed considerably worse than Illies' Freshwater Ecoregions. Therefore, we also negate the third research question. We were able to derive indicator taxa and typical communities for all three typologies and can thus confirm our fourth research question. There were more indicator taxa with higher mean indicator values for river typologies than those of random site combinations. The indicator values were generally in line with previous studies (Bonada *et al.*, 2006; Heino & Mykrä, 2006; Sánchez-Montoya *et al.*, 2007; Banks, Li & Herlihy, 2007). The typical communities were less similar than would be expected by chance, indicating a change in the most common families among types.

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

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

2.4.2 Data constraints

Due to the taxonomic resolution of the initial data sets and the varying sampling approaches, we conducted all analyses at the family level. Analyses at the genus or species level would have included more taxa, which means more discriminating entities and thus potentially more distinct assemblages. In the analysis of Moog *et al.* (2004), higher taxonomic resolution led to more distinct ecoregions. Similarly, Verdonschot (2006b) showed that a small improvement in classification strength was noticeable between ‘best-available’ (mostly species and genus) and family-level data on a pan-European scale. This improvement is plausible since responses to environmental conditions are determined by traits, which are captured most accurately at detailed (species or individual) taxonomic resolution (Poff, 1997; Wong & Carmona, 2021). At the same time, community composition is influenced by non-environmental factors like biotic interactions, dispersal, and stochasticity (Leibold *et al.*, 2004). If responses of congeneric species are more similar to each other than to those of more distantly related species (e.g., Hynes, 1975; Marchant, Barmuta & Chessman, 1995), using genus- or family-level data might reduce this “noise” (Bowman & Bailey, 1997). However, the degree to which species niches are determined at the family level likely depends on the degree to which speciation within the family was sympatric or allopatric (Cranston, 1990; Dolédec, Chessel & Gimaret-Carpentier, 2000). Hawkins *et al.* (2000) note that across taxa groups and typologies, a higher taxonomic resolution can occasionally even reduce classification strength. This notion is supported by our genus-level analyses and Mantel tests (Appendix, Fig. 6.5) and by many studies showing that differences between differently resolved data sets are usually small (e.g., Furse *et al.*, 1984; Rutt, Weatherley & Ormerod, 1990; Bowman

& Bailey, 1997; Waite *et al.*, 2004; Melo, 2005; Feio, Reynoldson & Graça, 2006; Heino & Soininen, 2007; Heino, 2008; Godoy *et al.*, 2019). Yet, some studies also find contrasting patterns, suggesting that higher taxonomic resolution confers significantly more information (e.g., Heino, 2014). Marchant *et al.* (1995) propose that the necessary degree of taxonomic resolution decreases with increasing spatial scale, with family-level data being sufficient for analyses that cover multiple catchments. This concurs with Moog *et al.* (2004), and if correct, would mean that family-level data is sufficient for our analysis.

The second measure we took to reduce the variation introduced by the varying sampling strategies was the transformation to presence-absence. Several studies have demonstrated that results can differ between presence-absence and abundance data (e.g., Thorne, Williams & Cao, 1999; Melo, 2005; Marshall *et al.*, 2006; Heino, 2008; Vasconcelos *et al.*, 2013). In comparison to abundance data, binary data put less weight on highly abundant taxa and more on rare ones, placing equal weight on each taxon, instead of each individual. The focus of the analysis thus moves from changes in relative abundances to changes in occurrences, which likely is the more important component of variation at the large spatial scales we considered in this study (Anderson *et al.*, 2005). How large the difference between presence-absence and abundance data is, thus likely depends on the spatial scale of the study. All of the above studies have considered smaller spatial scales (often the catchment scale) and might therefore overestimate the deviation for the spatial scale of the present study. This is in line with the finding that different basins can be differentiated with family-level presence-absence data (Heino, 2014). In conclusion, using species-level and abundance data would likely affect our results. To which degree cannot conclusively be determined until such data becomes available but given the arguments above and the results of the Mantel tests as well as the genus-level analysis, we are confident that our conclusions would hold.

2.4.3 Next steps for freshwater typologies

We showed that currently available pan-European typology systems require improvements when they are used to define bioceonotic reference conditions. This is not a fault in their construction, as they were not primarily derived for this purpose. However, we believe they might serve as a starting point for typology systems that can be used to this end. Hence, we propose three modifications that might improve the Broad River Types' capacity to delineate coherent and distinct biotic communities. First, the combination of regional and segmental typology systems would likely improve the typologies fit to large-scale ecological patterns. Regional and segmental systems capture important but distinct scales of variation: variation among large geographic areas and longitudinal changes along the river's course, respectively. When combined, regions spatially constrain river types. Instances of the same Broad River Type are thousands of kilometers apart. At such large spatial scales, dispersal limitation is a crucial determinant of community composition (Tonkin *et al.*, 2018). If species cannot reach favorable sites, due to historical or anthropogenic dispersal barriers (Leibold, Economo & Peres-Neto, 2010; Belletti *et al.*, 2020) or due to the sheer distance between sites, within-type similarity decreases. Such spatial structuring of benthic macroinvertebrate communities has already been observed at smaller spatial scales (e.g. , Mykrä, Heino & Muotka, 2007; Astorga *et al.*, 2012), indicating the potential benefit of spatially constrained types. The WFD System A typology system includes such a spatial constraint through the ecoregion descriptor. The Broad River Types, however, only differentiate between Mediterranean and non-Mediterranean regions. Including more elaborate regional descriptors such as Illies' Freshwater Ecoregions, the Hydroecoregions (Wasson *et al.*, 2007), the Biogeographic Regions, the Freshwater Ecoregions of the World (Abell *et al.*, 2008), or the Environmental Zones of Europe (Metzger *et al.*, 2012), would spatially constrain types and hence help to integrate dispersal limitations into the typology system. Problems can arise for rivers that run along or across ecoregion borders (Lazaridou *et al.*, 2013) and using all types that result from such a combination produces too many types to be useful. Therefore, ways to optimally aggregate the combined types should be derived in future work.

Second, intermittent rivers and ephemeral streams (IRES) are common throughout Europe (Datry, Larned & Tockner, 2014; Stubbington *et al.*, 2017; Messager *et al.*, 2021) and their prevalence is projected to increase with climate change (Jaeger *et al.*, 2014). Intermittent flow regimes increase the importance of dispersal and network connectivity (Cid *et al.*, 2020), reduce the importance of species sorting, and hence decrease the utility of purely environmental typology systems. The Broad River Types do not adequately account for this distinct and widespread river type by only recognizing them in the Mediterranean type. Simultaneously, they fail to capture the diversity of rivers in the Mediterranean region by aggregating them into two river types. The disregard for IRES mirrors the general lack of recognition for very small rivers (catchment size < 10 km^2) in the WFD (Stubbington *et al.*, 2018) and their public undervaluation (Armstrong *et al.*, 2012). This omission of very small rivers also neglects springbrooks, which are often distinct from nearby rhithral streams (Barquín & Death, 2006; Lusardi *et al.*, 2016).

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

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

2.4.4 Conclusion

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

CHAPTER 3

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

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Published in:
Science of The Total Environment 896 165081.
http://dx.doi.org/10.1016/j.scitotenv.2023.165081

Abstract

Typology systems are frequently used in applied and fundamental ecology and are relevant for environmental monitoring and conservation. They aggregate ecosystems into discrete types based on biotic and abiotic variables, assuming that ecosystems of the same type are more alike than ecosystems of different types with regard to a specific property of interest. We evaluated whether this assumption is met by the Broad River Types (BRT), a recently proposed European river typology system, that classifies river segments based on abiotic variables, when it is used to group biological communities. We compiled data on the community composition of diatoms, fishes, and aquatic macrophytes throughout Europe and evaluated whether the composition is more similar in site groups with the same river type than in site groups of different river types using analysis of similarities, classification strength, typical species analysis, and the area under zeta diversity decline curves. We compared the performance of the BRT with those of four region-based typology systems, namely, Illies Freshwater Ecoregions, the Biogeographic Regions, the Freshwater Ecoregions of the World, and the Environmental Zones, as well as spatial autocorrelation (SA) classifications. All typology systems received low scores from most evaluation methods, relative to predefined thresholds and the SA classifications. The BRT often scored lowest of all typology systems. Within each typology system, community composition overlapped considerably between site groups defined by the types of the systems. The overlap tended to be the lowest for fishes and between Illies Freshwater Ecoregions. In conclusion, we found that existing broad-scale river typology systems fail to delineate site groups with distinct and compositionally homogeneous communities of diatoms, fishes, and macrophytes. A way to improve the fit between typology systems and biological communities might be to combine segment-based and region-based typology systems to simultaneously account for local environmental variation and historical distribution patterns, thus potentially improving the utility of broad-scale typology systems for freshwater biota.

3.1 Introduction

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

Typology systems are models (Goodwin, 1999; Loveland & Merchant, 2004) that represent their subjects as members of discrete groups (types). In ecosystem typology systems, ecosystems are the subject and they are grouped according to their biotic and abiotic conditions. One simple, illustrative example is grouping rivers by the mean altitude of their catchment into lowland, mid-altitude, and highland rivers. Another example is grouping river segments longitudinally by the fish species that commonly occur in them, into the trout, grayling, barbel, and bream zones (Huet, 1949). Regarding each individual ecosystem as an instance of its type allows us to draw inferences and make predictions under a set of assumptions. An important assumption is that ecosystems of the same type are more similar to each other than to ecosystems of different types, with respect to a specific property of interest. Each typology system is optimized for one property (e.g., delineating homogeneous communities of mammals) and might fail to delineate meaningful patterns in other properties (e.g., background nitrogen concentration) (Loveland & Merchant, 2004).

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

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

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

Here, we aim to evaluate the fit between the BRT and the community composition of diatoms, fish, and aquatic macrophytes. We evaluated the coherence between community composition and the BRT with analysis of similarities, classification strength, typical species analyses, zeta diversity analyses. To contextualize the BRT's performance, we compared it to those of four region-based typology systems (Illies Freshwater Ecoregions (IFE, Illies, 1978), Biogeographic Regions (BGR, Evans, 2005)), Freshwater Ecoregions of the World (FEoW, Abell *et al.*, 2008), and Environmental Zones (EnZ, Metzger *et al.*, 2005)), and to spatial autocorrelation (SA) classifications. The SA classifications are naïve typology systems, consisting of simple geometric forms spread over Europe (Fig. 3.1). We aim to answer two questions: (Q1) Do the site groups delineated by the BRT host communities of diatoms, fish, and macrophytes whose composition is more similar within than among types? (Q2) Are the BRT a better classification of diatom, fish, and aquatic macrophyte communities, with regard to their composition, than the four region-based approaches?

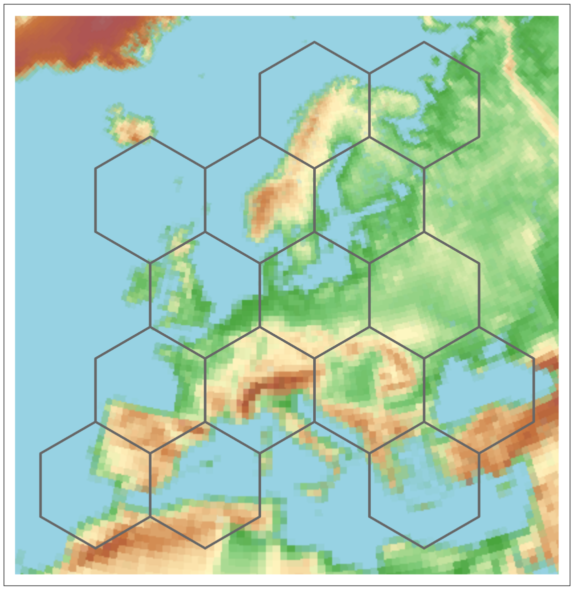

Figure 3.1: Hexagonal spatial autocorrelation (SA) classification with 15 cells. Each cell is a separate type. The SA classification is a naïve approach to classification capturing spatial autocorrelation but uninformed by ecologically relevant variables.

3.2 Methods

3.2.1 The Typology Systems

The BRT reduce the number of national WFD river types (1247) to a workable set, which can be used to compare water body status data across Europe (Lyche Solheim *et al.*, 2019). National types were combined based on altitude, catchment size, geology, region, and flow regime. Rare types were merged with the most similar type. The final BRT categorize 12 river types, as detailed in Table 3.1. We utilized the digital version of the BRT published by Globevnik (2019).

Table 3.1: Codes and names of the twelve Broad River Types proposed by Lyche Solheim et al. (2019). The sizes refer to catchment area: very small-small <100 km2, mediumlarge 100–10.000 km2 and very large >10.000 km2. Lowland denotes river segments <200 m above sea level (m.a.s.l.), mid-altitude 200–800 m.a.s.l. and highland >800 m.a.s.l. The geologies describe the prevailing lithological or pedological conditions in the catchments. Catchments are calcareous or siliceous if the respective soil types or minerals cover >50 % of the catchments area. If coverage is between 40 % and 50 % it is classified as mixed. Catchments with >20 % of their area covered by histosols are classified as organic. Mediterranean rivers are treated separately. For them the flow regime (perennial/temporary) is considered additionally.

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

The typology systems we used as reference points are shortly introduced below (for details and maps Appendix, Section 6.2.1). All reference typologies are region-based typologies as no other segment-based typologies are available for all of Europe. IFE divide between 25 regions based on the distribution of macroinvertebrate fauna, the BGR partition Europe into 12 regions based on their potential natural vegetation, the FEoW are a global system that classifies catchments based on their fish faunas, and the EnZ are 12 zones derived from principal component analysis of 22 environmental variables.

We created classifications that capture the spatial autocorrelation inherent in community composition data but are otherwise uninformed by biogeographic transition zones. These spatial autocorrelation (SA) classifications were created by laying regular, grids over Europe (Fig. 3.1), where each grid cell represents one type. We created four grids differing in cell size and form. The first SA classification has 15 hexagonal cells (Fig. 3.1), the second 36 hexagonal cells, the third 12 square cells, and the fourth 33 square cells. We chose 15 types as this approximately matches the average number of types from the other typology systems. The results of the four SA classifications agreed qualitatively and hence only the results of the 15 cell hexagonal classification are shown in the results section. Maps of and results for the additional SA classifications are provided in the supplementary information.

3.2.2 Data preparation

We compiled 21, 23, and 25 datasets for diatoms, fish, and macrophytes, respectively (Fig. 3.2) and Appendix, Tables 6.6 to 6.8). All sampling was conducted according to EU norms (EN 13946, EN 14407, and EN 15708 for diatoms, EN 14011 for fishes, and EN 14184 for macrophytes). We harmonized the datasets by transforming all data to presence-absence. This harmonization was necessary because abundance information was included in different formats or missing in the original datasets. However, analyses of the community structure (i.e., using abundance data) might come to different conclusions (Mueller, Pander & Geist, 2013) than ours. The samples were taken between 2000 and 2021, 1986 and 2021, and 2006 and 2021 for diatoms, fishes, and macrophytes respectively. The composition of communities has likely changed during these periods (Tison-Rosebery *et al.*, 2022) which might bias our results as within-type similarity is decreased by temporal fluctuations. However, the magnitude of this bias is small and it is unlikely to change our results quantitatively (see Appendix, section 6.2.3 for analysis). We reduced the effect of seasonal variations in community composition (e.g., Aberle & Wiltshire, 2006) by only including samples taken in summer. We use a broad definition of summer (May to September) to account for latitudinal differences in seasonal timing and phenology (Woods, Kaz & Giam, 2022; Dunn *et al.*, 2023). For each sampling site, we only used one sample (the most recent), since repeated measurements can spuriously increase the similarity within types (Fig. 3.3).

The diatom data required extensive harmonization because of varying nomenclatures, identification errors

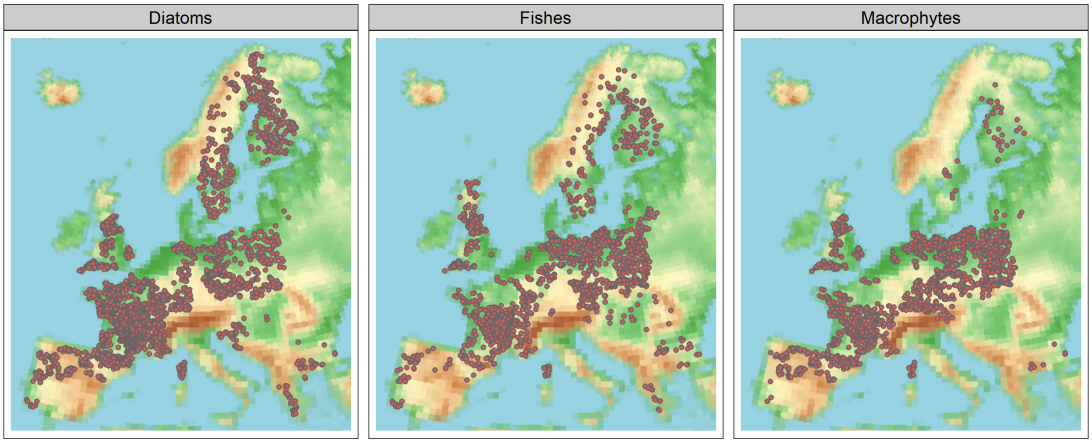

Figure 3.2: Spatial distribution of sampling sites for diatoms, fishes, and aquatic macrophytes. The map only shows sampling sites that we deemed least disturbed and could assign unambiguously to one stream in the digital representation of the Broad River Types. The spatial distribution of samples is driven by data availability and the extent of anthropogenic impacts and hence not balanced.

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

To prevent anthropogenic stressors from harmonizing communities across river types (McKinney & Lockwood, 1999; Petsch, 2016), we analyzed only the least disturbed sites (Stoddard *et al.*, 2006) (Fig. 3.3). We identified the least disturbed sites with a European database including the stressors total phosphorus and nitrogen load, alterations of mean and base flow, mixture toxic pressure, and extent of agricultural and urban land use at a sub-catchment scale (Lemm *et al.*, 2021). We standardized each stressor to the range from 0 to 1 and categorized all sub-catchment units where all scores were ≤ 0.24 as least disturbed (see Appendix, section 6.2.4 for rationale). In addition, we removed samples with ≤ 10 diatom species, ≤ 2 fish or macrophyte species, because we took the low richness as an indicator of a disturbance not covered by the approach described above. The thresholds are adjusted to average species richness of communities, which was notably higher for diatoms than for fish or macrophytes. Lastly, we visually validated the as-

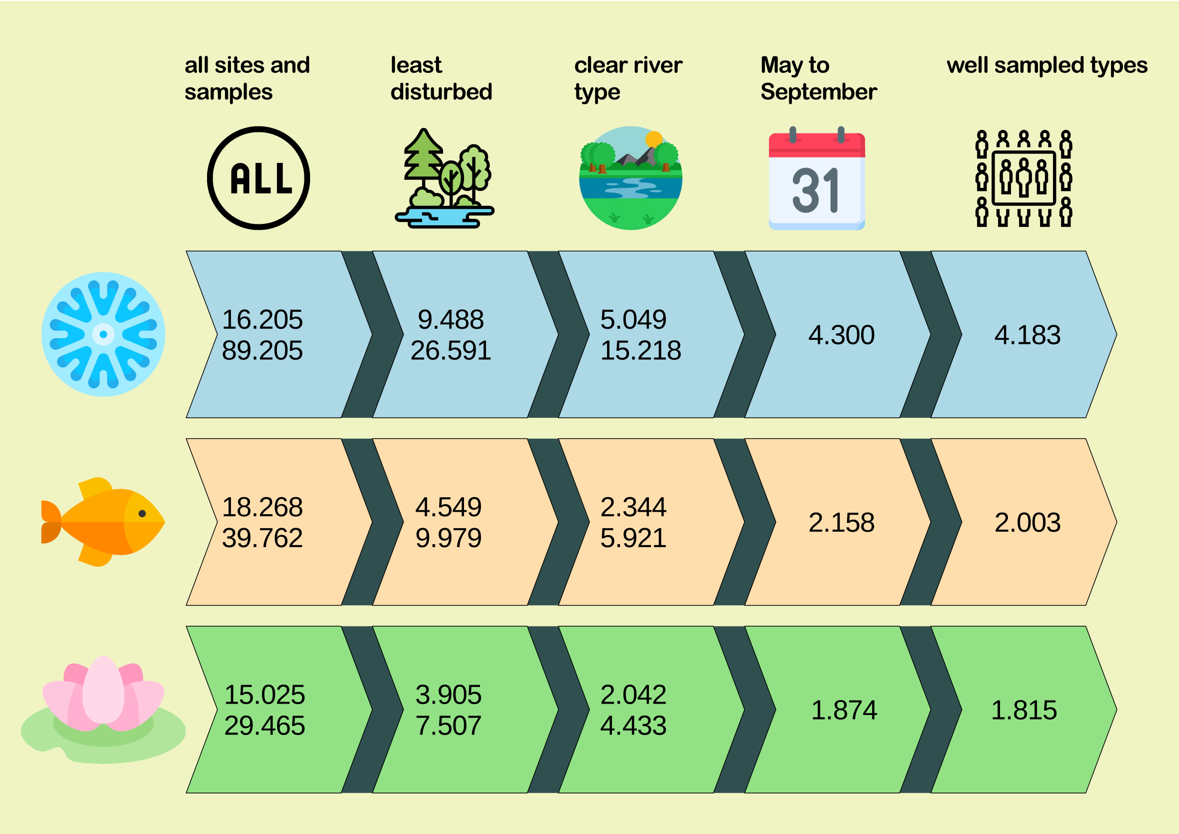

Figure 3.3: Overview of data processing and the resulting number of sites and samples. The rows are the taxonomic groups diatoms, fishes, and macrophytes. Within each box the upper number gives the number of sites and the lower is the number of samples. The first column gives the numbers before data processing. The second column gives the numbers after only least disturbed and not impoverished sites are retained. The third column provides the numbers after removing samples that could not unambiguously assigned a specific broad river type. The fourth column gives the number of samples after only the most recent sample and only samples between May and September were retained. As only one sample is kept per site, the number of samples and sites is the same. The last column gives the number of sites after those that were in ecosystem types with <20 samples were removed.

signment of samples to BRT by comparing the position of the sampling sites with the digital river network and the CaroDB.Positron base map through the mapview R package (Appelhans *et al.*, 2021) and removed samples from erroneous assignments. As a result of data availability and our data preparation the spatial distribution of samples in the analyzed dataset is not fully balanced. Some contiguous areas (e.g., parts of western Germany and the Netherlands, as well as eastern United Kingdom) have a high proportion of agricultural and urban land use and are consequently underrepresented in the final selection.

3.2.3 Evaluation of typologies

For each taxonomic group, we evaluated the river types for which we had at least 20 samples from the respective group (see Appendix, section 6.2.5) using analysis of similarities (ANOSIM, Clarke, 1993), classification strength (CS, Van Sickle, 1997), typical species analysis (TSA, Jupke *et al.*, 2022), and the area under the zeta diversity decline curve ($AUC\zeta$), a method proposed in this paper.

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

$\zeta_1 = 1$ and then computing the area under the curve that is created by drawing a line through all zeta diversities. Higher $AUC\zeta$ values imply a slower decline, i.e., more similar communities and thus a better typology system.

To evaluate the performance of individual typology types, we analyzed the type-specific classification strengths, TSA dissimilarities, and $AUC\zeta$. ANOSIM does not provide type-specific results and hence was omitted here. The type-specific CS were the difference between within-type similarity of a single type and between type similarity, which always considered all types. In contrast to the CS computed for the complete typology systems, this metric was not adjusted for sample size. For TSA dissimilarity, we computed the median dissimilarity of each type toward all others. For $AUC\zeta$, we used the zeta diversities computed for each type. For each taxon, typology system, and test, we scaled the results by their range. The best-performing type in each combination of typology system and taxonomic group had a range score of 1, while the worst-performing type had a range score of 0. Each type received nine range scores: one for each combination of taxon and test. For each type, we added these nine range scores. The highest possible range score is a nine, indicating that a type performed best for all taxonomic groups and tests. The worst possible range score is a zero, implying that a given type performed worst of all types in its typology system for all taxonomic groups and tests. Only types that were tested for all three taxa were considered for this analysis.

All analyses were conducted with R 4.2.2 (R Core Team, 2023). Data were prepared with data.table 1.14.2 (Dowle & Srinivasan, 2023), tidyverse 1.3.2 (Wickham *et al.*, 2019), and sf 1.0–9 (Pebesma, 2018). Analyses were conducted with zetadiv 1.2.0 (Latombe *et al.*, 2018), vegan 2.6–2 (Oksanen *et al.*, 2022) and parallelDist 0.2.6 (Eckert, 2022). Maps and figures were created with ggplot2 3.4.0 (Wickham, 2016), wesanderson 0.3.6 (Ram & Wickham, 2018), maptiles 0.4.0 (Giraud, 2022), and tmap 3.3–3 (Tennekes, 2018).

3.3 Results

The diatom data set comprised 1110 species and species complexes, from 176 genera and 60 families at 4183 least disturbed sites. The most common species/complexes were the *Achnanthidium minutissimum* complex (3835 occurrences, 92 % of samples), the *Gomphonema parvulum* complex (2894 occurrences, 69 % of samples), and *Planothidium lanceolatum* (2734 occurrences, 65 % of samples). The average species/complex occurred in 105.7 ± 340.6 (arithmetic mean ± standard deviation) samples and the average diatom species/complex richness per sample was 28.1 ± 11.0. The 265 singletons (24 % of the species/complexes) were omitted from further analyses. 87 % of observations had species/complexes-level information, > 99 % genus and family-level observations. Observations that lacked genus-level data were largely observations of undetermined Achnanthales (< 0.1 % of total observations). The fish data included 105 species from 69 genera and 21 families at 2003 least disturbed sites. The most common species were *Salmo trutta* (1208 occurrences, 60 % of samples), *Barbatula barbatula* (1029, 51 % of samples), and *Gobio gobio* (893, 45 % of samples). The mean number of occurrences was 140 ± 253. The average fish species richness was 7.3 ± 4.3. 17 species (16 % of species) were singletons and thus removed from subsequent analyses. 99 % of observations were at the species level. Most observations that were lacking species-level data were of Petromyzontidae (0.5 %) or *Lampetra* sp. (0.5 %). Lastly, macrophyte data included 299 species, 131 genera, and 67 families at 1815 least disturbed sites. The most common species were *Fontinalis antipyretica* (719 occurrences, 40 % of samples), *Lemna minor* (677 occurrences, 38 % of samples), and *Leptodictyum riparium* (567 occurrences, 32 % of samples). The mean number of occurrences was 44.1 ± 97.8. The average macrophyte species richness was 7.3 ± 4.2. The 63 singletons (21 % of taxa) were removed from further analyses. 98 % of observations had information at the species level. Callitriche, Carex, and Rorippa (all <0.01 %) are most frequent among observations without species-level data.

For all three taxonomic groups, the results of the different SA classifications differed minimally and without a discernible pattern. Below, we present the results of the 15-type hexagonal SA classification (see Appendix, section 6.2.6 for the results of the other SA classifications). For diatoms and fish, all ANOSIMS indicated weak separation between the types ($R < 0.5$, Fig. 3.4) and most typology systems performed similar to the SA classifications. For macrophytes, IFE, FEoW, and EnZ were good classifications ($R > 0.5$) and all typology systems outperformed the SA classifications, though the BRT only slightly. CS was low (< 0.1) for all analyses, except for IFE and fish (Fig. 3.4). The SA classification outperformed most typology systems for fish and macrophytes and always performed better than the BRT. The dissimilarity between TSA communities was lowest in macrophytes but the SA model outperformed most combinations of taxonomic group and typology systems, including the BRT for all the taxonomic groups. The complete list of typical communities is available in the accompanying Zenodo folder (Jupke, 2023). The median $AUC\zeta$ was lowest for macrophytes and the median $AUC\zeta s$ of the SA classification generally had a similar magnitude as those of the actual typology systems. The BRT's $AUC\zeta$ was always lower than that of the SA classifications. The typologies performance relative to the SA classifications and the best performing typology systems for each evaluation method and taxonomic groups are shown in Fig. 3.5.

The observed type-specific scores ranged from 6.6 (type *boreal* from BGR) to 0.3 (type *Mediterranean* from BGR) with a mean score of 3.1 (Fig. 3.6). Overall, we observed that the high latitude and altitude types tended to perform better than low latitude types across typology systems and taxa.

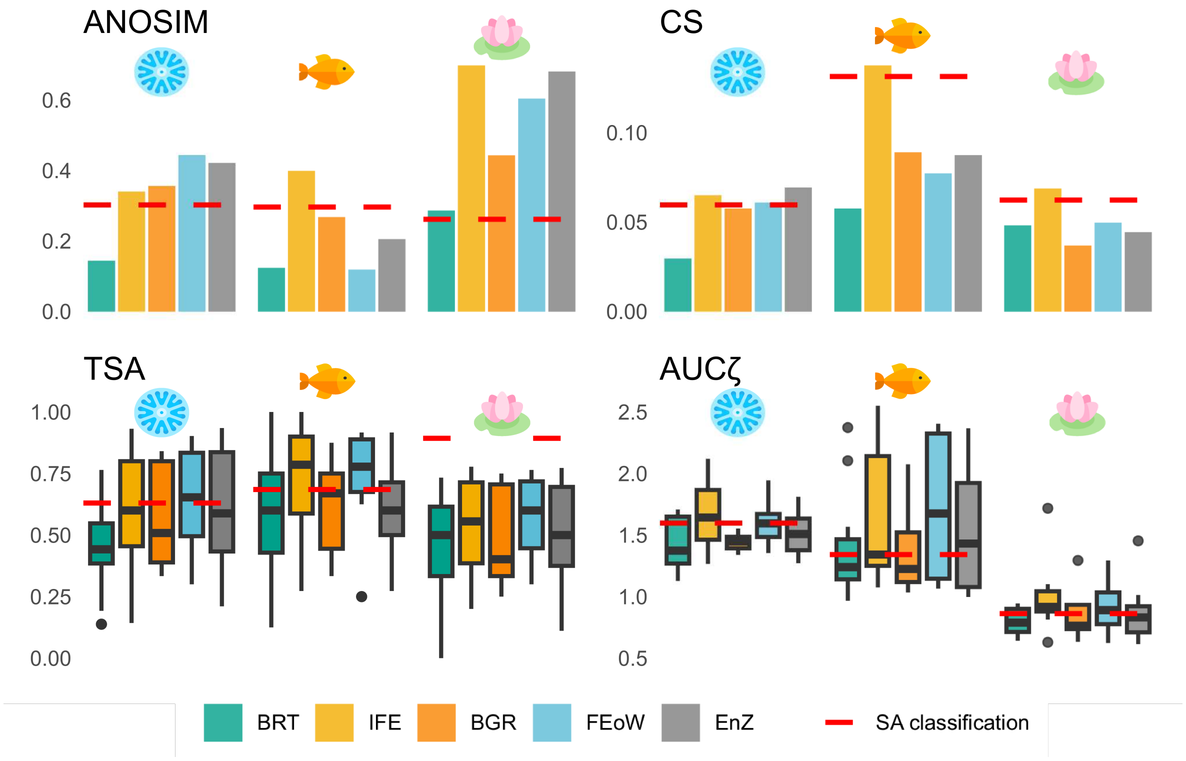

Figure 3.4: Results of the four cluster analyses, Analysis of similarities (ANOSIM), Classification Strength (CS), Typical Species Analysis (TSA), and area under the zeta diversity decline curve (AUCzeta), for the Broad River Types (BRT), Illies Freshwater Ecoregions (IFE), Biogeographic Regions (BGR), Freshwater Ecoregions of the World (FEoW), and Environmental Zones (EnZ) across diatoms, fishes, and macrophytes. For all four analyses, higher values imply a better classification. The dashed red line indicates the results for the 15-type hexagonal spatial autocorrelation (SA) classification. For ANOSIM, the R-statistic is shown. An R of 1 corresponds to a perfect classification where within-type similarities exceed among-type similarities. For the CS, the classification strength is shown. A high dissimilarity between the TSA communities of two types implies that the different species are common in each of the two types. Therefore, a good typology system would have high dissimilarities between TSA communities. For AUCzeta, the area under the zeta diversity decline curve is shown. If communities share fewer species, their zeta diversity decline curves will be steeper and hence enclose a smaller area over a fixed number of orders. A good typology would aggregate ecosystems with similar communities and hence with slowly declining zeta diversity curves and large areas under the decline curve. This analysis returns one area under the curve per type and taxonomic group. The distribution of these areas is shown here.

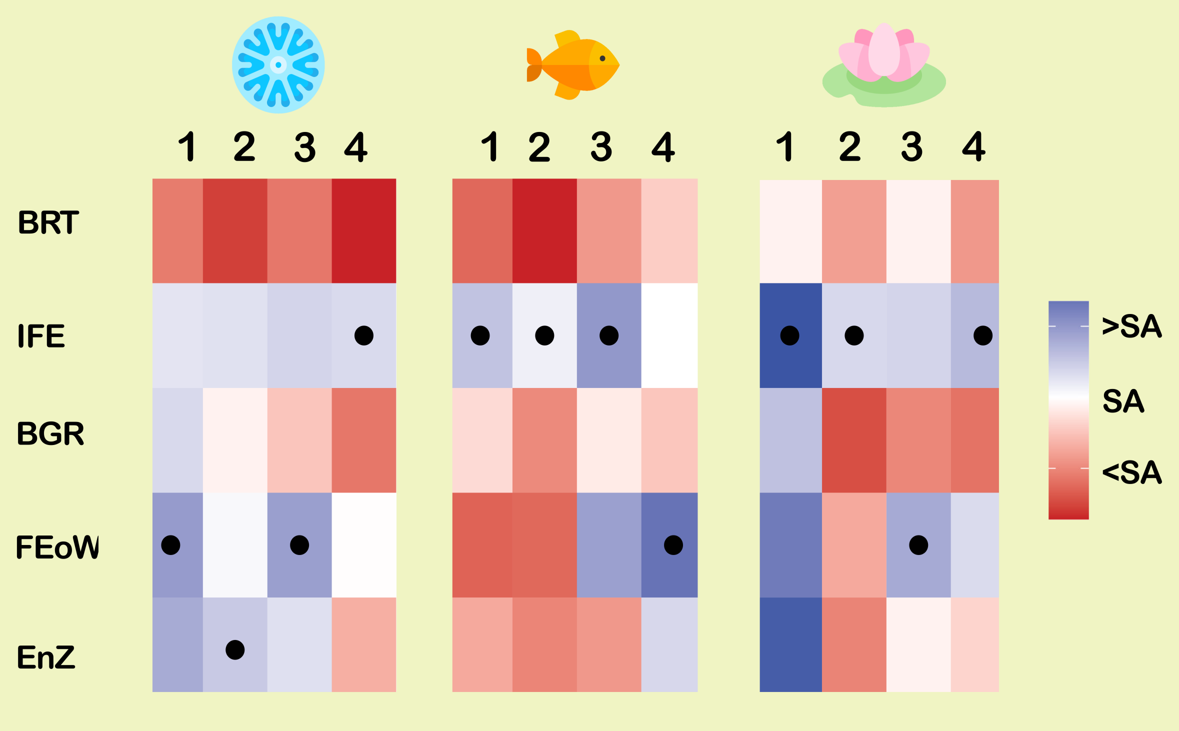

Figure 3.5: Summary of all results relative to the 15-type hexagonal spatial autocorrelation (SA) classification. The rows indicate the typology systems: Broad River Types (BRT), Illies Freshwater Ecoregions (IFE), Biogeographical Regions (BGR), Freshwater Ecoregions of the World (FEoW), and Environmental Zones (EnZ). The columns are the different analyses: Analysis of similarities (1), classification strength (2), Jaccard dissimilarity between typical species analysis communities (3), and area under the zeta diversity decline curve (4). All results are relative to the SA classification. Blue cells indicate that the typology received a higher score than the SA classification, red cells indicate the opposite. White cells show that the performance is similar to the SA classification. Black dots highlight the typology system that performed best for a given combination of taxonomic group and evaluation method.

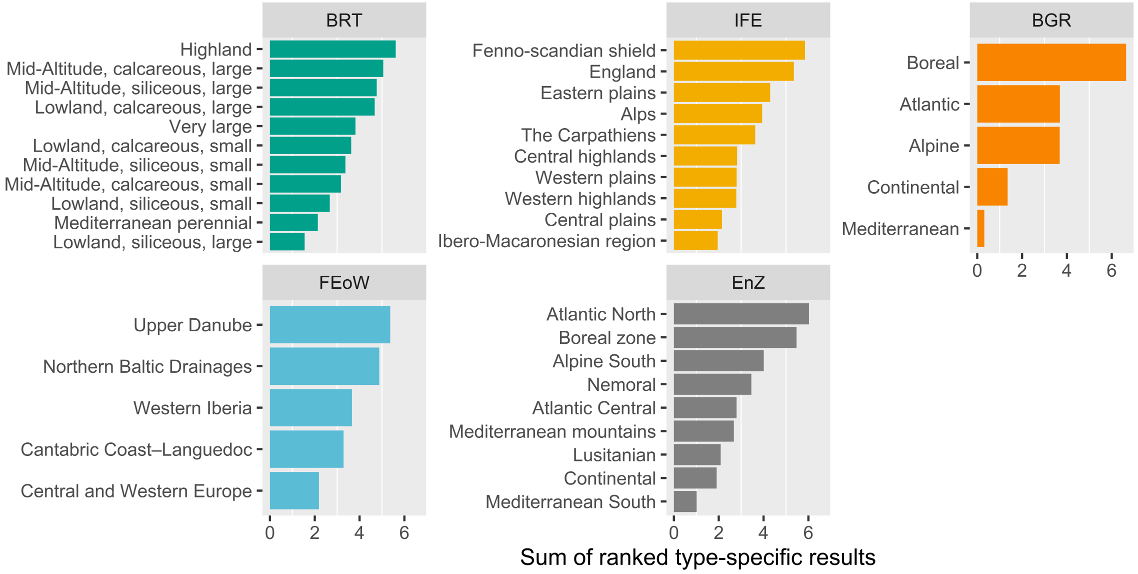

Figure 3.6: Performance of individual types across taxonomic groups and evaluation metrics for the Broad River Types (BRT), Illies Freshwater Ecoregions (IFE), Biogeographic Regions (BGR), Freshwater Ecoregions of the World (FEoW), and Environmental Zones (EnZ). Each score is the sum of scaled results across taxonomic groups and test. Scaling was conducted separately for each combination of taxonomic group, typology system, and test. The highest and best possible score is 9, the lowest and worst is 0. Only types that were evaluated for all three taxa are included

3.4 Discussion

We compiled datasets of diatom, fish, and macrophyte occurrences from rivers throughout Europe to determine whether spatial patterns in community composition follow broad-scale environmental covariates as captured by different ecosystem typologies. Our first research question was whether the site groups delineated by the BRT host communities of diatoms, fish, and macrophytes whose composition is more similar within than among types. This is not the case for any of the three taxonomic groups. The BRT failed to meet the predefined quality threshold for ANOSIM and CS and performed worse than the SA model in 11 out of 12 tests. Our second research question was whether the communities within BRT were more homogenous and distinct than those of the types of IFE, BGR, FEoW or EnZ. Here, the opposite was the case. In most analyses, the BRT were least reflected by the community compositions. Our analyses were based on presence-absence data. The results therefore pertain solely to the composition of communities and not their structure, i.e., the abundance of different taxa. Since patterns in community structure can deviate from those in community composition (Mueller *et al.*, 2013) we advise against generalizing our results to community structure. Further, we wish to emphasize again that our sampling sites are not uniformly distributed across types or within types. As such data do not exist on broad-scales we cannot evaluate the magnitude or direction of bias this might induce.

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

Fish assemblages often exhibit a spatial structure (Jackson & Harvey, 1989; Kilgour & Barton, 1999) and accordingly several studies indicated that fish assemblages are well described by a priori typology systems at fine (Hoeinghaus *et al.*, 2007; Vehanen, Sutela & Harjunpää, 2020) and broad scales (Frimpong & Angermeier, 2010). This partly reflects the fact that modern-day fish distributions are still strongly influenced by historical patterns (Vargas, Real & Guerrero, 1998; Reyjol *et al.*, 2007) but also that, among the taxa studied here, fish are the only group that disperses strictly within the river network, though we lack empirical data on possible zoochory in fish (Hirsch et al., 2018). Assuming that zoochory plays a subordinate role, dispersal between basins is only possible for euryhaline taxa such as *Anguilla anguilla*, *Alosa alosa*, or *Lampetra fluviatilis*, during river captures (Burridge, Craw & Waters, 2006), or with declining sea levels. The IFE capture fish community composition best of the evaluated typology systems. The bad performance of the BRT is surprising, given that longitudinal patterns, which only segment-based typology systems capture, are common in fish assemblages (Vila-Gispert, García-Berthou & Moreno-Amich, 2002). The influence of broad-scale factors and historical distribution patterns seems to override these longitudinal types.

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

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

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

3.4.1 Relevance of typology systems and ways forward

The availability of well-fitting typology systems matters. Typology systems are useful heuristics for researchers. Recent studies have used river typology systems to investigate type-specific temporal biodiversity trends (Powell *et al.*, 2022), inter-type differences in pollution pressure caused by man-made chemicals (Posthuma *et al.*, 2020), and the relevance of multiple stressors for different types of rivers (Birk *et al.*, 2020). Further, typology systems are crucial to the practical implementation of environmental policy. Policies need to define quantifiable standards and targets which requires distinct groups (Mau, 2017) to render complex matters legible to institutions (Scott, 2008). As a practical example, consider the environmental risk assessment of pesticides, which commonly derives a predicted exposure concentration and a, presumably safe, regulatory acceptable concentration. While exposure concentrations are predicted considering different types of ecosystems, the acceptable concentration does not take the receiving ecosystems into account. Introducing a typology system delineating biotic communities with different sensitivities represents a straightforward possibility to include spatial variation in sensitivity. If we neglect the potentially international nature of environmental issues, e.g., by relying on national tools to implement international policies, we risk being blindsided by transboundary harm (Knox, 2002) and transboundary crises (Boin, 2009). Together with Jupke *et al.* (2022), we show that European river typology systems fail to capture patterns in the community composition of aquatic biota considerably better than arrangements of simple geometric forms. It is important to note that the typology systems evaluated here were not designed for the specific purpose we evaluated them on. Hence, we do not wish to argue against the use of typology systems in general. Rather, we wish to highlight this research gap and encourage future efforts to close it.

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

Further, we might consider biological type descriptors in addition to abiotic ones, as is done in the IFE, BGR, and FEoW. While these three systems are based on expert knowledge about species ranges, others have created typology systems directly from observations. Several authors have derived diatom typologies for the evaluation of ecological indices (Grenier *et al.*, 2006; Lavoie, Dillon & Campeau, 2009; Goldenberg Vilar *et al.*, 2014; Tang, Stevenson & Infante, 2016). However, these typologies are at the subnational scale and were not meant to be generalized beyond their specific studies. For both macrophytes and fish, biotypes or -regions are commonly derived based on community composition and structure (Alahuhta & García-Girón, 2021; e.g., Holmes, Boon & Rowell, 1998; Riis, Sand-Jensen & Vestergaard, 2000; Pont *et al.*, 2007; Loewen *et al.*, 2021). If the purpose of the typology system is to define types with similar reference communities though, biotic type descriptors should not be used to avoid circularity (Bailey, Norris & Reynoldson, 2004; Stoddard *et al.*, 2006). A way to circumvent this circularity would be to use Generalized Dissimilarity Models (GDM, Ferrier *et al.*, 2007; Latombe, Hui & McGeoch, 2017). These models use spline functions to model the relationship between beta diversity (measured as dissimilarity metric, e.g.; Jaccard dissimilarity) and environmental variables. We can train such models to predict beta-diversity for the area of interest with the variables we want to use as type descriptors in our typology system. The predicted beta diversity, which is a function of the environmental variables, can then be clustered, instead of the environmental variables themselves. Effectively, this weights the variables by their importance for the taxonomic turnover of the focal taxon.

3.5 Conclusion

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

CHAPTER 4

Sensitivity of European macroinvertebrate assemblages toward three pesticides across river types

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Not yet published

Abstract

Anthropogenic stressors are a major driver of global biodiversity decline. While many studies examined the sensitivity of populations and communities to stressors, we lack knowledge of how sensitivities to stressors vary spatially in communities. Exposure to pesticides is a considerable stressor for ecological communities in freshwater ecosystems. Each pesticide undergoes an environmental risk assessment (ERA) to evaluate its risk to non-target taxa. ERA relies on generic methods, a few standard test organisms, and safety factors to determine concentrations that pose a low risk to ecosystems. This procedure neglects potential spatial variation in sensitivity and recommends a single safe concentration for each active substance. Elucidating spatial patterns in sensitivity to chemicals thus helps to close one of the major knowledge gaps in applied ecology and might improve ERA accuracy. We analyzed whether taxonomic turnover between field-sampled macroinvertebrate assemblages of different European river types results in systematic differences in assemblage sensitivity to Atrazine, copper, and Imidacloprid. To this end, we used an extensive database of macroinvertebrate assemblage compositions throughout Europe and predicted, for each assemblage, the concentration that would be harmful to 5% of taxa (HC_5) using hierarchical species sensitivity distribution models. Predicted HC_5 values varied over several orders of magnitude for all chemicals. However, variation within the 95% highest density intervals did not exceed one order of magnitude. Differences between the river types were minor for Atrazine and Imidacloprid and slightly higher for copper. For copper, the median HC_5 varied by a factor of 2.6 across river types. This level of variation is below what is commonly observed in toxicity tests of the species-chemical combination. We conclude that the differences in taxonomic composition between river types translate into relatively minor differences in assemblage sensitivity toward the three evaluated chemicals. However, several factors, e.g., differences in bioavailability, the interaction between environment and toxicity, or intraspecific sensitivity variation, may exacerbate differences in toxicant effects among river types in real-world ecosystems.

4.1 Introduction

Across the earth, ecosystems exhibit profound diversity in all their facets: the intricacies of geological features, the timing and amplitude of climatic patterns, and the abundance and scarcity of water. These factors and their interplay determine the existence and maintenance of biodiversity (Hutchinson, 1959; Humboldt & Bonpland, 2010). Ecologists investigate this diversity's characteristics, causes, and consequences, but vast gaps remain in our understanding. Closing these gaps requires concerted attention and effort, which are facilitated by categorizing the gaps: we likely have not yet identified most taxa (Linnean shortfall, Brown & Lomolino, 1998), their geographic ranges (Wallacean shortfall, Lomolino & Heaney, 2004), their phylogenetic relationships (Darwinian shortfall, Diniz-Filho *et al.*, 2013), or their functional traits (Raunkiæran shortfall, Hortal *et al.*, 2015). However, in light of the strong and growing human impact on ecosystems, a further gap might garner particular attention: the Hutchinsonian shortfall, defined by Hortal *et al.* (2015) as the lack of knowledge about the tolerance of species to abiotic conditions.

These shortfalls are especially pronounced in the highly diverse freshwater realm (García-Girón, Bini & Heino, 2023a), as they are more diverse than terrestrial or marine systems (Román-Palacios *et al.*, 2022) with many endemic species (e.g., Abell *et al.*, 2008; Murphy *et al.*, 2019), and fewer funds and efforts are allocated to freshwater research than to the other realms (Darwall *et al.*, 2011; Mazor *et al.*, 2018; Tydecks *et al.*, 2018). In addition to hosting highly biodiverse communities (Balian, 2008; Román-Palacios *et al.*, 2022), freshwater ecosystems are arguably the most threatened by human actions (Dudgeon *et al.*, 2006; Reid *et al.*, 2019; Albert *et al.*, 2021). They integrate stressors from the catchment scale (Hynes, 1975) and can propagate them through their network structure (Lorenz *et al.*, 2004; Gavrilescu, 2005), resulting in a potent mix of stressors (Schäfer *et al.*, 2016; Waite *et al.*, 2021). Agricultural land use contributes to many stressors that negatively affect freshwater ecosystems (Schürings *et al.*, 2023). High levels of agricultural land use in a catchment are related to nutrient enrichment (Jones *et al.*, 2001; Strokal *et al.*, 2016), increased sediment load (Jones *et al.*, 2001; Walling, 2008), and exposure to pesticides (Stehle & Schulz, 2015a). While the role of pesticides in broad-scale biodiversity trends remains poorly studied (Sylvester *et al.*, 2023), studies indicate they impact ecological communities at environmentally relevant concentrations (Cuppen *et al.*, 2000; Stehle & Schulz, 2015a; Liess *et al.*, 2021; Schürings *et al.*, 2023).

Pesticides must pass a prospective risk assessment before being released on the market to prevent unacceptable environmental effects. For each active substance, this assessment establishes a presumably safe concentration (Predicted no Effect Concentration, PNEC) and a concentration predicted to occur in the environment given the suggested application procedure (Predicted Exposure Concentration, PEC). If a compound's PEC is lower than its PNEC, it is considered safe (Boivin & Poulsen, 2017). PNECs are derived in a tiered approach, starting with a mandatory first tier, which involves standard toxicity tests under laboratory conditions using single species. The determined effect concentrations are divided by an assessment factor to obtain the PNEC. The assessment factor is meant to account for the uncertainty in extrapolating from laboratory conditions to the field. Higher tier tests may be conducted if the PEC exceeds the tier one PNEC. They involve increasingly complex scenarios such as multi-species and semi-field test systems and lower assessment factors.

This approach assumes that a single concentration (PNEC) can obtain a similar protection level across different ecosystems. The effect of this assumption is weakened by the use of assessment factors, as differences between ecosystems might be considered a part of the uncertainty that assessment factors account for. Nonetheless, it remains an open question whether the changes in taxonomic composition we observe among different types of ecosystems result in differences in sensitivity to pollutants. The question is also relevant in an applied context. If assemblage sensitivity varies systematically among river types, using a single PNEC would likely be inefficient and potentially ineffective. To date, few studies have investigated the broad-scale spatial patterns in sensitivity, partly because the sensitivities of most species towards most pesticides remain unknown (i.e., the Hutchinsonian Shortfall).

Few studies have investigated broad-scale patterns in sensitivity toward chemicals. Van den Berg *et al.* (2020) predicted relative sensitivity toward pesticides with models using information on functional traits and taxonomic relationships. They found considerable differences in the percentage of sensitive macroinvertebrate taxa between European ecoregions and UK river types. However, the magnitude of differences depended on the pesticide's mode of action. The data for Europe consisted only of species lists for ecoregions (Illies, 1978) and not of observed assemblages. Further, the study relied on a dichotomization of a relative sensitivity metric (mode-specific sensitivity, Rubach *et al.*, 2010), which is impacted by the included taxa and their taxonomic resolution. Field studies found negligible variation in assemblage sensitivity between central and northern European streams (Schäfer *et al.*, 2007; Schäfer *et al.*, 2012) but significant variability between water body types within regions (Biggs *et al.*, 2007). Together, these studies point toward broad-scale patterns in sensitivity, but patterns in field-sampled assemblage at the European scale have not been evaluated.

We investigate whether macroinvertebrate assemblage sensitivity toward three pesticides (Atrazine, copper, and Imidacloprid) differs systematically among European river types and whether the effect size of these differences exceeds partially significant threshold, thus meriting consideration in ERA. The chemicals we evaluate represent three different classes of pesticides (Herbicide, Fungicide, and Insecticide) and are relatively well-tested. We focused on non-target macroinvertebrates as they are among the groups facing the highest risk from pesticide exposure (Malaj *et al.*, 2014; Wolfram *et al.*, 2021). To predict the sensitivities of untested taxa, we used a *h*ierarchical *S*pecies *S*ensitivity *D*istribution model (hSSD, King *et al.*, 2015) that integrates chemical properties and taxonomic relatedness.

4.2 Methods

4.2.1 Data collection and harmonization

We compiled a database of macroinvertebrate assemblages in rivers throughout Europe from openly available and unpublished national monitoring datasets (see supplementary materials). All samples were collected in or after 2005 and with proportional multihabitat sampling similar to the STAR method (Consortium, 2003). To ensure comparability, we harmonized taxonomy across datasets with the taxonomic backbone of the Global Biodiversity Information Facility (www.gbif.org), only used samples collected between May and September, and restricted the data to phyla that occurred in all datasets (Annelida, Mollusca, and Arthropoda).

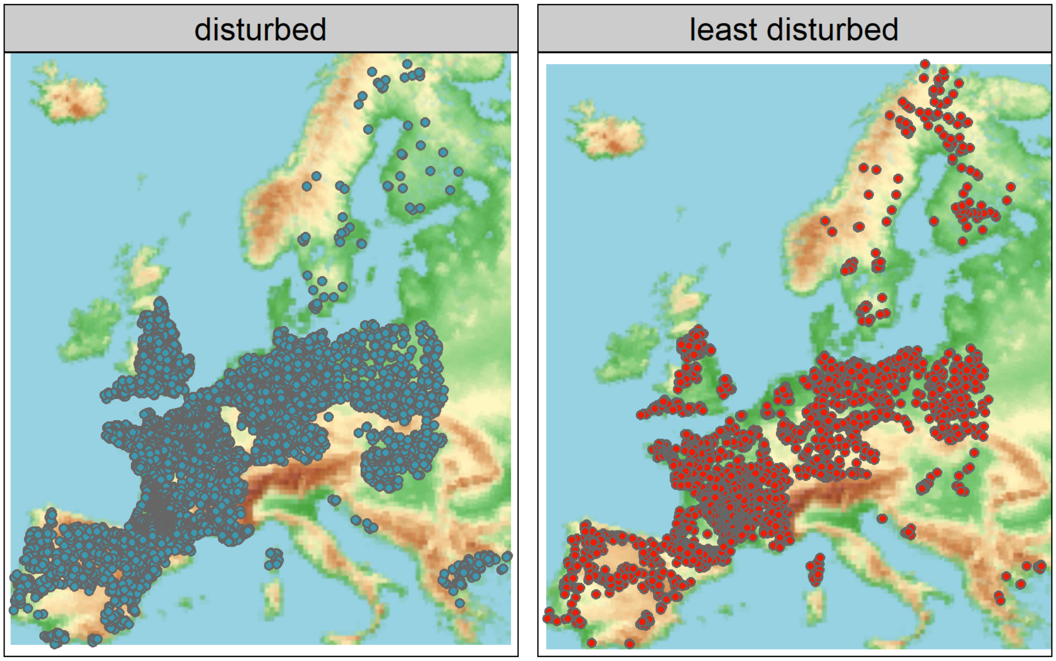

Figure 4.1: Spatial distribution of 10011 disturbed and 3587 least disturbed macroinvertebrate sampling sites across Europe.

We classified all sites as disturbed or least disturbed (sensu Stoddard *et al.*, 2006) based on a European stressor database (Lemm *et al.*, 2021). This database includes sub-catchment level data on seven indicators of anthropogenic stress: mixture toxic pressure, extent of urban and agricultural land use in the riparian zone, alteration of mean annual flow and base flow, and total phosphorus and nitrogen load. Sub-catchment units with values below the respective 24th percentile for each of the seven stressors were categorized as least disturbed. This threshold maximizes the ratio of least disturbed units with high or good ecological quality to least disturbed units with moderate, poor, or bad ecological quality (Jupke *et al.*, 2022). Subsequently, each sampling site was assigned the disturbance state of its sub-catchment unit.

We conducted all analyses twice, once with the only least disturbed sites and once with the complete dataset. Stressors can taxonomically homogenize biological communities across space (McKinney & Lockwood, 1999; Petsch, 2016). Thus, taxonomic differences between river types might be veiled if we consider disturbed sites. Notwithstanding, most sites in our database were disturbed, and removing such sites reduced our statistical power and spatial coverage substantially. The dataset comprised data from 13598 sampling sites; 3587 were least disturbed (Figure 4.1). As results differed little between the two datasets, the results only pertain to the least disturbed sites. Results for all samples are shown in the supplementary materials.

National river typology systems are available in all European states but differ strongly between countries. Therefore, we assigned each sampling site to one of twelve Broad River Types (Table 4.1), which are an aggregation of national Water Framework Directive typology types and currently the only pan-European river typology system that classifies river segments rather than regions (Lyche Solheim *et al.*, 2019). The taxonomic composition of biotic communities varies more strongly among types than within them, which is a crucial assumption for any typology system (Jupke *et al.*, 2022, 2023). While these differences are only marginal, superior alternatives are currently lacking. Still, we tested whether alternative typology systems, which classify contiguous regions rather than single stream segments, would produce different results. Besides the Broad River Types, we analyzed Illies Freshwater Ecoregions (Illies, 1978) and the Environmental Zones (Metzger *et al.*, 2012). The results for the alternative typology systems are qualitatively equal to those obtained for the Broad River Types. They are presented and discussed in the supplementary material.

Table 4.1: IDs and names of the 12 Broad River Types developed by Lyche Solheim et al. (2019). River segments are lowland if they are <200 meters above sea level (m.a.s.l.), mid-altitude for 200–800 m.a.s.l., and highland for >800 m.a.s.l. The catchment area determines segments size: very small-small <100 km2, medium-large 100–10.000 km2, and very large >10.000 km2. Depending on their lithology and pedology, catchments are calcareous or siliceous if the respective soil types or minerals cover >50 % of the their area. Catchments are mixed if coverage is between 40 and 50 %. Catchments with >20 % of their area covered by histosols are organic. The Broad River Types also consider Mediterranean rivers' flow regimes (perennial/temporary).

ID	Broad River Type
RT1	Very large
RT2	Lowland, calcareous or mixed, medium to large
RT3	Lowland, calcareous or mixed, very small to small
RT4	Lowland, siliceous including organic, medium to large
RT5	Lowland, siliceous including organic, very small to small
RT6	Mid-altitude, calcareous including organic, medium to large
RT7	Mid-altitude, calcareous or mixed, very small to small
RT8	Mid-altitude, siliceous including organic, medium to large
RT9	Mid-altitude, siliceous including organic, very small to small
RT10	Highland and glacial
RT11	Mediterranean perennial
RT12	Mediterranean temporary and very small

To each site, we assigned the broad river type of the spatially closest river segment in the digital representation of the Broad River Types provided by Globevnik (2019). Assigning sites to river segments is error-prone. The sampled segments might be missing from the digital river network, or the sites might be closer to other segments due to potential inaccuracies in the site coordinates or the spatial position of segments. To reduce the likelihood of such errors, we removed sites located > 300 m from the closest river segment. Further, we validated our assignment of sites to the river segments by visually comparing the site and segment location against the CaroDB.Positron base map with the mapview R package (Appelhans *et al.*, 2021).

4.2.2 Predicting assemblage sensitivity with hSSDs

We derived the sensitivity of the 13598 assemblage samples toward three pesticides: a herbicide (Atrazine), a fungicide (copper), and an insecticide (Imidacloprid). We predicted the sensitivity toward the selected chemicals for all taxa for which no test data was available. Of the 2149 unique taxa included in the dataset, sensitivity data were available for 27, 59, and 33 taxa for Atrazine, copper, and Imidacloprid, respectively. We predicted the sensitivity of taxa for which no data was available with hierarchical species sensitivity distribution models (hSSD, King *et al.*, 2015). These models expand upon Species Sensitivity Distributions (SSD), which estimate the probability distribution of sensitivities (usually log (EC_{50})) different taxa have toward one chemical (Kooijman, 1987; Posthuma, Suter & Traas, 2002). While SSDs are fit on sensitivities toward a single substance, hSSDs consider multiple chemicals and can accommodate sensitivity tendencies of taxa across chemicals. Since sensitivities are partly phylogenetically preserved (Guénard *et al.*, 2011, 2014; Malaj *et al.*, 2016), we can use the relatedness between taxa to predict sensitivities (van den Berg *et al.*, 2021).

We trained our hSSD model on acute toxicity data from the US EPA ECOTOXicology Knowledgebase (Olker *et al.*, 2022, available at http:/www.epa.gov/ecotox/). The toxicity data consisted of EC_{50} (immobility) or LC_{50} values for aqueous exposure with durations of 1-7 days. Using the parameter values estimated in the model training, we predicted the log EC_{50} for all untested taxa in our assemblages (Figure 4.2).

We employed the hSSD model proposed by Craig (2013). The model follows the basic structure:

$$y_{ijk} = \mu_{ik} + \epsilon_{ijk} \tag{4.1}$$

Where i,j, and k are indices over chemicals, species, and measurements, respectively. y_{ijk} is the k-th measured log-sensitivity of species j toward chemical i. μ_{ik} is the true log-sensitivity of species j toward chemical i and ϵ_{ijk} is the measurement error. The true log-sensitivity is modeled as

$$\mu_{ik} = \mu + \alpha_i + \beta_j + \psi_{ij} \tag{4.2}$$

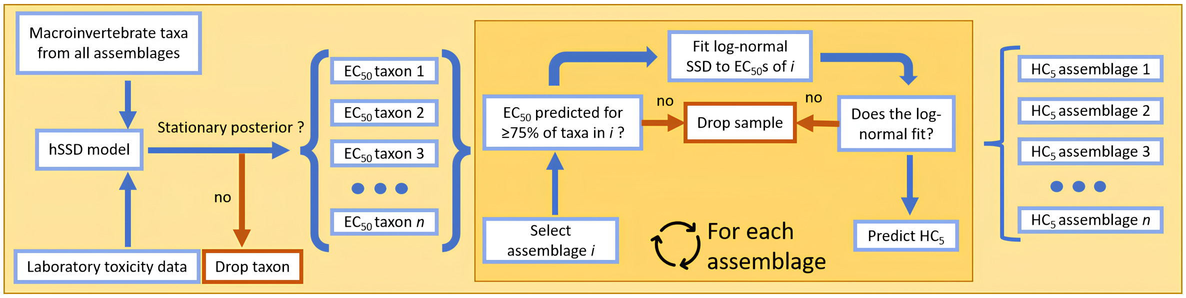

Figure 4.2: Workflow of the analysis. We used hierarchical species sensitivity distribution models (hSSD) to predict the sensitivity of 2149 taxa toward Atrazine, copper, and Imidacloprid. After removing taxa for which no reliable prediction could be made because the posterior distribution of the log (EC50) did not reach a stationary state, we fit log-normal distributions to the predicted log (EC50) values of each observed macroinvertebrate assemblage. Given that the log-normal was a reasonable approximation of the empirical distribution of log (EC50) values, we determined the assemblage HC5 as the fifth percentile of the fitted distribution.

where μ is the mean log-sensitivity across chemicals and species, α_i is the difference between the overall mean and the mean for chemical i, β_j is the sensitivity tendency of species j, and ψ_{ij} is an interaction term which allows the position of species j in the SSDs to vary between chemicals. ψ_{ij} is modeled as

$$\psi_{ij} = \phi_i + \xi_{ij} \tag{4.3}$$

where ϕ_i gives the variability for chemical i and ξ_{ij} is directly comparable between chemicals. Both β_j and ξ_{ij} are taxonomically structured as follows

$$\beta_j = \beta_{species_j} + \beta_{genus_j} + \beta_{family_j} + \ \dots \tag{4.4}$$

and

$$\xi_{ij} = \xi_{i_{species_j}} + \xi_{i_{genus_j}} + \xi_{i_{family_j}} + \ \dots \tag{4.5}$$

Hence, the model captures phylogenetically conserved sensitivity patterns in both β and ξ. We estimated model parameters with a Metropolis within block Gibbs approach, a Markov Chain Monte Carlo (MCMC) algorithm, and used the taxonomic levels genus, family, order, class, and phylum. The MCMC had a burn-in of 8000 runs per chemical, and the predicted log (EC_{50}) values were calculated from 10.000 samples drawn with a thinning of 15. For Imidacloprid, we increased the number of samples to 30.000 to increase the number of species with stationary posteriors.

We removed all taxa for which a Heidelberger-Welch test (Heidelberger & Welch, 1981) indicated that the posterior was non-stationary (at an α of 0.05). Removing those taxa reduced the total number of taxa to 2008, 2115, and 1366 for Atrazine, copper, and Imidacloprid, respectively. For each sample, we calculated the fraction of the remaining taxa. Samples where this fraction was lower than 75% were omitted from further analyses, reducing the number of samples to 11423, 13291, and 12648 for Atrazine, copper, and Imidacloprid, respectively.

We build assemblage SSDs by fitting log-normal distributions to the predicted $\log(EC_{50})$ values of each observed assemblage. We followed the guidance in EFSA (2013) and only fit SSDs to assemblage with at least eight taxa. Using the Kolmogorov-Smirnov test (Kolmogorov, 1933; Smirnov, 1948), we tested the distributional fit of the log-normal distribution and removed assemblages where the test suggested a statistically significant (at $\alpha = 0.05$) deviation between the fitted distribution and the underlying data. This reduced the number of samples to 4046, 12945, and 11352 for Atrazine, copper, and Imidacloprid, respectively. Tables with the predicted EC_{50} values are available in the supplementary materials. Lastly, we predicted the concentration that would affect 5% of taxa from the assemblage (Hazard Concentration 5, HC_5) as the fifth percentile of the distribution fitted to its $\log(EC_{50})$ values. The HC_5 is a good summary statistic to express the potential effects of chemical exposure on assemblages (Schäfer *et al.*, 2013).

4.2.3 Detecting patterns in sensitivities

The predicted HC_5 values had strongly skewed and non-normal distributions (Fig 4.3). Hence, we used the non-parametric effect size estimate Cliff's d, which is robust towards non-normality and outliers (Cliff, 1993) as it does not compare mean values or other indicators of distribution location. Cliff's d is the sample approximation of δ, which is the probability that a value (HC_5) from one group is higher than those from another group (Eq. (4.6)).

$$\delta = Pr(x_i > x_j) - Pr(x_i < x_j) \tag{4.6}$$

This probability is approximated by computing the proportion of values in one group that exceed those in the other (Eq. (4.7)).

$$d = \frac{\Sigma_{i=1}^{m} \Sigma_{j=1}^{n} [x_i > x_j] - [x_i < x_j]}{mn} \tag{4.7}$$

The $[\cdot]$ are Iverson brackets, defined to take the value one if the contained statement is true, and m and n are the respective group sizes. According to Romano *et al.* (2006), $|d|$ values above 0.47 strongly support group differences.

The Cliff's d provided us with an estimate of whether HC_5 values differ between groups but not with an estimate of the size of the difference. What magnitude of difference between river types merits changes to the current ERA practices? We defined two heuristic thresholds:

1) the differences between river types should exceed those between different tests of the same chemical-species combination.

2) the differences between river types should be larger than a factor of six.

Testing the sensitivity of one species towards one compound can produce vastly different estimates of endpoints (Hickey *et al.*, 2012; Craig, 2013). As our predicted sensitivities rely on the results of such single-species tests, variation within these tests constitutes an inherent uncertainty. If the magnitude of test uncertainty exceeds the observed differences between river types, we cannot be sure these differences are genuine. The second threshold builds upon current risk assessment practices. When determining regulatory acceptable concentrations with SSDs, the EFSA recommends assessment factors of three to six for invertebrates (EFSA, 2013). Among the suggestions to choose a value within that range is to consider the quality of the toxicity data used to construct the SSD. As most of our toxicity data are predictions from the hSSD, we prefer to err on the side of caution and use the larger assessment factor of six. This aligns with the precautionary principle that guides environmental policy in the European Union (EC, 2008).

To facilitate comparisons among chemicals, we scaled the HC_5 values by dividing the HC_5 values by the median HC_5 of the chemical and then taking the decadal logarithm of the quotient.

4.2.3.1 Determining variation in single-species toxicity tests

For all taxa present in our dataset, we downloaded toxicity data for all three chemicals using the standartox R package (Scharmüller, Schreiner & Schäfer, 2020). We only considered combinations of species and chemicals for which at least five tests were available in the database. Of the 2149 taxa in our dataset, 490 had associated LC/EC50 data in the standartox database, and 80 had LC/EC50 data for at least one of the three focal chemicals. We further reduced this dataset by the following inclusion criteria: (i) only test durations for which ≥ 3 different taxa were available; (ii) only combinations of taxa and chemicals for which ≥ 3 tests were available; (iii) mortality (i.e., LC_{50}) as a response, (iv) only aquatic exposure tests. Further, we removed tests flagged as outliers in the standartox database. We computed the quotient of the highest to the lowest recorded $LC_5$0 value for each taxon-chemical combination for each test duration. Lastly, we compared the quotient between median HC_5 values of the Broad River Types to the median of quotients across taxa but within chemicals and test durations.

4.2.4 Software

We conducted all analyses in R 4.3.0 (R Core Team, 2023). For data wrangling, we used the packages tidyverse 2.0.0 (Wickham *et al.*, 2019), data.table 1.14.8 (Dowle & Srinivasan, 2023), and sf 1.0-12 (Pebesma, 2018). For analyses, we used the packages vegan 2.6-4 (Oksanen *et al.*, 2022), MASS 7.3-58.3 (Venables &

Ripley, 2002), effsize 0.8.1 (Torchiano, 2020), standartox 0.0.2 (Scharmüller, 2022), and HDInterval 0.2.4 (Meredith & Kruschke, 2022). We created visualizations with ggplot2 3.4.2 (Wickham, 2016), tmap 3.3-3 (Tennekes, 2018), and cowplot 1.1.1 (Wilke, 2020).

4.3 Results

Assemblage HC_5 values varied by up to two (Atrazine, copper), or three (Imidacloprid) orders of magnitude (Fig. 4.3). Within the 95% highest density interval (HDI), i.e., the smallest possible interval that includes 95% of the area under the curve, the predicted HC_5 values only varied by one (copper, Imidacloprid) magnitude or less (Atrazine).

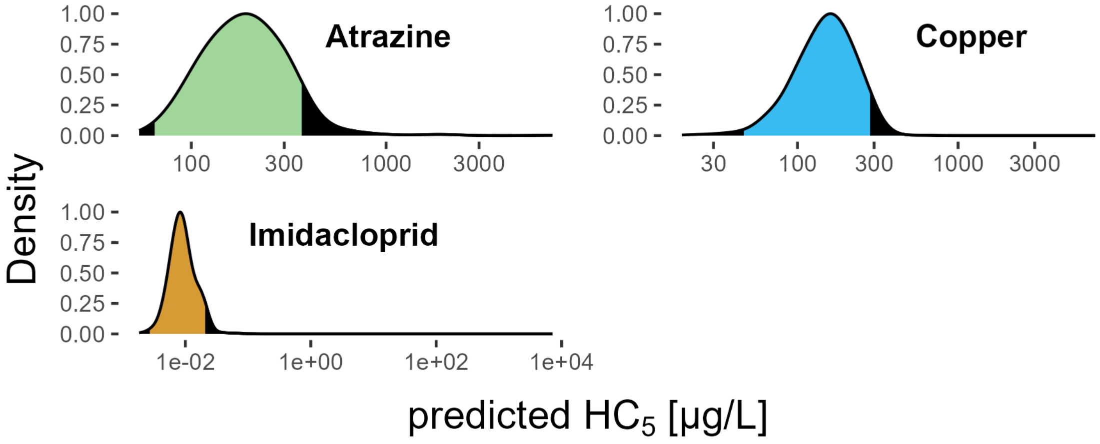

Figure 4.3: Density of assemblage Hazard concentration 5 (HC5) for the three focal chemicals. HC5 values outside the 95% highest density interval for the respective chemical are shaded black. Only the least-disturbed sites are included. The x-axis is log10-scaled, and the x-axis ranges vary across chemicals.

The predicted HC_5 values varied more strongly within than among Broad River Types (Fig. 4.3). The largest among-type differences are apparent for copper, where the median scaled HC_5 of very large rivers (RT1) is -0.30, i.e., at approximately 50% of the overall median HC_5 for copper and highland rivers (RT10) are at 0.2, i.e., approximately 1.6 times the overall median for copper. A version of Figure 4.4 with log(HC_5) on y-axis is available in the supplementary materials.

The analysis of Cliff's d confirmed this impression (Fig. 4.5). Differences between river types exceeded the heuristic threshold of 0.47 for two of three compounds, but most notably for copper HC_5 values. For Atrazine, highland rivers (RT10) tended to be the least sensitive (highest HC_5), which lead to noticeable differences to the more sensitive lowland types (RT2 - 5), as well as to large mid-altitude siliceous rivers (RT8). For copper, lowland rivers (RT1 - 5), especially very large rivers (RT1), were more sensitive than mid-altitude (RT6 - 9), highland (RT10), and Mediterranean rivers (RT11,12). Across altitude levels, as-

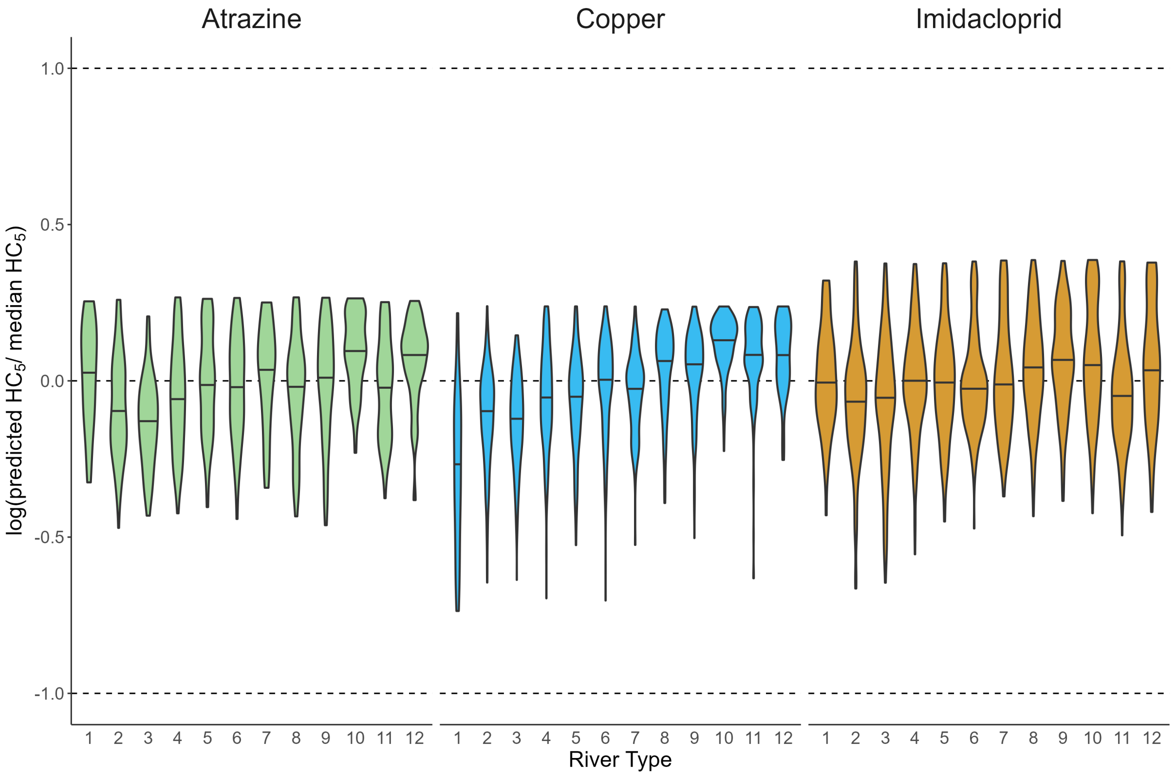

Figure 4.4: Density distribution of scaled Hazard concentration 5 (HC5) values for each chemical and river type. Scaling was achieved by dividing HC5 values by the median HC5 for the chemical across river types and taking the decadal logarithm of this quotient. Values of zero thus imply that the value is equal to the chemical's overall median, and values of 1 indicate that the value is one order of magnitude greater than the overall median. Horizontal lines within the density curves are medians. This plot shows the least disturbed sites and values within the 95% highest density interval.

semblages from calcareous rivers were more sensitive towards copper than those from siliceous rivers. For Imidacloprid, all among-type differences fell below the 0.47 threshold for Cliff's d.

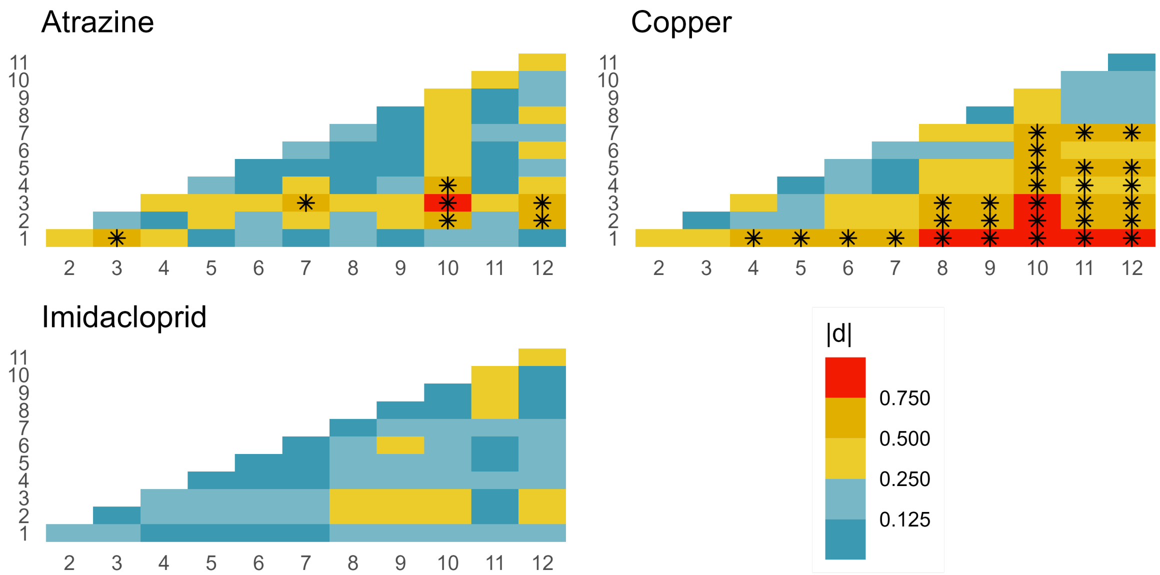

Figure 4.5: Differences between the assemblage hazard concentration 5 (HC5) values of different river types expressed as the absolute value of Cliff's d. X- and Y-Axis give the Broad River Type ID (Table 4.1). Dark blue cells indicate the smallest differences, and dark red cells mark the largest observed differences. An asterisk marks Cliff's d values that exceed the threshold of 0.47. Values are based on the least disturbed sites only.

We quantified the differences between river types by computing all quotients of river-types specific median HC_5 values (Fig. 4.6). These quotients were below six for all three chemicals, i.e., average river type HC_5 differed by less than a factor of six. The highest quotient between median HC_5 values was 2.7, which we observed for copper between very large rivers (RT1) and highland rivers (RT10). Further, the differences were below those for single-species toxicity tests, except for Atrazine. The variation between tests depended on study length but ranged from 1.7 to 7.5 for copper and 1.8 to 30.7 for Imidacloprid. Only one study length (48 hours) fulfilled our selection criteria for Atrazine. For this length, the sensitivity varied by a factor of 1.3.

4.4 Discussion

We used phylogenetic models to predict the sensitivity of macroinvertebrate assemblages toward three different chemicals and used the predicted sensitivities to compare the assemblage sensitivity between river types. Our Cliffs' d analysis indicated sensitivity differences between river types. We observed the largest difference in the median HC_5 for copper between very large rivers (highest sensitivity) and highland rivers

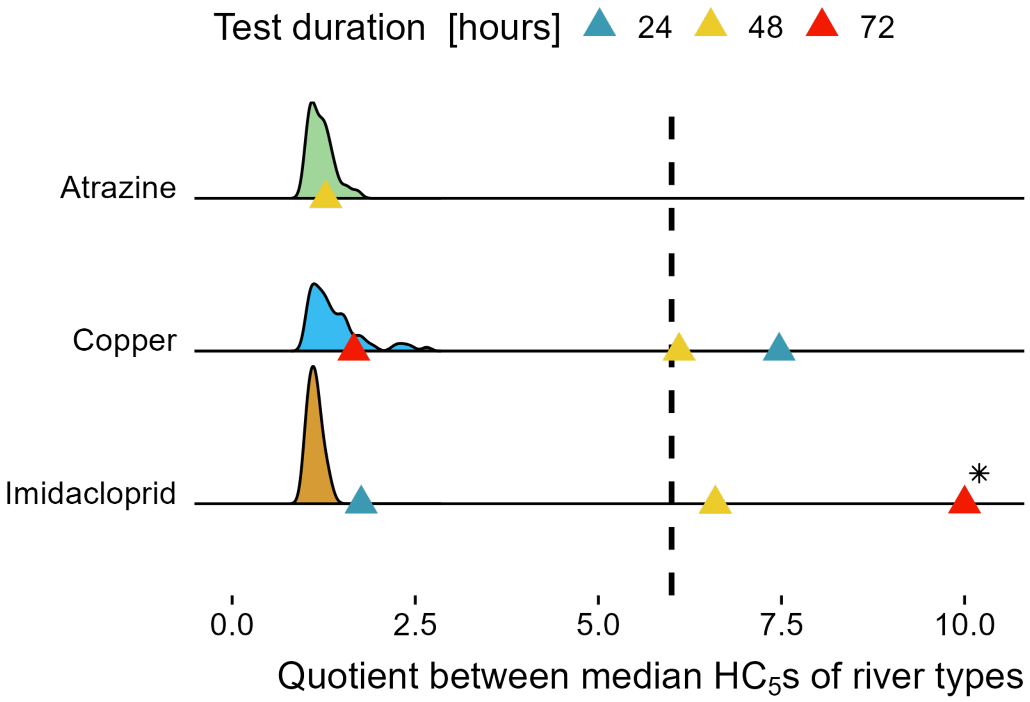

Figure 4.6: The factor of variation between median HC5s of Broad River Types. The triangles show the variation in sensitivity (LC50) from single-species toxicity tests. Their color indicates the test duration in hours. For Atrazine, only one test duration (48h) fulfilled all criteria (at least three taxa with at least three tests; tests with aquatic exposure and mortality as endpoint). The triangle marked with an asterisk for Imidacloprid identifies a value exceeding 10 (31). For the sake of clarity, we censored the x-axis at 10. The black dashed vertical line marks a factor of six differences, the upper limit for assessment factors suggested by the EFSA for deriving RACs with macroinvertebrate SSDs.

(lowest sensitivity). The median HC_5s differed by a factor of 2.7. This variation was lower than that between toxicity tests and our predetermined threshold factor of six. It was also below the lower threshold (3) for assessment factors suggested for regulatory acceptable concentrations derived from macroinvertebrate SSD (EFSA, 2013). Overall, sensitivity differed between river types but in an unpredictable and chemical-dependent manner. Our results suggest that variation in macroinvertebrate assemblage sensitivity, solely due to taxonomic composition, exists but is neither pronounced nor well captured by existing freshwater typology systems.

4.4.1 Are river types suitable to capture sensitivity variation?

We evaluated the differences in assemblage sensitivities among distinct river types rather than continuous changes in sensitivity along spatial or environmental gradients. Hence, we assumed that, generally, a discrete representation of space is suitable and, specifically, that the Broad River Types are a good representation. While the terms typology system and river type are uncommon in ERA parlance, they relate to the more familiar environmental scenarios (Rico *et al.*, 2016; Franco *et al.*, 2017). Environmental scenarios are also discrete entities designed to represent specific combinations of abiotic (exposure, bioavailability, other stressors) and biotic (community composition, specific ecosystem function) conditions. Typology systems originating from other research areas might aid in identifying relevant and realistic combinations of conditions for environmental scenarios. A river-type-specific ERA could be implemented in the same ways outlined for ecological scenarios (Franco *et al.*, 2017). On the effect side, we would need to identify typical taxa, taxa with special protection status, or desirable levels of ecosystem service provision for each river type to formulate respective protection goals and to derive type-specific PNECs that support those goals. On the exposure side, typical environmental conditions of the different types could be used as exposure scenarios in models. We used the Broad River Types because they are the only pan-European segment-based river typology. Alternative typology systems either classify regions instead of individual river segments (e.g., Illies, 1978; Metzger *et al.*, 2012) or extend beyond Europe (Ouellet Dallaire *et al.*, 2019). Region-based typology systems can be superior in capturing biogeographic patterns but fail to integrate longitudinal variations along rivers.

Further, previous studies suggest that sensitivity variation is likely more significant among river types within regions than among regions (Biggs *et al.*, 2007; Schäfer *et al.*, 2012). Our analyses for two region-based typology systems yielded similar results. However, Jupke *et al.* (2022) showed that the taxonomic community composition of macroinvertebrates differed almost as strongly within Broad River Types as among them. As we predicted assemblage sensitivities through the taxonomic composition, larger sensitivity differences between river types are more likely for river types with stronger differences in community composition. Therefore, other units of comparison might have elicited more pronounced differences.

4.4.2 Spatial ERA is still worth pursuing

Our results lend no support for a spatially explicit ERA. Notwithstanding, we argue that a spatially explicit ERA that accounts for the specifics of exposure and species vulnerabilities of receiving ecosystems, may deliver more reliable results for three reasons: 1. the environment influences bioavailability, 2. the environment moderates effects, and 3. sensitivities vary within species.

4.4.2.1 The environment influences bioavailability

A chemical's bioavailable fraction drives the effects of the chemical and can be much lower than the total load (Lu *et al.*, 2019b). Bioavailability, i.e., the extent to which a contaminant is available for uptake by organisms, is determined by how strongly the chemical adsorbs to available surfaces, its speciation, and its degradation rate. All three factors are governed by water pH (e.g., Xing *et al.*, 2012; Ding *et al.*, 2018; Khatikarn *et al.*, 2018), temperature (Kim *et al.*, 2010; Patra *et al.*, 2015), and size as well as the organic carbon content of suspended solids (Hodge *et al.*, 1993; Haitzer *et al.*, 1998; Ding *et al.*, 2018). The type of dissolved organic carbon also strongly impacts their capacity to form chemical complexes (De Schamphelaere *et al.*, 2004). Water hardness reduces the uptake of metals because the calcium cations compete for the same membrane transport proteins as the metals (Soucek *et al.*, 2011; Marchand *et al.*, 2013; Hundt *et al.*, 2016). Temperature, pH, organic carbon content, and water hardness are affected by factors that are or could easily be, implemented in typology systems, such as altitude, bedrock geology, or dominant soil type in a catchment. The bioavailable fraction, and therefore the effect of a chemical, might differ between river types, even when the inherent sensitivity of the assemblages is similar. Future studies could investigate bioavailability in different river types or define river types according to the expected bioavailability and determine the toxicity towards typical species under test media conforming to the water chemical conditions of these different types. Further, such differences in bioavailability might be integrated into the zonation scenarios of exposure models, such as FOCUS (Linders *et al.*, 2003).

4.4.2.2 The environment moderates effects

Many, potentially most, aquatic ecosystems face exposure to multiple stressors at or above ecologically relevant thresholds (Schäfer *et al.*, 2016; Waite *et al.*, 2021). Hence, organisms exposed to pesticides in the field are likely already in a stressed state before the exposure. The simultaneous or antecedent occurrence of other, chemical or non-chemical, stressors can strongly impact a pesticide's ecological effects (e.g., Blanck & Wängberg, 1988). The toxicity of Pyrethroids increases with decreasing temperature (Coats *et al.*, 1989; Hasenbein, Poynton & Connon, 2018) and with increasing salinity (Hasenbein *et al.*, 2018). Under hypoxic conditions, some metal cations occur in lower valency states (e.g., Cu^+), which differ in toxicity from higher valency forms (e.g., Shaw *et al.*, 2007). For example, Van Der Geest *et al.* (2002) observed a 50% mortality in the mayfly *Ephoron virgo* when independently non-lethal oxygen reduction and copper levels were combined. Nanoparticles can affect the concentration of pesticides in the aqueous phase depending on other environmental conditions (Seitz *et al.*, 2012, 2015). These examples are by no means exhaustive (see Holmstrup *et al.* (2010) and Steinberg (2012) for reviews on these topics) but demonstrate the potential for interactions between environmental conditions and chemicals. A meta-analysis of such interactions found synergistic interactions (i.e., the combined effect exceeds the sum of independent effects) in 62% of cases (Laskowski *et al.*, 2010). Conversely, models only using the dominant stressors best explained the observed effects in a study investigating the combined effects of climate change and additional stressors (Morris *et al.*, 2022). Several field studies reach the same conclusion: the most toxic compound accounts for most of the observed effects (Verro *et al.*, 2009; Schäfer *et al.*, 2013; Knillmann *et al.*, 2018; Liess *et al.*, 2021).

The prevalence and magnitude of many stressors differ between river types (Schäfer *et al.*, 2016; Birk *et al.*, 2020; Leitner *et al.*, 2021), as can the responses of taxa to the same stressor (Charles *et al.*, 2006; Alahuhta *et al.*, 2017; Denison *et al.*, 2021). In a spatially explicit risk assessment, we might be able to anticipate likely river-type-specific combinations of stressors or chemicals. A key challenge for including stressor interactions in prospective risk assessment is the large number of possible combinations (combinatorial explosion, Lundstedt *et al.*, 1998). Both multiple stressor and mixture toxicity research are currently active, though poorly integrated, fields of science (Orr *et al.*, 2020; Schäfer *et al.*, 2023). One potential integration pathway could be identifying the most common type-specific stressor combinations. We might use available field data (e.g., Schreiner *et al.*, 2016; Liess *et al.*, 2021) or a combination of high-resolution crop classification at national (Blickensdörfer *et al.*, 2022; Asam *et al.*, 2022) or continental level (Pflugmacher *et al.*, 2019; d'Andrimont *et al.*, 2021) and inventories of crop-specific active ingredients (Jarvis *et al.*, 2020) to predict common mixtures of pesticides. Pistocchi *et al.* (2023) took first steps in this direction by predicting the concentrations and cumulative toxicities of 148 active substances throughout Europe. Field data or predictions on other stressors such as nutrients (Lemm *et al.*, 2021), flow regime shifts (Lemm *et al.*, 2021), temperature (Karger *et al.*, 2017), salinity (Le *et al.*, 2019), are also available on broad spatial scales and could be used to identify common and type-specific combinations of non-chemical and chemical stressors. This approach cannot address second-order effects following the primary changes to the species composition or food web structure (Pace *et al.*, 1999; Wisz *et al.*, 2013; Feld *et al.*, 2023). If biological data with a high spatio-temporal resolution were at hand, we could take on this issue with latent variable models that include environmentally constrained interaction effects (Kissling *et al.*, 2012; Tikhonov *et al.*, 2017; but see Blanchet, Cazelles & Gravel, 2020) or copula models (Anderson *et al.*, 2019; Ghosh *et al.*, 2020).

4.4.2.3 Intraspecific variation in sensitivity

Considerable sensitivity variation between exists between individuals or populations in Cladocerans (Baird *et al.*, 1991; Bossuyt & Janssen, 2005), Dipterans (Nowak *et al.*, 2008), Gastropods (Jensen & Forbes, 2001), Collembolans (Crommentuijn *et al.*, 1995), Anurans (Bridges & Semlitsch, 2000; Hoskins & Boone, 2017), Algae (Behra, Genoni & Joseph, 1999; De Laender *et al.*, 2014; Esteves *et al.*, 2017), Fish (Petitjean *et al.*, 2021), and aquatic macrophytes (Dumont *et al.*, 2019). While the studies show different magnitudes of intraspecific variation, the taxonomic breadth highlights the ubiquitous of the phenomenon. In sampled populations, these differences can arise by dint of acclimatization through previous exposures (Naylor, Pindar & Calow, 1990; Bossuyt & Janssen, 2005; Becker *et al.*, 2020). Life stages and functional traits like body size can explain part of the variation in populations without acclimatization (Gerritsen, van der Hoeven & Pielaat, 1998; Gergs *et al.*, 2013; Kulkarni, Daniels & Preuss, 2013; Gergs, Kulkarni & Preuss, 2015). River types could be defined to coincide with different management contexts and, hence, acclimatization scenarios as laid out above. Additionally, mean functional traits of populations of the same species might differ between river types. Populations in environments with longer favorable seasons can have more generations per year (Tauber, Tauber & Masaki, 1986; Välimäki *et al.*, 2008; Altermatt, 2010), and body size can vary with temperature and trophic state (Havens *et al.*, 2015; Classen *et al.*, 2017; Karpowicz *et al.*, 2020). Interspecific variation can potentially distort our results if the variation is systematic and captured by river types. If individuals or populations of some species are systematically more or less sensitive in river type A than in river type B, this would affect the validity of our results. However, the variation would have to be large and occur in a substantial faction of the species pool. Even when most species sensitivities vary systematically among types, the direction of the effect must be the same for a systematic bias to occur. Overall, intraspecific variation is therefore unlikely to distort our results, even if it is common.

4.4.3 Conclusion

Current ERA practices fail to protect non-target organisms. One way to improve ERA might be to account for differences between ecosystems in biotic and abiotic conditions. In the present study, the differences in macroinvertebrate assemblage sensitivities between river types were negligible compared to the variation in toxicity tests and the uncertainty accounted for via assessment factors in regulation. Therefore, our study does not add support to this avenue. However, our predictions solely build upon the taxonomic assemblage composition. The predictions omit potential differences in bioavailability, multiple stressor context, and sensitivity variation within species. Thus, our study does not refute the potential benefits of spatial ERA schemes. Further, our study represents a large step towards elucidating broad-scale patterns in sensitivity and hence toward curtailing the Hutchinsonian shortfall.

CHAPTER 5

General Discussion

We evaluated the biological validity of the BRT typology system and estimated differences in assemblage pesticide sensitivities among its types. We showed marked differences between biotic assemblages within broad river types relative to the observed among-type variation. In most cases, this ratio of within-to-among-type differences was higher than for alternative ATS. All tested ATS failed to reach commonly used thresholds for good classification performance. We found minor differences in assemblage sensitivity between the BRT-types. The relative sensitivity of river types and the magnitude of differences between types depended on the chemical, thus prohibiting the identification of a most sensitive type. Further, the differences between river types were smaller than those observed between laboratory tests of the same species-compound combination and below the assessment factor used for macroinvertebrate SSDs in ERA. Thus, we interpreted the differences as irrelevant for ERA. Hence, the study does not directly support a type-specific ERA. However, the study is a first step in evaluating spatial patterns in assemblage sensitivity. It does not decisively prove the absence of such patterns. The bioavailability of pesticides, the stressor context, and species sensitivity can differ between river types, engendering inter-type differences independent of species composition. As part of this project, we compiled the largest database of field samples on the four biological quality elements of the WFD currently available and motivated improvements to the BRT system (Lyche-Solheim, personal communication). We also developed new statistical methods to evaluate the concordance between ATS and biological assemblages (typical species analysis and the area under the ζ-diversity decline curve).

In the following, we will discuss the two main findings of this thesis:

1. Variation in assemblage sensitivity does not follow ATS types.
2. Current pan-European ATS fail to capture biotic assemblage composition.

Concerning the first finding, we will discuss further possibilities to find patterns in sensitivity, other developments that might improve the specificity and protectiveness of ERA, and non-ERA-related measures to reduce the burden of pesticide pollution on freshwater biodiversity. Regarding the second finding, we will address the reasonable expectations toward the biological validity of broad-scale ATS, how we might develop new ATS systems, and argue that we should do so.

5.1 Variation in assemblage sensitivity does not follow ATS

5.1.1 Addressing the Hutchinsonain Shortfall

Our study aimed to find generalizable spatial patterns in the pesticide sensitivity of macroinvertebrate assemblages. Looking for such patterns is necessary because we lack knowledge of most species' tolerance to different pesticides or environmental gradients in general (the Hutchinsonian Shortfall). We observed slight assemblage sensitivity differences between river types. The effect size was insufficient to advocate for changes to ERA or the BRT as a means to generalize sensitivity patterns. We might thus conclude that we failed to identify spatial patterns in macroinvertebrate assemblage sensitivity. This failure might indicate that such patterns do not exist, are incongruent with any of the tested ATS, or that our predicted sensitivities were biased. Each conclusion implies a different avenue to address the Hutchinsonian Shortfall further. If assemblage sensitivities do not have a spatial structure, a different set of approaches would be required. If the spatial structure is inconsistent with the current ATS, we must develop a new ATS. We must use or develop new prediction methods if the predicted sensitivities are biased. We address the first and the third scenarios below and the second scenario in section 5.2.2, which discusses possibilities for novel ATS.

Currently, we derive most of our knowledge of the pesticide sensitivity of organisms from laboratory tests. While laboratory tests doubtlessly will increase our knowledge, they are resource-intensive, slow, and require animal testing. New approach methodologies aim to circumvent these issues. They include *in silico*, *in vitro*, and *in chemico* testing (e.g., Rivetti & Campos, 2023). Among them, computer models scale best because they do not require laboratory work. However, all algorithms require training data, which highlights the interconnection between biodiversity knowledge shortfalls (Hortal *et al.*, 2015). Besides the Hutchinsonian Shortfall, we lack knowledge on the existence of some species (Linnean Shortfall, Lomolino & Heaney, 2004), their geographical distributions (Wallacean Shortfall, Lomolino & Heaney, 2004), their traits (Raunkiæran Shortfall, Hortal *et al.*, 2015), their abundances (Prestonian Shortfall, Cardoso *et al.*, 2011), their interactions (Eltonian Shortfall, Hortal *et al.*, 2015), and their phylogenies (Darwinian Shortfall, Diniz-Filho *et al.*, 2013). We cannot address these shortfalls in isolation, as they are highly interrelated (Table 5.1) (Hortal *et al.*, 2015).

5.1.1.1 The impact of other Biodiversity Shortfalls

Table 5.1: How do the other six Biodiversity Shortfalls impact the study of the Hutchinsonian Shortfall? An overview of shortfalls and their consequences for studies of the Hutchinsonian Shortfall.

Biodiversity Shortfall	What is missing	Consequences for Hutchinsonian Shortfall
Linnean	Taxa	Species not considered for assemblage sensitivity
Wallacean	Geographic ranges	Biases evaluation when natural gradients are used, small impact on estimates based on physiology and laboratory tests
Raunkiæran	Functional traits	Reduces performance and applicability of trait-based models
Darwinian	Phylogeny	Reduces performance and applicability of phylogeny-based models
Prestonian	Abundances	Changes in assemblage structure cannot be studied
Eltonian	Interactions	Potential effects of interaction networks (buffer, cascades) cannot be studied

Our analyses neglect all species we do not yet know. Therefore, the Linnean Shortfall is the most fundamental. Using the rates of newly described aquatic insect species as a proxy, we see that undescribed taxa are distributed unevenly in space (Sánchez-Campaña *et al.*, 2023) and possibly among ecosystem types. The uncertainty caused by undescribed taxa might vary between river types. Europe is among the taxonomically best-described areas (Meyer *et al.*, 2015), so the number of undescribed taxa can be assumed to be relatively low in the area of our studies. However, cryptic taxa, formally a particular case of undescribed taxa, remain an issue in this region. Their prevalence differs between realms and organism groups, but they are common among aquatic standard test organisms (Jourdan *et al.*, 2023) and can vary in sensitivity (Feckler *et al.*, 2012). To bias the results of our study, cryptic species would need to make up a considerable fraction of the species pool. A large proportion of them would additionally need to differ markedly in sensitivity and these differences would need to systematically differ between river types. Therefore, we think it is unlikely that cryptic species had a strong impact on our study. However, from a theoretical perspective, we need a more complete inventory of organisms to tackle the Hutchinsonian Shortfall.

Existing algorithms often use data on functional traits or phylogeny to extrapolate sensitivity to untested organisms (van den Berg *et al.*, 2021). As captured in the Raunkiæran and Darwinian Shortfalls, these data are often missing, preventing the application of predictive algorithms (e.g., Rubach *et al.*, 2011; Van den Brink *et al.*, 2011; Van den Berg *et al.*, 2019). Functional and phylogenetic data is not merely available or missing but can be available in different resolutions and qualities. Information on functional traits can be available at coarse taxonomic resolutions or only for selected traits. For animals, data are often collected on easily measurable rather than functionally relevant traits (Hortal *et al.*, 2015). Most traits databases for macroinvertebrates contain data on external, visibly discernible traits that can be linked to toxicokinetics, while internal traits (e.g., the existence of receptors) that might predict toxicodynamics are rarely included (Rubach *et al.*, 2011; van den Berg *et al.*, 2021). When data are available for all relevant traits, the database could still be improved by allowing intraspecific variability. After all, traits are properties of individuals, not of species. While Mcgill *et al.* (2006) argue that traits should vary more between than within species to be useful to ecology, traits vary between members of the same species (Violle *et al.*, 2012; Des Roches *et al.*, 2018), and this variation occasionally exceeds the interspecific variation (Albert *et al.*, 2010; De Laender *et al.*, 2014). The explanatory capacity of a trait determines its usefulness, not the ratio of intra- to interspecific variation. Hence, trait databases should contain data at the individual level or on several moments of the trait's distribution over all measured individuals.
Similarly, phylogenetic data can be available at different resolutions. The highest resolution includes intraspecific genetic diversity and convergence time as a continuous measure of taxonomical relatedness. However, most broad-scale limnological studies use taxonomy instead of phylogeny to operationalize relatedness (Alahuhta *et al.*, 2019) since phylogenetic data is only available for selected areas and taxa (e.g., Zhou *et al.*, 2016; Betancur-R *et al.*, 2017; Múrria *et al.*, 2018). While phylogenetic predictive models can use divergence time as a continuous metric for relatedness, omitted species can bias these estimations (Nee, May & Harvey, 1994; FitzJohn, Maddison & Otto, 2009), further highlighting the interconnection between shortfalls. Ongoing work addresses the dearth of data for both shortfalls and at each level (García-Girón *et al.*, 2023a).

In all our analyses, we used presence-absence data, a constraint imposed by the data, as some datasets lacked abundance information, and others used different ways to measure abundance. Thus, our analyses were affected by the Prestionian Shortfall. Several studies indicate that the numerical resolution of the analyzed data influences the results (e.g., Heino, 2008; Lavoie *et al.*, 2009; Sály *et al.*, 2011). In this context, the most pertinent consequence is that shifts in assemblage sensitivity due to shifts in assemblage structure could not be detected. Previous studies have shown such shifts in species abundance distributions after the herbicide exposure of algae (De Laender *et al.*, 2014). With abundance data, we might weigh the different sensitivities in the SSD by the relative abundances of the respective taxa to obtain a concentration that affects $X\%$ of individuals rather than $X\%$ of taxa. Considering assemblage structure would go beyond what ERA requires in Europe, as it aims to protect invertebrate populations rather than individuals (EC, 2009; EFSA, 2013). Still, considering assemblage structure in evaluations of assemblage sensitivity is an interesting option for further research.

The Eltonian Shortfall refers to our lack of knowledge about the strength and consequences of biotic interactions. A species' sensitivity, as assessed in laboratory tests, is independent of biotic interactions. However, the real-world effects of pesticides and other stressors depend on the network of biotic interactions entangling each individual (Bruder *et al.*, 2019). Parasitism and exposure to chemicals often interact synergistically (Cedergreen, Pedersen & Fredensborg, 2023), as can chemical exposure and predation (Bruder *et al.*, 2017; Ito *et al.*, 2020). Vice versa, Albertson *et al.* (2021) conclude in their meta-analysis that the presence of stressors seems not to interfere with facilitative biotic interactions. Our studies conceptualized assemblages as lists of spatiotemporally co-occurring species. We add further complexity and potential between-type variation if we also consider the interactions between the species. Properties of ecological networks, such as connectivity and modularity, can influence the response of the assemblage to external perturbations (Bruder *et al.*, 2019). Effects can propagate through networks (e.g., Alexander *et al.*, 2013). Predicting the occurrence and effects of interaction cascades requires knowledge of the network structure and is vital since indirect interaction effects on fitness are common (Cosmo *et al.*, 2023). Uncovering this structure remains a formidable task. Food webs are among the most studied and best-understood ecological networks, as we can use gut content analysis (Jones & Waldron, 2003) or stable isotope analysis (Pringle, 2020) to unveil them. Still, our understanding of food webs remains fragmentary (Pringle, 2020). Even with a network structure, higher-order effects are hard to predict, and most modeling focuses on unrealistically simple networks (Levine *et al.*, 2017). The integration of biotic interactions into biogeography is at an early phase (Thuiller *et al.*, 2023), and whether or not biotic interactions matter for the broad-scale distribution of taxa is contested (Soberón & Nakamura, 2009; Wisz *et al.*, 2013). Efforts to compile data on biotic interactions are ongoing (e.g., Poelen, Simons & Mungall, 2014) but only consider a small fraction of described taxa and usually consider interaction as binary (interact: yes/no) rather than a continuum (Gómez, Iriondo & Torres, 2023). Hence, we cannot address the Hutchinsonian Shortfall in isolation. Even when we rely on *in silico* approaches, we need to learn more about extant species, their traits, phylogenies, abundances, and interactions.

5.1.1.2 Computer models

The success of predictive models depends not only on the availability of such data but also on the use of suitable models. We used the hSSD model proposed by Craig (2013), which extrapolates measured sensitivities to taxa for which no sensitivities are available. The extrapolation uses estimates of species sensitivity across chemicals, a chemical's toxicity across species, and several additional parameters. The model incorporates relatedness because multiple parameters are taxonomically structured. The hSSD model assumes one shared variance parameter in sensitivity between species in a genus, one for all genera in a family, and one variance between all families in an order. The value of this variation parameter is independent of the identity of the species, genus, family, or order. This crude notion of relatedness only requires a few model parameters to be estimated, thus easing the model fitting. The approach requires no additional data, such as functional traits or phylogenetic trees, but lacks a robust mechanical basis. Relatedness-based approaches that use phylogenetic trees (e.g., Guénard *et al.*, 2014; Malaj *et al.*, 2016) represent relatedness on a continuous gradient based on divergence time (Kumar *et al.*, 2022; but see Louca & Pennell, 2020). Possibilities to include phylogeny are phylogenetic mixed models, where the covariance matrix of a random factor has a phylogenetically informed variance-covariance matrix (Ives & Helmus, 2011), or phylogenetic eigenvector maps which decompose a weighted matrix representation of the phylogenetic tree to estimate a phylogenetic covariance matrix (Guénard, Legendre & Peres-Neto, 2013). Compared to our approach, these methods have a stronger mechanical foundation but suffer from the Darwinian Shortfall. Existing studies have also used far fewer taxa than we have ($\sim$ 30, Guénard *et al.*, 2014; Malaj *et al.*, 2016).

An alternative approach is the prediction of sensitivities with functional traits (e.g., Rubach *et al.*, 2011). External functional traits can be related to toxicokinetics (van den Berg *et al.*, 2021). For example, larger organisms have a higher uptake rate, and organisms with a high degree of sclerotization have a lower elimination rate (Rubach *et al.*, 2012). While trait-based sensitivity predictions occasionally contradict current theory (Hamilton *et al.*, 2020), traits offer a more robust mechanic basis than a non-phylogenetic notion of relatedness. Lastly, several recent studies have successfully predicted sensitivities with machine learning techniques. Zubrod *et al.* (2023) trained Random Forests (Breiman, 2001) and Local Cascade Ensembles (Fauvel *et al.*, 2022) with chemical fingerprints and parameters from the Dynamic Energy Budget Model (Nisbet *et al.*, 2000), which captures traits related to toxicodynamics. Their models successfully predicted the sensitivity of fish and macroinvertebrates to different pesticides. Wu (2022) predicted approximate LC_{50} of fishes with different machine learning methods, including Random Forests. These approaches have recently been encouraged by Schür *et al.* (2023), who initiated sensitivity prediction challenges based on the extensive ADORE database they compiled. Machine learning techniques generally require more data than statistical regression models, as they impose less structure and use more parameters. Hence, while these studies are promising, this avenue will not lead past the abovementioned biodiversity knowledge shortfalls. Many alternative, potentially more accurate approaches exist to predict sensitivities. The broad taxonomic scope of our study would have made the application of data-intensive methods that require information on traits or phylogeny difficult, but future studies might consider using fewer taxa but more elaborate prediction methods.

5.1.2 No support for type-specific risk assessment

Our comparison of assemblage pesticide sensitivities has revealed minor differences between broad river types. Hence, these results do not directly support the notion that considering the recipient ecosystem type might improve ERA's precision. However, such amendments should not be discouraged based on our results alone. Our study considered the effect of taxonomic compositions, not whether ATS might capture patterns in bioavailability, stressor context, or intraspecific sensitivity. At least for bioavailability and stressor context, such spatially structured variation has been shown (Birk *et al.*, 2020; Leitner *et al.*, 2021) or can be expected (Kim *et al.*, 2010; Soucek *et al.*, 2011; Xing *et al.*, 2012). Interspecific variation in sensitivity has been shown in field (e.g., Alahuhta *et al.*, 2017; Denison *et al.*, 2021) and laboratory studies (e.g., Bossuyt & Janssen, 2005; Nowak *et al.*, 2008), but we lack studies that investigate its spatial distribution.
Further, the study included only three chemicals: Atrazine, copper, and Imidacloprid. This selection is feasible, as plenty of toxicity data is available for these compounds, but small. We discourage extrapolations from this selection to the universe of chemicals (Drakvik *et al.*, 2020). Differences among species in absolute sensitivity vary significantly between chemicals (Nagai, 2016), as do the relative sensitivity rankings (Van den Berg *et al.*, 2020). No single species is the most sensitive toward all chemicals (Cairns, 1986). In our analyses, no river type had the most sensitive macroinvertebrate assemblages across chemicals, and the magnitude of inter-type differences varied among chemicals. Hence, we might observe more pronounced differences between river types for other compounds. Lastly, we only evaluated the sensitivity of aquatic macroinvertebrates. Other organism groups relevant to ERA, such as fish, algae, or earthworms were not considered but might show conspicuous and structured variation.

5.1.3 Alternative ways to improve ecological risk assessment

If we assume that, despite the arguments above, type-specific ERA cannot improve precision and protectiveness, what might? Along with the criticism of the current ERA scheme comes a series of recommendations (e.g., Schäffer *et al.*, 2018; Schäfer *et al.*, 2019; Topping, Aldrich & Berny, 2020). The fastest way to increase the protectiveness of ERA would be to increase safety factors (Schäfer *et al.*, 2019; Drakvik *et al.*, 2020). While this might lead to an overly restrictive ERA, it would align with the precautionary principle that guides EU environmental policy (EC, 2008). Following the risk management archetypes developed by Aven (2016), we might advance from the precautionary to a discursive strategy, in which we reduce uncertainty and involve stakeholders. Along this line, we need to improve exposure models. Threshold exceedances (e.g., Wolfram *et al.*, 2021) and comparisons between model predictions and measured concentrations (Knäbel *et al.*, 2012, 2014) have demonstrated the inadequacy of the current FOCUS exposure models. When predicted environmental concentrations are inaccurate, a comparison with threshold concentrations will not reliably lead to a protective ERA, even if the threshold concentrations are accurate.

Novel methods are currently under development (e.g., Boström *et al.*, 2019; Yan *et al.*, 2022) but lack detailed field data to validate their predictions. Further, these models should more strongly consider the specific environmental context, e.g., through environmental scenarios (Rico *et al.*, 2016; Franco *et al.*, 2017), which might build upon broad-scale ATS.

On the effect assessment side, each novel compound's risk-benefit ratio should be benchmarked against existing compounds (Schäfer *et al.*, 2019; Sousa *et al.*, 2022). The novel compound should not be authorized if such analyses indicate that existing compounds are preferable. Benchmarking would lower the likelihood of regrettable substitutions, which Siviter & Muth (2020) observed after the recent neonicotinoid ban. Further, future effect assessments should consider co-occurring stressors, including other anthropogenic chemicals, and integrate the landscape context. Concurrent stressors acting on the community determine a compound's effect. Such stressors include biotic interactions (Cedergreen *et al.*, 2023), temperature (Verheyen & Stoks, 2023), or other chemicals (Moschet *et al.*, 2014). The potential for synergistic stressor interactions complicates their assessment since the number of combinations prohibits individual assessments. In the case of multiple chemicals, this challenge might be answered with additional assessment factor (Drakvik *et al.*, 2020), component-based analyses (Posthuma *et al.*, 2019), and identification of priority mixtures (Drakvik *et al.*, 2020). Concerning other stressors, we might be able to predict the interactions in computer models. However, such models do not currently exist and would likely require extensive training data.

A temporary option for provisional authorization combined with post-registration monitoring will grant time for developing such models and provide the necessary data. Post-registration monitoring requires a network of demonstration farms with intensive monitoring. These farms would need to cover a representative selection of catchments, the identification of which would benefit from broad-scale ATS. These catchments would be extensively monitored regarding the application (dates and doses) but also the environment, including non-target screening (Brack *et al.*, 2019), e-DNA-based biomonitoring (Hering *et al.*, 2018), and effect-based monitoring (Escher *et al.*, 2018). The monitoring efforts must exceed the lackluster WFD monitoring (Brack *et al.*, 2017). For these intensively monitored efforts, we could determine the role of landscape connectivity and the upstream riverine landscape, both crucial for recovery through immigration dynamics (Schriever *et al.*, 2007; Focks, 2014; Topping *et al.*, 2015). We can further identify priority mixtures from the gathered monitoring data. These priority mixtures will likely consist of different substance classes, e.g., pharmaceuticals, pesticides, industrial chemicals, or food and feed additives (Neale *et al.*, 2020), currently regulated under different policy frameworks. A successful mixture assessment will entail a deeper policy integration, with common protection goals and authorization criteria (Kortenkamp & Faust, 2018; Rotter *et al.*, 2018; Sousa *et al.*, 2022). Policy integration would also allow for linkages between ERA (including non-pesticide chemicals), the WFD, and the Common Agricultural Policy. Catchment-level cap and trade schemes for agro-chemicals could be combined with agri-environmental schemes (AGS) and

RBMPs. Catchment-specific caps for chemicals could be determined by the amount of buffer strips (Reichenberger *et al.*, 2007; Vormeier *et al.*, 2023), the landscape heterogeneity (Tscharntke *et al.*, 2021), or the fraction of land managed organically or under Integrative Pest Management (EEA, 2023). Current AGS already reward many of these behaviors but are not catchment-specific and often not focused on improving water quality (Jones *et al.*, 2017).

The complexity of managing multiple stressors within a landscape of metacommunities and social incentives necessitates *in silico* approaches to estimate the effects of interventions. Current landscape-scale simulation models consider the effects of multiple farming practices on different dimensions of local landscapes through multi-criteria decision analysis (Topping, Dalby & Valdez, 2019), for example, with the ALMaSS (Topping *et al.*, 2003; Topping, 2022), GeSoN (Paparella, Cembalo & Topping, 2023), or MAgPIE models (Dietrich *et al.*, 2019). The catchment-level results could be subsequently scaled up through stochastic metacommunity models (Lerch *et al.*, 2023) or metaecosystem models (Harvey *et al.*, 2023), which enable us to estimate ecosystem functions, and hence service provision, in different scenarios and at different scales. Catchment-scale digital twins could use the data from monitoring farms for near-term forecasting (De Koning *et al.*, 2023). Such forecasts have been successfully used to predict cyanobacterial blooms in lakes (Lofton *et al.*, 2022). They could also inform application rates in precision agriculture, a promising non-ERA way to reduce pesticide burdens.

5.1.4 Non-ERA ways to reduce the burden of pesticide pollution on freshwater biodiversity

Effective gatekeeping through ERA is but one way to manage and reduce the risk that pesticides pose to ecosystems. This section discusses four ways to improve risk management and reduce agriculture's pesticide reliance. As alluded to above, precision agriculture has the potential to improve modeling by generating vast amounts of data, but it could also reduce pesticide application itself (Timmermann *et al.*, 2001; e.g., Khakural *et al.*, 1999). Precision agriculture refers to the integration of digital techniques and monitoring in farming. Farmers can use fine-scale (pests, plant health, adjacent ecosystems) and broad-scale data (precipitation, wind, slope) to fine-tune the application rates of pesticides and fertilizers (Sishodia, Ray & Singh, 2020). As weed density often varies within fields (Khakural *et al.*, 1999; Clay *et al.*, 1999; Gaston *et al.*, 2001), constant herbicide application rates create an unnecessary risk for surrounding ecosystems. In addition to the spatial distribution, farmers can optimize the temporal distribution of applications to avoid critical developmental windows, such as the aquatic emergence of short-lived organisms (Jones, Ali & Egerstedt, 2016). We can weigh the expected market value of produce within field sections (e.g., Capmourteres *et al.*, 2018) against the expected risk created by pesticide application. Field areas with low expected market value and near non-field habitats, such as rivers, might receive lower pesticide input than high-productivity areas in the center of the field.

A strong ERA incentivizes the industry to develop compounds that meet the ERA's constraints. It encourages advances in sustainable, green, and benign-by-design chemicals, which contributes to reducing the risk through pesticides (Blum *et al.*, 2017). Early *in silico* approaches tried to identify chemical properties that predict the biological activity of chemicals (Kostal *et al.*, 2015). However, this is insufficient for chemicals designed to show biological effects, like pesticides or pharmaceuticals. Recent advances in machine learning techniques allow the identification of candidate molecules with receptor-specific activity (Zhavoronkov *et al.*, 2019; Zhou *et al.*, 2019), a technique that might also have great potential for the design of highly specific pesticides (Sparks & Bryant, 2022; Zhao, Huang & Hao, 2022). However, the market share and hence expected revenue of highly specific substances is small relative to that of broad spectrum substances, thus disincentivising their development.

Incentivization might also work when applied to the farmers. Denmark, Norway, Sweden, and France have introduced risk-based taxes on pesticide sales. In these countries, high-risk pesticides have higher tax rates than their low-risk alternatives. Since the introduction of the tax, the sale of pesticides has decreased in Denmark (Nielsen *et al.*, 2023) but increased in France (Guichard *et al.*, 2017). The fact that these taxes were part of larger policy packages complicates causal analyses of their effects (Böcker & Finger, 2016). In all cases, the announcement of the tax led to hoarding by retailers and farmers, partly explaining why the decline in application rates is slower than in sales (Böcker & Finger, 2016). Conceptually, the efficacy of the taxes depends strongly on the farmers' price elasticity toward pesticides. Earlier studies report relatively low elasticities, which could explain the mixed effects we observe (Falconer & Hodge, 2000; Skevas, Stefanou & Lansink, 2012). Several studies have reported low price elasticity of pesticides (Falconer & Hodge, 2000; Skevas *et al.*, 2012), which would reduce the effectiveness of such internalizing taxes.

As mentioned in the previous section, the currently available AGS support various measures that potentially reduce pesticide reliance. Among the supported practices that benefit biodiversity are organic farming (Geiger *et al.*, 2010; Tuck *et al.*, 2014; Gong *et al.*, 2022), crop diversification (Beillouin, 2021), agroforestry (Udawatta, Rankoth & Jose, 2019), the maintenance of extensively managed fallows (Tarjuelo, Margalida & Mougeot, 2020), and flowering strips (Albrecht *et al.*, 2020). Notably, most of these studies exclusively focus on benefits to terrestrial biodiversity. How and if AGS can benefit freshwater diversity directly is poorly studied (Jones *et al.*, 2017). While all of these are possible pathways to reduce the burden of pesticide pollution on freshwater biodiversity, the continued detection of legacy compounds (EEA, 2023) and the ongoing international trade of prohibited compounds, including but not restricted to pesticides (Zou *et al.*, 2023), show that preventing harmful chemicals from entering the market remains the most effective mechanism.

5.2 Current pan-European ATS fail to capture community composition

We have shown that currently available pan-European ATS fail to delineate patterns in the assemblage composition of aquatic macroinvertebrates, diatoms, fishes, and aquatic macrophytes. Since ATS can be of tremendous value to basic science and the practical management of freshwater bodies, we will try to chart a way to improve the performance of broad-scale ATS in this regard. To save words, *the performance* of ATS will henceforth refer to the coherence between ATS- types and assemblage composition. We will explore three questions in this discussion: (i) What level of performance can we reasonably expect from broad-scale ATS?; (ii) how can we improve the performance of broad-scale ATS?; and (iii) why and when are broad-scale ATS more useful than fine-scale ATS?

5.2.1 What performance can we reasonably expect from broad-scale ATS?

Can we reasonably expect ATS to perform better than what we observed? Did the evaluated ATS perform poorly because of their design or because ATS cannot capture patterns in assemblage composition at the spatial scale we evaluated? We cannot know the performance of the optimal ATS, but we can consider theoretical arguments and empirical findings to create a reasonable expectation. Typology systems based on biotic instead of abiotic data tend to perform better (e.g., de Vries *et al.*, 2020b). However, such ATS rely on circular logic (Kelly *et al.*, 2012) and use temporally highly variable descriptors, which is inadvisable for typology systems (Pennak, 1971; Robertson, Saad & Heisey, 2006). Thus, we will only consider abiotic ATS in this discussion.

From a theoretical perspective, assemblage composition is at least partially determined by abiotic variables. Species sorting prevents establishment in habitats outside a species' fundamental niche. Therefore, a local assemblage will primarily consist of the subset of the regional species pool, which tolerates the local conditions. Abiotic ATS constructed from the relevant abiotic drivers should be able to capture these subsets. ATS will perform best if species niches are narrow, have little overlap (Leibold *et al.*, 2022), and are conserved in the considered area. However, current abiotic conditions are not the only factor determining assemblage composition. Delayed species sorting can occur when past conditions shape current composition (Harding *et al.*, 1998), for example, if extinctions lag behind the changes in environmental conditions that cause them (Tilman & Lehman, 1994). In addition, dispersal limitation can prevent species from reaching favorable ecosystems. Mass effects resulting from strong dispersal can mask species sorting, as high immigration rates prevent local extinctions (Wilson & Shmida, 1984; Leboucher *et al.*, 2021). Interactions with other taxa also impact assemblage composition, especially in benign environments (Menge, 1976; Poff & Ward, 1989; Wisz *et al.*, 2013). Lastly, stochasticity or drift are essential facets of assemblage composition (e.g., Hubbell, 2001; Vellend, 2016; Munoz & Huneman, 2016). The degree to which each process determines different species' abundances will likely vary between species and sites (Leibold *et al.*, 2022). Their functional traits might structure this variation between species. For marine invertebrates, Pandit, Kolasa & Cottenie (2009) found that environmental processes governed generalists' abundance while dispersal drove specialists' abundance. The harshness of environmental conditions can structure the variation between sites. Datry *et al.* (2016) showed that for freshwater invertebrates and fish, sites with benign conditions are less dispersal-limited than sites with moderately harsh conditions. Neither spatial nor environmental distance predicted assemblage composition well in sites with very harsh environments, potentially alluding to a more decisive role of drift. How we can or whether we should integrate these non-species-sorting processes into ATS or biomonitoring in general are open questions (Cid *et al.*, 2020). Thus, from a theoretical perspective, we can expect abiotic ATS to capture patterns in assemblage composition to the degree that species sorting drives them.

A further restriction on the performance of ATS is the gradual nature of change in assemblage composition. Place-independent and regional ATS commonly have distinct and sharp boundaries. Instead of smooth transitions, they implicitly assume distinct assemblage types, demarcated by compositional break points - reminiscent of Clement's superorganisms (Clements, 1916). Such biogeographic breakpoints have been shown for aquatic macrophytes (García-Girón *et al.*, 2023b), macroinvertebrates (Heino & Alahuhta, 2015; Heino *et al.*, 2015; He *et al.*, 2020), fish (Henriques-Silva, Lindo & Peres-Neto, 2013; Tan *et al.*, 2021), and diatoms (Heino *et al.*, 2015). However, the strength of these breakpoints often varied between catchments (Heino *et al.*, 2015) or depended on abiotic variables (Tan *et al.*, 2021). Some studies failed to find such breakpoints (Tonkin *et al.*, 2016; He *et al.*, 2020). Additionally, Schmera *et al.* (2018) have highlighted several flaws with the statistical method underlying these studies, the elements of metacommunity structure framework (Leibold & Mikkelson, 2002). Considering regional ATS, we might regard boundaries as biogeographical transition zones (Ignacio Ferro *et al.*, 2014; Ferro, 2022). Some studies have removed observations within a fixed distance of the boundaries to account for transition zones (e.g., Soininen, Paavola & Muotka, 2004). More sophisticated approaches might estimate the size of each transition zone individually (De Klerk, Burgess & Visser, 2018). Individual estimation is feasible for regional ATS, which have relatively few boundaries, but less for place-independent ATS, where boundaries and transitions are ubiquitous. We conclude that using sharp boundaries to delimit types might suit some taxonomic groups at some places or under certain conditions, but allowing for gradual transitions might improve performance. Gradual transitions are further discussed below.

Considering past performances of broad-scale ATS adds an empirical side to our theoretical considerations. While many studies have evaluated ATS performance, almost all analyses are at the scale of federal or national states (e.g., Hawkins *et al.*, 2000; Turak & Koop, 2008; Mykrä *et al.*, 2009). Most pertinent for us are the few studies conducted at a pan-European level. Several studies evaluated the performance of a WFD

System A ATS (Annex II, EC, 2000) at the European scale. The WFD System and the BRT share many variables and thresholds. Therefore, these empirical findings are not entirely independent of our results as the ATS they test is conceptually similar to the one we analyzed. Verdonschot (2006a) considered macroinvertebrates, Baattrup-Pedersen *et al.* (2006) considered aquatic macrophytes, and Kelly *et al.* (2012) considered diatoms. Using different methods and rationales, all three conclude that the WFD System A ATS performs poorly on a European scale. Verdonschot (2006a) considers the selection of descriptors the main problem. Rather than focusing on geology and altitude, the ATS should be based on temperature and current but keep catchment size. However, their ordination of biotic communities identified three groups (lowland, highland, and Mediterranean), thus confirming the existence of broad-scale groups. Baattrup-Pedersen *et al.* (2006) base their rejection of the System A ATS on the fact that a biotic classification showed slightly higher performance. However, the differences between the System A and the biotic ATS were minor, the analysis used only 60 samples, and taxonomic turnover was noticeable among the System A types. Hence, this study neither strongly supports nor opposes broad-scale ATS. Kelly *et al.* (2012) refute their ATS (Van de Bund *et al.*, 2004), which differed slightly from System A, based on the visual inspection of an ordination diagram, in which samples from different types overlap. Their analysis of similarities indicates weak but existing separation among types ($0.25 < ANOSIM\ R < 0.5$). Diatom assemblage composition differed more strongly among member states than river types. Kelly *et al.* (2012) interpret this as a sign that the sampling and analysis methods of the individual countries bias the results, as has been shown elsewhere (e.g., Prygiel *et al.*, 2002; Kahlert *et al.*, 2009). The existence of species complexes and cryptic species further complicates such analyses (Mann, 1999; Evans *et al.*, 2008). Therefore, the results of Kelly *et al.* (2012) are also inconclusive.

Hence, while the three studies discussed above, together with Jupke *et al.* (2022) and Jupke *et al.* (2023), find a relatively low performance, all identify confounding factors or highlight potential improvements to their ATS. Given the theoretical considerations above, broad-scale ATS will never perfectly predict assemblage composition. The question we cannot conclusively answer is how good they can be. Existing studies use an assortment of methods and benchmarks to evaluate ATS performance. All agree that existing ATS at all scales are generally better than random allocations of sites. However, given the diversity of tests, no generally agreed-upon demarcation for good performance exists. Most studies also lack a neutral model or benchmark other than a completely random distribution of taxa across sites. Spatial autocorrelation classifications, as were used by Wolock, Winter & McMahon (2004), Frimpong & Angermeier (2010), and Jupke *et al.* (2023), represent a more reasonable baseline against which to compare ATS than complete randomness. Further, ATS should outperform these systems in multiple metrics to ensure that results are not artifacts of the employed tests. Lastly, the two methods we proposed, typical species analysis (Jupke *et al.*, 2022) and area under the ζ-diversity decline curve (Jupke *et al.*, 2023), represent valuable additions to the existing toolkit because they supply type-specific results.

None of the methods commonly used to evaluate ATS have been evaluated on simulated data. Using simulated data gives us complete control over the data's properties and transparent cause-effect relationships between the generation process and results (e.g., Jupke & Schäfer, 2020; Leibold *et al.*, 2022). Simulating meta-communities along gradients of species sorting, biotic interactions, mass effects, and stochasticity could show which methods are most robust or sensitive toward which process (e.g., Thompson *et al.*, 2020; Lerch *et al.*, 2023).

5.2.2 How can we improve the performance of broad-scale ATS?

Given that theoretical considerations and current studies imply that better-performing ATS are possible, we propose four improvements. We discussed three of them briefly in Jupke *et al.* (2022) and Jupke *et al.* (2023). While we cannot be sure that ATS following these guidelines will outperform existing ATS, the proposals are well-founded in theory: *(i)* add or change type descriptors, *(ii)* indirectly use biological data, *(iii)* use mixed ATS, and *(iv)* use probabilistic type memberships (Fig. 5.1).

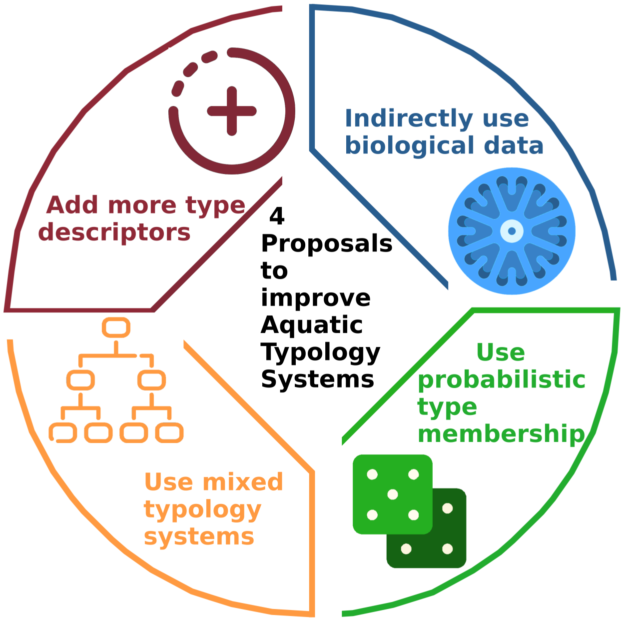

Figure 5.1: Four ways that might improve broad-scale aquatic typology systems: Add more descriptors, indirectly use available biological data, use mixed typology systems, and use probabilistic type memberships.

5.2.2.1 Add or change type descriptors

An increasing amount of geospatial data is available to classify streams, catchments, or valley segments (Lee & Kang, 2015). The envisaged river types aim to predict, as best as possible, abiotic patterns that entail differences in biotic assemblage composition. Constructing such ATS is a predictive task, and predictive models tend to improve by including more predictors (Gelman, Hill & Vehtari, 2021; James *et al.*, 2021). The BRT include five descriptors - fewer than alternative recent ATS. For example, the ATS proposed by Borgwardt *et al.* (2019) considered 30 different descriptors, and McManamay & DeRolph (2019) used 66. The most predictive variables will likely differ between taxa. Diatoms respond strongly to pH (Rimet *et al.*, 2004; Smucker & Vis, 2011; Jyrkänkallio-Mikkola *et al.*, 2017), conductivity (Soininen *et al.*, 2004; Grenier *et al.*, 2006), and altitude (Göthe *et al.*, 2013; Bottin *et al.*, 2014), while climate and relief determine fish community composition (Shelley *et al.*, 2019; Loewen *et al.*, 2021; Kirk, Rahel & Laughlin, 2021). Taxon-specific ATS will likely show the highest performance (Loveland & Merchant, 2004; Melles *et al.*, 2014; Edler *et al.*, 2017), but ATS with a large selection of descriptors have a higher probability of including the relevant ones and are easier to adapt to other taxonomic groups.

Four descriptors are worth highlighting because they affect assemblage composition but are largely lacking from available broad-scale ATS: sediment type, pH, conductivity, and flow. Sediment type determines the available habitats for macroinvertebrates (Boyero, 2003; Barnes, Vaughan & Ormerod, 2013), pH and conductivity are crucial for diatoms (Rimet *et al.*, 2004; Soininen *et al.*, 2004) and aquatic macrophytes (Riis *et al.*, 2000; Gillard *et al.*, 2020), and flow has been considered a master variable for rivers (Poff *et al.*, 1997). Besides information on the amount and timing of discharge, flow data can also encompass the influence of lakes and wetlands on a given river or valley segment. Including lakes and wetlands has been suggested by Melles *et al.* (2014) as it more fully incorporates the idea of a riverine landscape and because these ecosystems strongly influence dynamics in rivers (Jones, 2010). Snelder, Biggs & Woods (2005) provide a pertinent example of how lakes' influence could be operationalized. Most of the discussed variables are available for many sampling locations (Orgiazzi *et al.*, 2018; Mazzetti *et al.*, 2020; Müller, Middelburg & Sluijs, 2021). In some instances, extrapolations for larger areas (e.g., nation states) are available (Irving *et al.*, 2018), while other variables would need to be extrapolated.

A further consideration is to include metrics of spatio-temporal variation. Integrating temporal changes in ATS was recommended by Goodwin (1999), who emphasized that this would integrate the idea of rivers as processes through time rather than as things in space (Pinet, 1997). Fluctuations in environmental conditions can be summarized in summary statistics, as is commonly done for discharge time series (Olden & Poff, 2003). Alternatively, some classification approaches can directly incorporate time series (e.g., Bharath & Srinivas, 2015; Masanta & Vemavarapu, 2020). The ongoing nature of time series is a pertinent reminder that ATS should be dynamic and continuously updated (Frissell *et al.*, 1986). Updates are necessary as our understanding evolves and ecosystems are changing. Human actions create novel ecosystems that might be worth acknowledgment in ATS and preservation (Hobbs *et al.*, 2006; Hobbs, Higgs & Harris, 2009; Santana, 2022). Climate change might shift the boundaries of ecoregions (Troast, Paperno & Cook, 2020), and new ecosystems emerge as glaciers retreat (Bosson *et al.*, 2023).

5.2.2.2 Indirectly use biological data

Using abiotic variables to define ATS does not prevent us from using biotic data to inform the selection and weighting of variables. A straightforward way to ensure that taxonomic turnover occurs along the gradients of the selected variables would be to fit multivariate regression models (e.g., Wang *et al.*, 2012; Yee, 2015; Ovaskainen & Abrego, 2020) and to select only statistically significant variables. A further approach might be to first classify sites based on their biotic assemblages, using species-archetype models (Dunstan *et al.*, 2011), regions of common profile (Foster *et al.*, 2013), or Latent Dirichlet Allocation (Blei, Ng & Jordam, 2003; Valle *et al.*, 2014; Shimizu, Izbicki & Valle, 2023), using discriminant analysis to identify the abiotic variables that best discriminate between the groups and weigh the variables according to their discriminatory power. However, we will focus on an approach based on Generalized Dissimilarity Models (GDM, Ferrier *et al.*, 2002, 2007; Ferrier, 2002). GDMs model the compositional turnover of biological assemblages along environmental gradients. They account for the variable turnover rate along such gradients (Whittaker, 1977; Wilson & Mohler, 1983; Oksanen & Tonteri, 1995). While previous methods unrealistically assumed a linear relationship between biological and environmental distance (Manly, 1986), GDMs account for the non-linearity by transforming the environmental variables. Each environmental variable x_p is transformed into smooth functions of itself $I(x_p)$ with I-spline basis function (Ramsay, 1988). The regression parameters a weigh the distance between the smooth functions of two sites ΔI against the taxonomic turnover between the sites. The functions and parameters thus estimated can be used to create constrained environmental classifications, based on the environmental variables transformed by their smooth functions. While we are still classifying environmental variables, they are informed by the biological data. This is comparable to how constrained ordinations arrange biological samples within an ordination space determined by environmental variables. The intercept of this regression is comparable to the nugget of a variogram. It indicates variation in coincident sites, which might signal that abiotic variables are missing or hint at the magnitude of non-species-sorting metacommunity processes. To reduce the impact of rare species without completely removing them, we might also use ζ instead of β diversity to measure turnover. This approach further allows us to consider more than two sites simultaneously because ζ diversity naturally scales to multiple sites. Appropriately, GDMs that employ ζ diversity are called multi-site GDMs (Latombe *et al.*, 2017). Using ζ instead of β diversity disposes of the need to choose a distance metric. Standard distance metrics such as Sörensen or Bray Curtis can fail to capture the mean-variance relationship of the data (Warton, Wright & Wang, 2012).

5.2.2.3 Use mixed ATS

There are three types of ATS: place-independent, regional, and mixed. Place-independent ATS have small mapping units (river reaches, segments, or valley segments) that can be distributed across the whole area of the ATS. Regional ATS create larger contiguous areas as mapping units. All small mapping units within one such region are assigned the same type. Mixed ATS have regions with different sets of place-independent types inside each region. Place-independent and regional ATS have drawbacks that mixed systems can address. Place-independent ATS are blind toward broad-scale biogeographic processes, such as dispersal barriers, glaciation history, and diversity gradients. Regional ATS fail to capture the longitudinal changes along rivers. Mixed systems simultaneously capture broad- and small-scale patterns. For this reason, several authors have suggested that mixed typology systems are most appropriate for ATS (Naiman *et al.*, 1992; Mandrak, 1999; Hawkins *et al.*, 2000; Snelder & Biggs, 2002; Melles *et al.*, 2014).

Mixed ATS can easily be integrated into current limnological theory frameworks, a crucial point for any ecosystem typology system (Goodwin, 1999; Melles *et al.*, 2012; Keith *et al.*, 2022). We can regard the regions as macrosystems (Heffernan *et al.*, 2014) and the place-independent mapping units as functional process zones (FPZ, Thorp, Thoms & Delong, 2006). Macrosystems are the unit of study in macrosystem ecology, regional or continental in scale (McCluney *et al.*, 2014; Heffernan *et al.*, 2014). Macrosystems ecology integrates landscape ecology and macroecology. It takes a mechanistic perspective on small spatial units to understand broad-scale processes. Macroecology works on the same spatial scale but aims to identify patterns rather than generate mechanistic understanding (Gaston & Blackburn, 2000; McGill, 2019). By defining our regions as macrosystems, we situate them firmly within the context of ongoing research while remaining flexible in which variables and classification approaches we choose.
FPZ are the basic units of rivers in the *Riverine Ecosystem Synthesis* (RES, Thorp *et al.*, 2006; Thorp, Thoms & Delong, 2010). RES follows Pringle *et al.* (1988), Townsend (1989), and Poole (2002) in conceptualizing rivers as arrays of patches, thus integrating patch dynamics theory into limnology. This trend is a turn away from the continuous view of river ecosystems espoused in the river continuum concept (Vannote *et al.*, 1980) toward one of punctuated gradients (Perry & Schaeffer, 1987) and serial discontinuity (Ward & Stanford, 1983). This view holds that compositional turnover is not slow and continuous but happens episodically, e.g., at river confluences (Benda *et al.*, 2004). The patches in RES are called hydrogeomorphic patches, and if the patch size is assumed to be at the scale of reaches or valley segments, they are called FPZ. Some studies have found agreement between the discrete notion of FPZs and macroinvertebrate assemblage composition (Elgueta *et al.*, 2019; Maasri *et al.*, 2019). Other studies find that a combined notion of patchy gradients (Collins *et al.*, 2018) integrating FPZs and Strahler order to predict assemblage composition performs even better (Maasri *et al.*, 2021b). Thorp *et al.* (2023) suggested hydrogeomorphic patches as subunits in riverine macrosystems and started to integrate the two theories.

Many limnologists recognize the advantages of mixed ATS since Frissell *et al.* (1986) discussed hierarchy in river networks. Consequently, mixed ATS are common. Melles *et al.* (2014) reviewed 81 ATS and found that 64% contained multiple hierarchical levels, and of those, two-thirds used a regional system as the highest level. Watson *et al.* (2021) recommend nesting the BRT in regions before using them as the basis

for the new EUNIS freshwater typology system. The BRT already recognize the difference between the Mediterranean and non-Mediterranean regions. Each broad river type occurs only in either region. While the BRT are a mixed system in this sense, this dichotomy is an insufficient regionalization.
The easiest way forward would be the combination of an existing place-independent ATS with an existing regionalization. In considering the topic, Watson *et al.* (2021) propose combining the BRT with the Environmental Zones (Metzger *et al.*, 2005). Such a combination would result in many types if the constituent ATS are not simplified beforehand. Combining the BRT with the environmental zones results in 138 types. Combining them with Illies Freshwater Ecoregions, which tended to perform best in Jupke *et al.* (2022) and Jupke *et al.* (2023), results in 226 types. While typologies with a higher number of types can perform better (Frimpong & Angermeier, 2010), classifications with fewer types are, in general, *ceteris paribus*, more useful (Hynes, 1975; Dodkins *et al.*, 2005; Melles *et al.*, 2013). Some older systems with global extent had several hundred thousand or even million types (e.g., Pennak, 1971; Rosgen, 1994), which is barely more useful than naming segments (Hynes, 1975). While we can not *a priori* derive a threshold above which there are too many types in an ATS, 138 and 226 are at least towards the upper end of what might be considered functional. An alternative option would be to create new and bespoke regionalizations. The following section presents several possible avenues for this.

5.2.2.3.1 Developing new Regionalizations Regionalizations are classifications. Their unique feature is their spatial nature. The derived types should be spatially continuous rather than randomly distributed in space. Spatial autocorrelation in abiotic conditions can lead to cohesive regions without explicit incorporation of cohesion restrains (e.g., Metzger *et al.*, 2005; Stidl, 2023) but not necessarily (e.g., Pessoa, Blanco & Gomes, 2018; Lusiana, 2023). Spatially-restrained clustering methods are available and preferable for this task. Before we turn to the appropriate algorithms, we must identify meaningful mapping units, i.e., the individual elements to be grouped into regions. Two evident options are catchments and raster cells. Catchments are areas where all incoming water drains toward the same river segment. Catchments are naturally meaningful and standard management units of riverine landscapes (van Rees *et al.*, 2021). Raster cells are squares that do not correspond to naturally occurring elements. However, they are the dominant data model for large geospatial databases. Any data associated with river catchments would thus be summaries of the raster cells therein. Therefore, raster cells represent the highest resolution option.

Most standard techniques to derive regions do not explicitly constrain their clusters to be spatially contiguous. These techniques include self-organizing maps (Kohonen, 1982; Wang *et al.*, 2015) and fuzzy c-means clustering (Dunn, 1973; Bezdek, 2013; Wang *et al.*, 2015; Lasram *et al.*, 2015; Lusiana, 2023). Spatially non-constrained clustering methods can be coerced toward spatial coherence by increasing the number of types until resulting clusters are coherent (e.g., Smith & Nichols, 2009) or by splitting non-spatially contiguous clusters into parts (Abraham *et al.*, 2013). Such *ad hoc* approaches might lead to satisfactory results but are highly subjective. Other clustering methods have explicitly incorporated spatial continuity as a constraint in their algorithm, creating continuous and reproducible classifications. One approach is to grow regions by iteratively combining neighboring patches (e.g., Lu, Jiang & Zang, 2003; Heller *et al.*, 2006; Blumensath *et al.*, 2013). However, these methods currently only maximize within-cluster similarity but not among-cluster variability. Additionally, these algorithms are not iterative; once merged, cells remain merged, which makes the algorithms sensitive to noise and outliers (Baldassano, Beck & Fei-Fei, 2015). Spectral clustering approaches use network theory to represent their data as a graph $G(V,E)$, where V is the set of nodes and E is the set of edges. For our interest, the nodes represent the raster cells or catchments and the edges connect neighboring units. The edge between nodes v and u is weighted ($w(u,v)$) by the similarity of the nodes $s(u,v)$. The set of all nodes $\mathbf{V}$ can be partitioned into disjoint sets $\mathbf{A}$ and $\mathbf{B}$ with $\mathbf{A} \cup \mathbf{B} = \mathbf{V}$ by cutting edges. The optimal partitioning of nodes is defined as the one that minimizes some cost function. Wu & Leahy (1993) suggested using the *cut cost* as the cost function, i.e., the total weight of cut edges.

$$cut(A,B) = \Sigma_{u \in A, v \in B}\ w(u,v)$$

This function severs only the edges with the least weight, i.e., the connection between the least similar nodes. Stopping criteria can be the number of clusters or an edge weight threshold above which edges cannot be cut. Unfortunately, this cost function tends to create clusters with only one or a few members (Shi & Malik, 2000). We can avoid such behavior by using the *normalized cut cost* (Ncut) instead, which scales the *cut cost* by the sum of edge weights from nodes of the respective partitions to all other nodes, i.e.,

$$Ncut(A,B) = \frac{cut(A,B)}{assoc(A,V)} + \frac{cut(A,B)}{assoc(B,V)}$$

, where $assoc(A,V) = \Sigma_{u \in A, t \in V}\ w(u,t)$ (Shi & Malik, 2000). This method, NCUT, has been favorably compared to other spectral clustering techniques and Gaussian mixture modeling (Shen, Papademetris & Constable, 2010). It has been used to create a whole-brain fMRI atlas (Craddock *et al.*, 2012) and to elucidate the connectome of the *Drosophila* mushroom bodies (Li *et al.*, 2020). It has not been used for ecological applications or ecoregion delineation.

Fuzzy C-means (FCM, Dunn, 1973; Bezdek, 2013) is a fuzzy classification, meaning that objects can belong to multiple classes. Fuzzy clustering builds upon the fuzzy set theory of Zadeh (1965), which similarly lifts the constraint imposed by the ordinary set theory that elements can only belong to a single set. Instead, each cell i has a degree of membership u_{ij} between 0 and 1 for class j, under the constraint that $\Sigma_{j=1}^{J} u_{ij} = 1, \forall i \in [1, ..., I]$, where I is the number of cells and J is the number of classes. The closer u_{ij} is to 1, the more representative i is of j. The classification is represented by a fuzzy membership matrix $\mathbf{U}$

$$\mathbf{U} = \begin{pmatrix} u_{11} & \cdots & u_{1J} \\ \vdots & \ddots & \vdots \\ u_{I1} & \cdots & u_{IJ} \end{pmatrix}$$

Further, the centroid of cluster i is described by a vector v_i of length M, where M is the number of environmental variables used in the classification. The FCM algorithm starts by randomly assigning cells to clusters and computing centroids by averaging the descriptors x weighted by the membership values u of the observations.

$$v_j = \left(\Sigma\, u_{ij}^m \cdot x_{ij}\right) / \left(\Sigma\, u_{ij}^m\right)$$

The parameter m determines the fuzziness of the classification, where a smaller m leads to crisper classifications. Next, we compute the distance d_{ij} between each cell i and cluster centroids v_j using an appropriate distance metric. Lastly, we recompute the fuzzy membership matrix.

$$u_{ij} = \frac{1}{\Sigma(\frac{d_{ij}}{d_{lj}})^{2/m-1}}$$

This algorithm iterates until it finds a local minimum. In its original form, FCM is not spatially constrained. None of the above steps implies continuous regions. However, several ways to introduce such constraints have been proposed to reduce the *salt-and-pepper noise* common in the results of the original algorithm (Ahmed *et al.*, 2002; Szilagyi *et al.*, 2003; Chen & Zhang, 2004; Chuang *et al.*, 2006; Cai, Chen & Zhang, 2007; Krinidis & Chatzis, 2010; Zhang *et al.*, 2018). These spatial constraints bias the cluster identity of any cell toward the identity of the surrounding cells by adding a term to the updating of u_{ij}. The resulting classification is more likely to consist of continuous regions rather than scattered cells.

While FCM is quite commonly used to create spatial regions, e.g., catchment types (Ahani & Mousavi Nadoushani, 2016; Senent-Aparicio *et al.*, 2017; Pessoa *et al.*, 2018), agricultural management units (Roell *et al.*, 2020; Dad & Shafiq, 2021; Jena *et al.*, 2022), or ecoregions (Lusiana, 2023), none of these applications use a spatially constrained version. A further modification of FCM is possibilistic FCM (Krishnapuram & Keller, 1993; Pal *et al.*, 2005). Possibilities are not constrained to sum to one across classes for each cell. Thus, outliers are not forced into clusters and do not distort the cluster centroids. However, possibilistic clustering requires additional and strongly influential hyperparameters (De Cáceres, Oliva & Font, 2006).

Lastly, we will consider spatial signatures (Nowosad, 2021). This algorithm does not necessarily create continuous regions, but it breaches the gap between the raster cell and the catchment as the basic mapping unit and is thus worth considering. A spatial signature is a property of an area, i.e., a collection of raster cells. If there is no natural structure, this area is usually a square, but the catchment is a meaningful unit for river networks. For each area, we compute an adjacency matrix of the following form (Table 5.2).

Table 5.2: Example Adjacency matrix of a landcover raster. In this example, 272 cells with the type agriculture are next to other cells of the type agriculture, while 32 cells of the type grassland are next to cells of the type forest.

	agriculture	forest	grassland	water
agriculture	272	218	4	0
forest	218	38,778	32	12
grassland	4	32	16	0
water	0	12	0	2

We turn the adjacency matrix into a vector, drop duplicate elements that exist as the matrix is symmetrical, and normalize the vector, which now has the same properties as a probability density function. These transformations allow us to use distance metrics developed for density functions, such as the Jenson-Shannon distance, to compute the environmental distance between areas. Multivariate adjacency matrices allow for polythetic classifications and integrate the spatial configuration of multiple environmental variables within the catchment. In contrast to alternative approaches, spatial signatures directly incorporate the frequency and spatial configuration of environmental variables. A drawback of this method is that we can only use categorical variables, as adjacency matrices cannot be defined for continuous variables. To our best knowledge, this approach has only been applied in a recent Bachelor's thesis (Stidl, 2023) and merits further investigation.

An extensive review of all available methods is far beyond the scope of this discussion. Generally, all of the methods described above might provide good regionalizations. Which proves most useful will need to be determined through trial and error. Given that we must construct these classifications to evaluate them, it presents a good opportunity to use ensemble clustering (Golalipour *et al.*, 2021). Instead of relying on a single classification, we compute multiple partitions and combine them. This identifies regions with support from multiple algorithms and regions where the algorithms differ in judgment. We might regard these regions as less certain and treat them similarly to biogeographic transition zones or ecotones. Integrating uncertainty into ATS, through this or other means, is the last proposal we will discuss.

5.2.2.4 Use probabilistic type membership

Most ATS use crisp classes, i.e., each unit is exclusively part of one type. ATS with crisp classes are straightforward to use but mask the uncertainty of class membership. Whenever we use models, the results are associated with uncertainty due to the model selection and construction and uncertainty due to the apparent randomness of the study object (Matthies, 2007). The fuzzy membership value u_{ij} can be interpreted as the probability that unit i is part of cluster j (Zadeh, 1965). Since probability can quantify uncertainty (e.g., Stigler, 1986), u_{ij} express our uncertainty about the membership of i in j. We can further quantify our uncertainty across observations with the Shannon-Wiener entropy (Shannon, 1948) or Gini-coefficient (Gini, 1921). Optimally, we would have low uncertainty, i.e., only membership values close to 1, in which case the fuzzy classification would be similar to a crisp classification (McBratney & Moore, 1985). Especially in broad-scale applications, however, this is unlikely. Areas of high uncertainty are likely to occur due to low sample density or higher intrinsic variability.

Besides uncertainty, the membership value can also indicate a transitory environment between types, also known as ecotones or, at broader scales, biogeographic transition zones. Recent results indicate that freshwater ecosystems are best described as a patchy continuum (Collins *et al.*, 2018; Maasri *et al.*, 2021a). While the unrestrained continuum perspective in ordinations misses the opportunity to generalize from types, crisp classifications impose artificially strong retrains. Fuzzy classifications represent a middle ground that can combine continuity with patchiness (Feilhauer *et al.*, 2021).

As such, they have been used to estimate the location and width of ecotones in terrestrial systems (Brown, 1998; Olivero, Márquez & Real, 2013; De Klerk *et al.*, 2018), and similar approaches are feasible for freshwater ecosystems.

There is little to no literature on how current policy applications of ATS would need to change, how they might benefit, or how they might suffer from changing to a probabilistic perspective. For the WFD, reference conditions might be determined as the weighted product of crisp reference conditions. High-entropy units might constitute exceptional cases and merit increased monitoring efforts. On the one hand, they represent rare ecosystems, and on the other hand, their idiosyncratic nature might indicate that extrapolations from other sites are error-prone. Ecosystem managers are constantly required to make decisions under uncertainty (Milner-Gulland & Shea, 2017). While classifications aim to reduce this uncertainty, they should not hide it, and we should still be able to communicate it (Jansen *et al.*, 2022). There is nothing to lose in starting with a fuzzy approach since we can always collapse them into crisp classifications, while the opposite is impossible.

5.2.3 Synthesis

This section will summarize the four suggestions and clarify how they would interlock. The proposed ATS consists of multiple hierarchical levels. The highest level is a regional ATS, created with spatially constrained algorithms like NCuts, FCM, or spatial signatures. The regions are conceptualized as macrosystems. Within each macrosystem, we define place-independent FPZ types. Each FPZ type is constrained to occur within a single macrosystem. We use abiotic variables to delineate macrosystems and FPZs but transform them with Generalized Dissimilarity Models to weigh them according to their relevance to the turnover rate and to incorporate the non-linear nature of turnover along environmental gradients. This step regularizes the environmental variables, as gradients with minimal biotic turnover receive weak weights. For this reason, because the ATS consists of nominal types, and because we focus on prediction, the initial selection of variables can be broad and does not need to concern itself with parsimony. We should use of the diversity of available spatial data, consider all parts of the riverine landscape, interpolate variables where necessary, and incorporate temporal dynamics more strongly. Lastly, we must validate the ATS with synthetic and field data in iterative tests. Metacommunity models can provide many independently simulated data sets for bespoke combinations of spatial signals, biotic interactions, stochasticity, and species sorting. These can be used to identify the strengths and weaknesses of current systems and create reasonable baselines for ATS performance.

5.3 Why we should develop broad-scale ATS

The ATS we tested and used cover Europe. Some of them are used, at least indirectly, in practical applications. Illies Freshwater Ecoregions are part of the System A proposal for national WFD ATS (EC, 2000), the Biogeographic Regions inform the distribution of Natura 2000 sites (Evans, 2012), and the BRT are discussed as a new EUNIS freshwater typology system (Watson *et al.*, 2021). Simultaneously, the BRT have quickly become a standard tool for broad-scale limnological studies in Europe (Borgwardt *et al.*, 2019; Poikane *et al.*, 2019; Birk *et al.*, 2020; Posthuma *et al.*, 2020; Gerke *et al.*, 2021; Leitner *et al.*, 2021; Lemm *et al.*, 2021; Büttner *et al.*, 2022; Vigiak *et al.*, 2023). These facts illustrate the interest of both applied and basic ecologists in broad-scale ATS. Beyond these benefits, broad-scale ATS are crucial for international environmental policy.

ATS and ecosystem management remain national affairs in Europe as member states implement the WFD. However, environmental problems cross political borders, which are usually independent of ecological ones (Hundloe, 1998; Dallimer & Strange, 2015). Of the 111 river basin districts delineated in the WFD, 40 cross national borders, covering 60% of EU territory (Lyche Solheim *et al.*, 2012). Principle 21 of the Stockholm Declaration calls on nations to ensure that “activities within their jurisdiction or control do not cause damage to the environment of other States or areas beyond the limits of national jurisdiction" (UN, 1972). However, given the daily occurrence of such transboundary harms, there is a large discrepancy between *de jure* and *de facto* (Bodansky, 1995; Knox, 2002). As examples, consider the recent disaster in the Oder River (Schulte *et al.*, 2022; Free *et al.*, 2023; Sobieraj & Metelski, 2023), acid rain (Likens, Bormann & Johnson, 1972; Singh & Agrawal, 2007), or Climate change (IPCC, 2021). Accumulating transboundary harm can result in hard-to-manage transboundary crises that commonly entail significant damages (Boin, 2009, 2019). In addition to harm, services transcend borders. López-Hoffman *et al.* (2010) show multiple examples of how conservation of habitats benefits societies in multiple countries. Conservation projects that contribute to maintaining this transboundary flow of services are hindered by socio-political borders when the latter reduce connectivity between protected areas (Opermanis *et al.*, 2012). Connectivity between habitats on both sides of borders is important, as border regions often harbor communities high in diversity and endemism (Huang *et al.*, 2012; Erg *et al.*, 2015; Fowler *et al.*, 2018), and climate change is likely to cause transboundary range shifts (Titley *et al.*, 2021). Kark *et al.* (2009) showed that multinational conservation projects have the potential to be more effective and cheaper than national ones. An international environmental policy is needed to account for flows of harms and services across political borders and would greatly benefit from suitable typology systems to define reference conditions or design monitoring programs. These typology systems need to be at the scale of the policy, and hence, international policy requires broad-scale typology systems.

Typology systems are used to optimize the spatial distribution of monitoring sites. For national monitoring, as conducted under the WFD, national ATS are sufficient. However, Maasri *et al.* (2021a) recently identified broad-scale biomonitoring efforts as one of 15 freshwater biodiversity science priorities. Such broad-scale monitoring will be required to tackle the ongoing biodiversity crisis. A common theme running through this thesis is the need for more and more accurate data. We will need better chemical monitoring to estimate the exposure ecosystems face. We will need more sensitivity data to estimate the burden this exposure entails. We will need broad-scale biomonitoring to close the biodiversity shortfalls (García-Girón *et al.*, 2023a), detect biodiversity trends (Haase *et al.*, 2023), and compute meaningful indices that track our progress toward global biodiversity policy targets. The Global Biodiversity Framework has formulated 23 measurable targets for 2030. Measuring progress towards the targets of international environmental treaties is difficult (Balsiger & Prys, 2016) as it requires harmonized data at the relevant spatial scale, which for the biodiversity framework is global (Gonzalez *et al.*, 2023). The current global data repositories suffer from geographic and taxonomic biases (Hughes *et al.*, 2021), and their samples are mostly nonprobability samples (Boyd, Powney & Pescott, 2023). Data that do not suffer from these issues are needed to accurately derive variables of interest, such as essential biodiversity variables (Pereira *et al.*, 2013; Schmeller *et al.*, 2018) and essential ecosystem service variables (Balvanera *et al.*, 2022). Only broad-scale harmonized biomonitoring based on probabilistic survey design can generate such data (Hawkins & Yuan, 2016; Harper *et al.*, 2021). Efforts to create such monitoring networks are underway in the form of the Global Biodiversity Observation System (Gonzalez *et al.*, 2023) or the Global Lake Ecological Observatory Network (Weathers *et al.*, 2013). Broad-scale typology systems will be crucial for an informed distribution of sampling sites, the detection and assessment of trends against reference conditions, and, hence, the successful implementation of international biodiversity policy.

5.4 Conclusion

Broad-scale typology systems are a potentially crucial tool to many aspects of international environmental policy, including ecological risk assessment. Currently, European broad-scale aquatic typology systems are not up to this task, as they do not capture patterns in biotic assemblage composition. This thesis highlights the many ways in which various fields of limnology would benefit from functional typology systems and proposes several steps for developing more functional systems. Beyond new variables and algorithms, a conceptual synthesis and a validation of testing approaches are necessary to ensure scientific rigor, and to stop *ad hoc* approaches and seemingly arbitrary quality thresholds. We cannot conclusively answer whether assemblage sensitivity toward pesticides is spatially structured in Europe. While our analyses do not suggest such patterns, doubt concerning the suitability of the typology systems and the model used to predict sensitivities are justified. Nonetheless, the study can be an important stepping stone for future studies into the surprisingly understudied area of spatial sensitivity distribution.

CHAPTER 6

Appendix

6.1 Supplementary Materials for *Evaluating the biological validity of European river typology systems with least disturbed benthic macroinvertebrate communities*

6.1.1 SM 1 - Data Sets

Table 6.1: Overview of individual data sets. The number of samples and sites refers to sites within 500 meters of a river reach in the digital representation of the broad river types. pMHS abbreviates proportional multihabitat sampling. To avoid repetition, we summarized the following sampling schemes by their names AQEM (pMHS with kicknet; 20 sampling units; 25x25cm frame; 500 µm mesh size), PERLA (pMHS with kicknet; 3 minutes; 25x25cm frame; 500 µm mesh size), and AFNOR XP T 90 333 (MHS with kicknet; 12 samples, 20x25cm frame; 500 µm mesh size; not fully proportional but 50 percent of samples are taken on the dominant substrate)

ID	data set	all samples (sites)	least disturbed samples (sites)	sampling method
1	Project AQEM (Romania)	258 (97)	18 (7)	AQEM
2	Project AQEM (Sweden)	76 (38)	68 (34)	AQEM
3	Project Biodrought	18 (9)	4 (2)	PERLA
4	Cantabria and Picos de Europa	65 (65)	37 (37)	AQEM
5	Monitoring Spain	2068 (1569)	889 (679)	AQEM
6	Koutajoki Basin	8 (8)	8 (8)	pMHS with kicknet; 4 samples, 30s each; 300 µM mesh
7	Naiades	5238 (3159)	1737 (1053)	AFNOR XP T 90 333
8	Monitoring Czech Republic	3114 (1410)	506 (235)	PERLA
9	Project STAR	14 (14)	10 (10)	AQEM

ID	data set	all samples (sites)	least disturbed samples (sites)	sampling method
10	Monitoring France (RCS Network)	2252 (2252)	808 (808)	AFNOR XP T 90 333
11	Monitoring Germany	11573 (8300)	2599 (1634)	AQEM
12	Monitoring Greece	97 (97)	36 (36)	pHMS with kicknet; 3 minutes; 25x23cm frame; 900 µM mesh
13	Monitoring Netherlands	755 (483)	57 (32)	pHMS with handnet; 5 meters; 30x15 cm frame; 500 µM mesh
14	Monitoring Poland	1499 (1264)	794 (675)	AQEM
15	Monitoring Portugal	516 (501)	227 (220)	pMHS with kicknet; 6 samples each with 1m length, all microhabitats; 25x25cm frame; 500 µM mesh
16	Monitoring Slovakia	22 (22)	4 (4)	AQEM
17	Project WISER	1590 (1590)	292 (292)	AQEM
18	Monitoring UK	4180 (2153)	870 (444)	pHMS with kicknet; 3 minutes; 1000 µM mesh
19	Monitoring Finland	288 (288)	268 (268)	pMHS with kicknet; 4 samples, 30s each; 500 µM mesh
20	Monitoring Croatia	31 (31)	15 (15)	AQEM
21	Monitoring Norway	51 (51)	51 (51)	pMHS with kicknet; 9 samples each 20sm 1m. 25x25cm frame; 250 µM mesh

6.1.2 SM 2 - Determination of least disturbed sites

We used the WFD ecological status assessment for each sub catchment unit (FEC), to determine the optimal threshold for least disturbed sites. We computed the percentage of FECs with high or good ecological status (henceforth denoted as good) and the percentage of FECs with moderate, poor, or bad (henceforth shortened to bad) ecological status at threshold values ranging from 0.05 to 1 (Fig. 6.1). The percentage of good and bad FECs increased with an increasing threshold value. For low threshold values (approximately < 0.3), the percentage of good FECs increased faster than that of bad FECs. The difference between them was maximized at a threshold of 0.24 (Fig. 6.2).

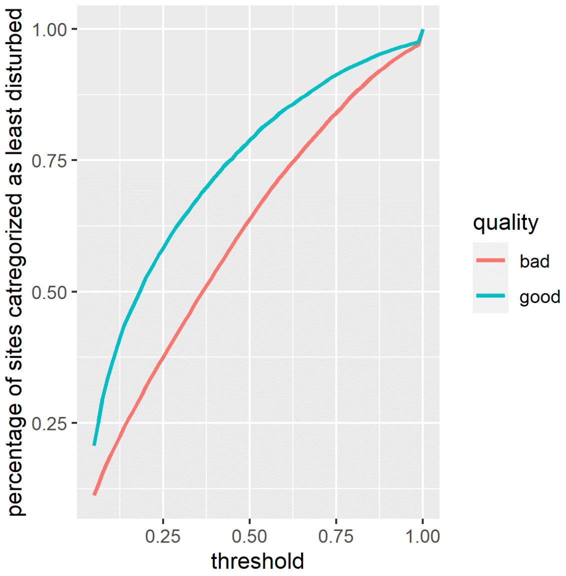

Figure 6.1: Percentage of sites with good or high (good) or moderate, poor, and bad ecological status (bad) that were classified as least disturbed as a function of the delineation threshold.

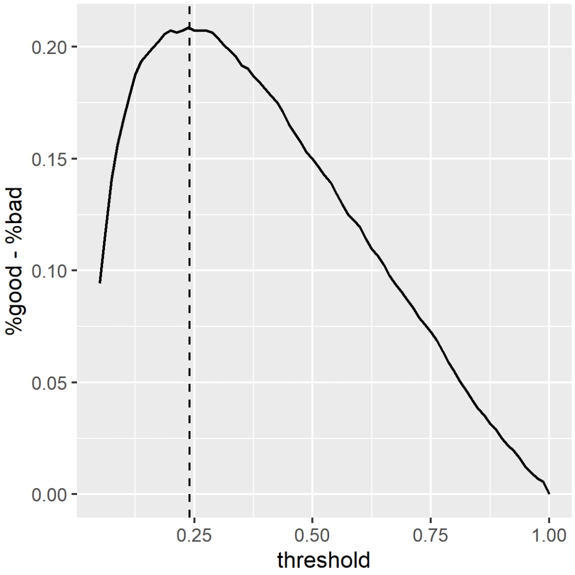

Figure 6.2: Difference between the percentage of FECs with good or high (good) and FECs with moderate, poor, or bad ecological status (bad) as a function of the delineation threshold. A dashed line marks the curve's maximum at a threshold of 0.24.

We provide the mean and standard deviation of the seven pressure variables in least disturbed FECs (Table 6.2).

Table 6.2: Mean values and standard deviation for the seven pressure variables in subcatchment unit classified as least disturbed. For more information the Broad River Types see table 2.1 or Lyche Solheim et al. (2019). msPAF stands for multi-species potentially affected fraction.

	Total Phosphorous Load		Total Nitrogen Load		Urban Area		Agricultural area		mean annual flow		mean annual base flow index		msPAF [Ratio]	
Broad River Type	mean	sd	mean	mean	mean	mean	mean	mean	mean	mean	mean	mean	mean	mean
RT1	19.1	15.33	5.9	4.58	0.06	0.06	0.09	0.07	4.91	5.41	2.32	5.08	0.02	0.03
RT2	31.7	24.72	10.8	8.22	0.06	0.06	0.08	0.08	1.29	2.95	1.25	3.57	0.04	0.05
RT3	46.2	54.79	13.9	9.22	0.04	0.06	0.04	0.07	0.46	1.73	0.86	2.84	0.05	0.06
RT4	22.5	35.55	6.6	9.39	0.05	0.05	0.06	0.07	0.97	2.87	0.55	2.29	0.02	0.04
RT5	39.4	61.14	10.3	13.18	0.04	0.05	0.04	0.06	0.38	1.75	0.45	2.13	0.03	0.04
RT6	36.5	18.17	10.9	4.75	0.10	0.07	0.07	0.08	1.54	3.47	0.74	2.75	0.05	0.05
RT7	33.4	16.92	11.3	5.27	0.06	0.07	0.04	0.06	0.28	1.26	0.66	2.50	0.05	0.05
RT8	19.6	17.14	6.0	5.66	0.05	0.07	0.03	0.05	1.04	3.14	0.39	2.12	0.01	0.03
RT9	25.4	30.28	7.4	7.36	0.03	0.05	0.02	0.04	0.31	1.63	0.35	1.89	0.02	0.04

	Total Phosphorous Load		Total Nitrogen Load		Urban Area		Agricultural area		mean annual flow		mean annual base flow index		msPAF [Ratio]	
Broad River Type	mean	sd	mean	mean	mean	mean	mean	mean	mean	mean	mean	mean	mean	mean
RT10	28.1	14.78	7.1	3.61	0.05	0.06	0.02	0.04	0.78	2.62	0.83	3.18	0.02	0.03
RT11	21.3	15.05	5.9	2.89	0.03	0.05	0.10	0.08	2.97	5.46	1.57	4.14	0.04	0.04
RT12	20.9	15.63	5.9	3.26	0.03	0.05	0.07	0.08	0.88	2.43	1.75	4.65	0.05	0.05

6.1.3 SM 3 - Distribution of samples between types and seasons

We analyzed combinations of types and seasons for which we had more than 15 samples from the least impaired catchments. For the Broad River Types, we analyzed all twelve types for spring and summer and omitted Mediterranean, temporary, and very small streams (RT12). For Illies Freshwater Ecoregions and the Biogeographic Regions, we omitted more types (Fig.s 6.3 and 6.4).

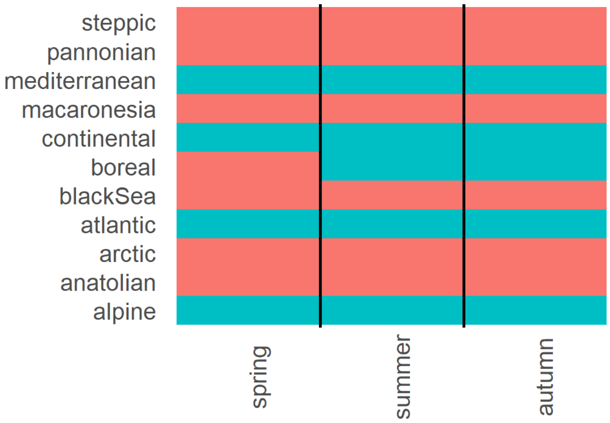

Figure 6.3: Combinations of Biogeographic Regions and seasons that were analyzed. The blue cells indicate that the combination of type and seasons was analyzed. The red cells indicate that the combination was not analyzed.

The number of sites available for each type differed strongly between types and seasons. The number of samples for the types of each typology system are provided in the tables 6.3 to 6.5.

Table 6.3: Number of samples for each Broad River Types and season.

Broad River Type	Spring	Summer	Autumn
RT1 - Very Large Rivers	53	104	57
RT2 - Large lowland rivers, calcareous	611	477	422
RT3 - Small lowland rivers, calcareous	356	197	231
RT4 - Large lowland rivers, siliceous	394	318	410
RT5 - Small lowland rivers, siliceous	375	267	319

Broad River Type	Spring	Summer	Autumn
RT6 - Large mid-altitude rivers, calcareous	208	289	165
RT7 - Small mid-altitude rivers, calcareous	139	104	85
RT8 - Large mid-altitude rivers, siliceous	501	636	588
RT9 - small mid-altitude rivers, siliceous	511	384	346
RT10 - Highland/glacial river	90	339	214
RT11 - Mediterranean rivers, perennial	122	281	93
RT12 - Mediterranean rivers, intermittent	56	108	0

Table 6.4: Number of samples for each Biogeographic Region and season.

Biogeographic Region	Spring	Summer	Autumn
alpine	98	195	208
atlantic	911	805	956
boreal	0	26	239
continental	2,184	1,985	1,390
mediterranean	223	493	137

Table 6.5: Number of samples for each Freshwater Ecoregion and season.

Freshwater Ecoregion	Spring	Summer	Autumn
Alps	62	71	44
Borealic uplands	0	0	74

Freshwater Ecoregion	Spring	Summer	Autumn
Central highlands	848	429	442
Central plains	1,015	542	418
Dinaric western Balkan	16	0	0
Eastern plains	240	96	39
England	538	65	515
Fenno-scandian shield	0	26	226
Hungarian lowlands	45	18	35
Ibero-Macaronesian region	229	388	97
Italy and Corsica	0	22	0
Pyrenees	0	64	65
The Carpathiens	50	22	39
Western highlands	248	776	402
Western plains	125	985	534

6.1.4 SM 4 - Mantel Tests

To evaluate the correlation between distance matrices at different taxonomic and numerical resolutions, we conducted mantel tests (Mantel, 1967) for every data set where this was feasible (Fig. 6.5). The mantel tests were conducted with the mantel function from the vegan R package (Oksanen *et al.*, 2022) with 999 permutations. For presence-absence data, we used the Jaccard distance, and for abundance data the Bray-Curtis distance. In some data sets, some sites had only observations with low taxonomic resolutions (i.e., family- or order-level). We removed such sites from the data set, as the mantel test requires distance matrices with the same dimensions, i.e., number of sites.

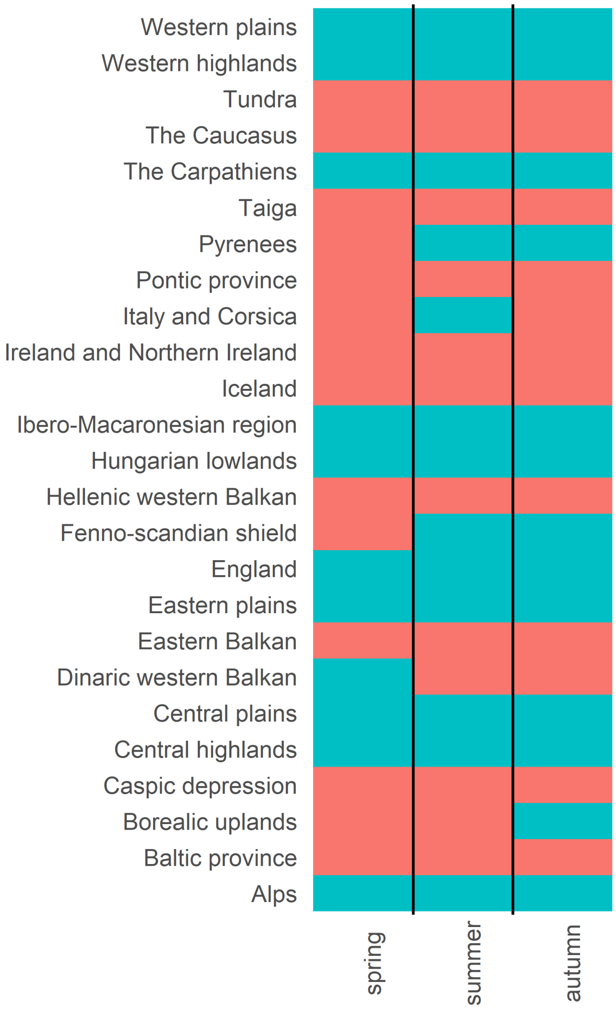

Figure 6.4: Combinations of Illies' Freshwater Ecoregions and seasons that were analyzed. The blue cells indicate that the combination of type and seasons was analyzed. The red cells indicate that the combination was not analyzed.

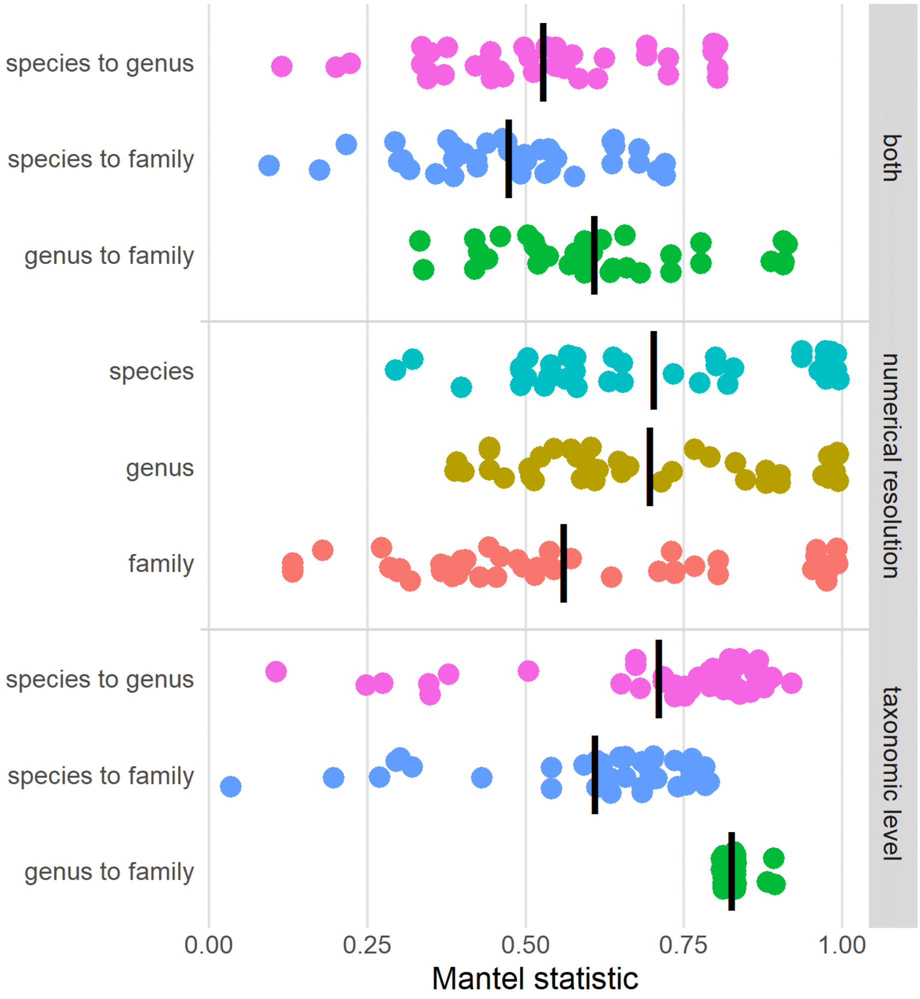

Figure 6.5: Correlation between distance tables of different numerical and taxonomic resolutions. Each point shows the mantel test statistic for one data set and season. The black vertical lines show the mean values.

6.1.5 SM 5 - Genus-Level Analysis

We repeated all steps of the main analysis with a data set that was resolved to genus-level and consisted of relative abundances. Henceforth, we will refer to this analysis as the genus-level analysis and to the analysis from the main text as the family-level analysis. We omitted the data sets 8, 10, 12, 14, 20, and 21 (Table 6.1) because they only contained presence-absence information and the data sets 5 and 15 (Table 6.1) because genus information was missing from 97 % and 100 % of observations, respectively. In the remaining data sets, genus information was missing from 2.3 % (data set 3) to 28 % (data set 7) of observations, with genus information missing from 11 % of observations on average. In total, the number of sites and samples was reduced to 4.154 and 6.323 compared to 6.965 and 9.976 in the family-level analysis (cf. Fig. 2.1 and Fig. 6.6).

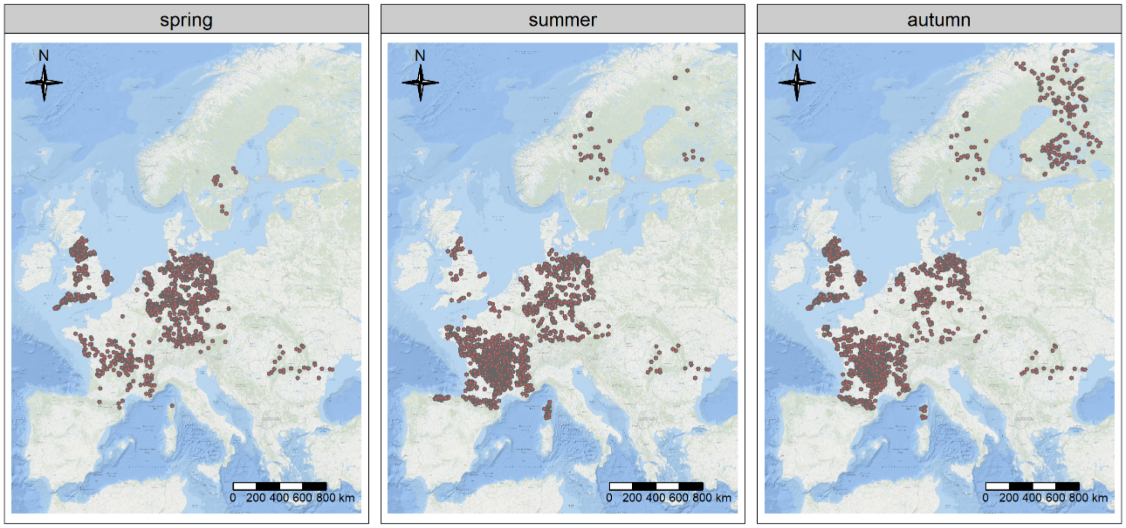

Figure 6.6: Spatial distribution of sampling sites. Each facet shows a different season.

After removing genera that occurred in less than 1 % of samples, the seasonal data sets contained 244, 238, and 234 different genera respectively. That is, the number of genera was 2.6, 2.3, and 2.4 times higher than the respective number of families.

All analyses were conducted in the same way as for the main analysis in the manuscript. We used Bray-Curtis distance instead of the Jaccard distance to account for the abundance data. Except for the spring samples of the Biogeographic Regions, biotic communities were more similar within than between types (i.e., ANOSIM and CS: p-value < 0.05; Fig. 6.7), but differences were rather small ranging from Illies' Freshwater Ecoregions ($\overline{R_{ANOSIM}} = 0.20$; $\overline{CS} = 0.07$) to the Broad River Types ($\overline{R_{ANOSIM}} = 0.14$; $\overline{CS} = 0.05$) and the Biogeographic Regions ($\overline{R_{ANOSIM}} = 0.05$; $\overline{CS} = 0.03$). All these test statistics were lower than for the analysis of family-level presence-absence data.

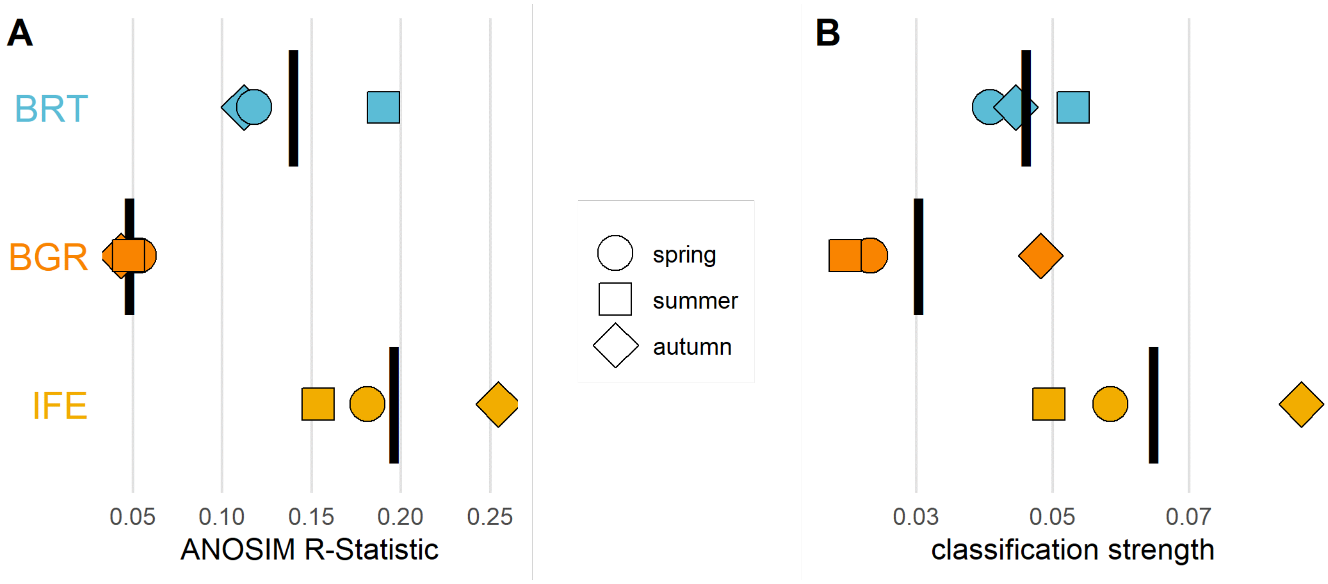

Figure 6.7: Comparison of within-type and between-type. In both panels, larger values imply a larger difference between within-type and between-type similarity and hence a better classification performance. Y-axis and colors indicate the typology system: the Broad River Types (BRT), Biogeographic Regions (BGR), and Illies' Freshwater Ecoregions (IFE). The shapes indicate the season (circle = spring, square = summer, and diamond = autumn). The vertical black lines are mean values across seasons. (A) Results of the ANOSIM. (B) Results of the classifications strength analysis.

Within type similarity was generally lower than in the family-level analysis (Fig. 6.8). The within-type similarities of the genus-level analysis matched those of the family-level analysis, i.e., similarities are higher within mid- and high-altitude types than within lowland types.

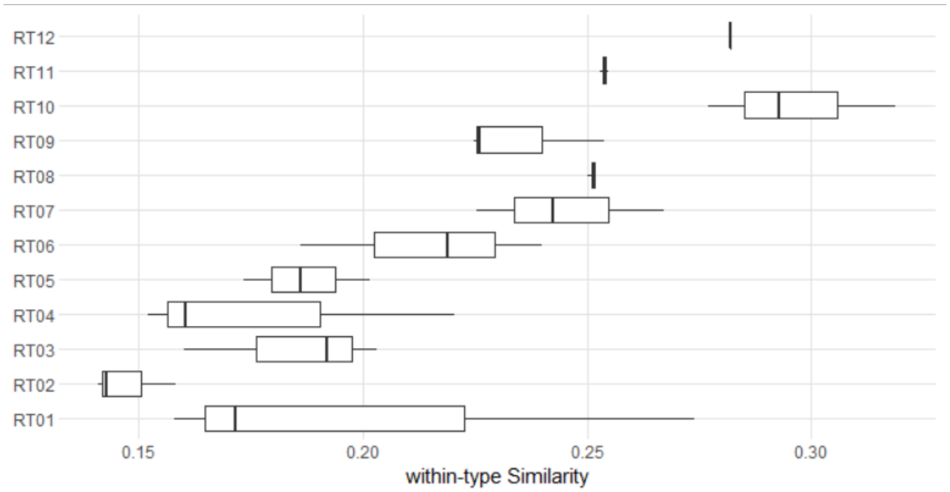

Figure 6.8: The within-type similarity of Broad River Types. Each boxplot summarizes the values for the three seasons (except for RT12 where only spring and summer were analyzed). See Lyche Solheim et al. (2019) or Table 2.1 for a description of the types.

The mean indicator value of indicator genera as well as the number of statistically significant indicator genera was higher in all combinations of typology systems and seasons than in random permutations (pseudo-p-value < 0.05). Compared to the family-level analysis, the mean value across seasons decreased from 0.49 to 0.44 for the Biogeographic Regions, from 0.49 to 0.37 for Illies' Freshwater Ecoregions, and from 0.38 to 0.31 for the Broad River Types. The strongest seasonal trend was observed for the Biogeographic regions with a mean indicator value of 0.58 for spring and 0.37 for autumn (Fig. 6.9). The high spring value corresponds to the lowest observed number of indicator genera (40) which is far below the overall average of 136. The two patterns that were observable in the main analysis, namely higher number of indicative families in the Broad River Types and higher number of indicative families in autumn are both missing in the genus-level analysis.

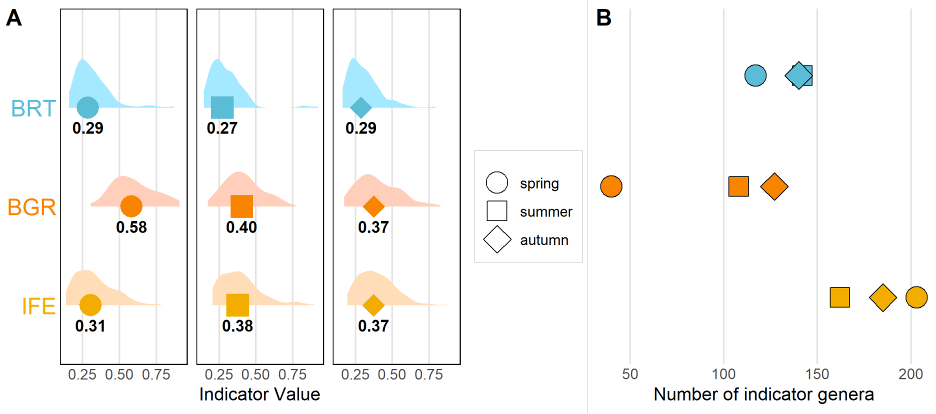

Figure 6.9: Indicator taxa for the Broad River Types (BRT), the Biogeographic Regions (BGR), and Illies' Freshwater Ecoregions (IFE). (A) Distribution of indicator values. Values can range between 0 and 1, where 1 indicates a perfect indicator taxon. The points within the density curves show the median, which is also provided as a number. Three panels show the three different seasons (summer, spring, and autumn), which are also highlighted by the symbol of the median, (B) The number of indicator families. Point shapes indicate seasons and point colors the typology systems.

The mean indicator value of indicator genera as well as the number of statistically significant indicator genera was higher in all combinations of typology systems and seasons than in random permutations (pseudo-p-value < 0.05). Compared to the family-level analysis, the mean value across seasons decreased from 0.49 to 0.44 for the Biogeographic Regions, from 0.49 to 0.37 for Illies' Freshwater Ecoregions, and from 0.38 to 0.31 for the Broad River Types. The strongest seasonal trend was observed for the Biogeographic regions with a mean indicator value of 0.58 for spring and 0.37 for autumn (Fig. 6.10). The high spring value corresponds to the lowest observed number of indicator genera (40) which is far below the overall average of 136. The two patterns that were observable in the main analysis, namely higher number of indicative families in the Broad River Types and higher number of indicative families in autumn are both missing in the genus-level analysis.

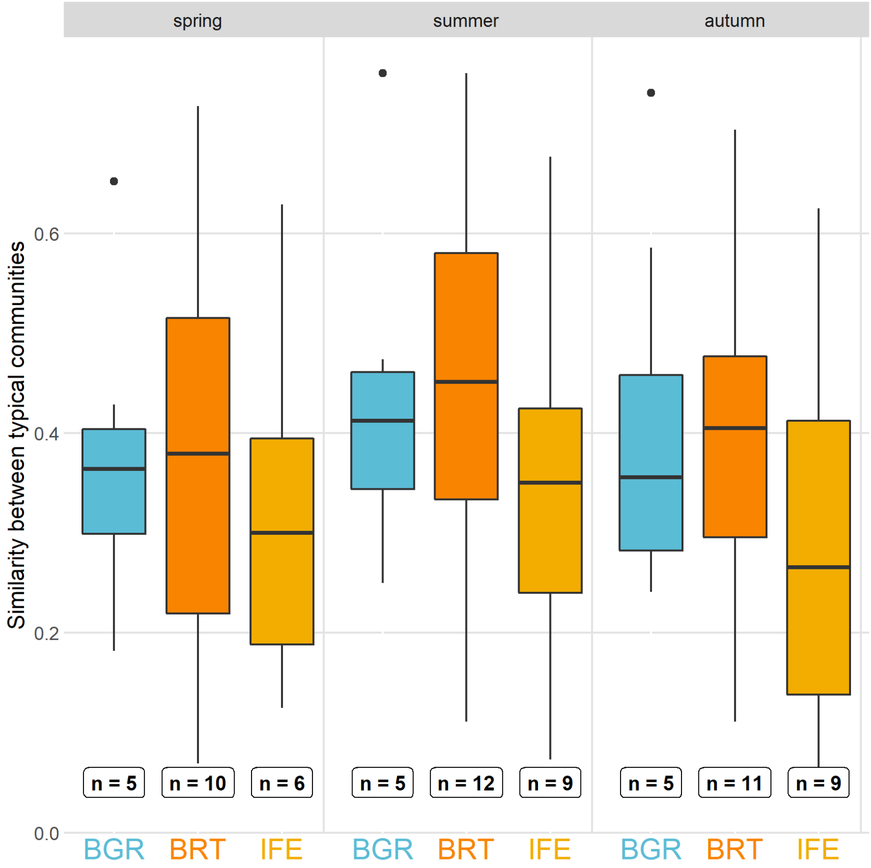

Figure 6.10: Bray Curtis similarities between typical communities for the Broad River Types (BRT), Biogeographic Regions (BGR), and Illies Freshwater Ecoregions (IFE). A similarity of 1 implies identical communities, while a similarity of 0 implies no shared taxa. The three horizontally ordered panels show different seasons (spring, summer, and autumn). The n below the boxplots is the number of individual types in the comparison.

6.1.6 SM 6 - Within and between type similarities

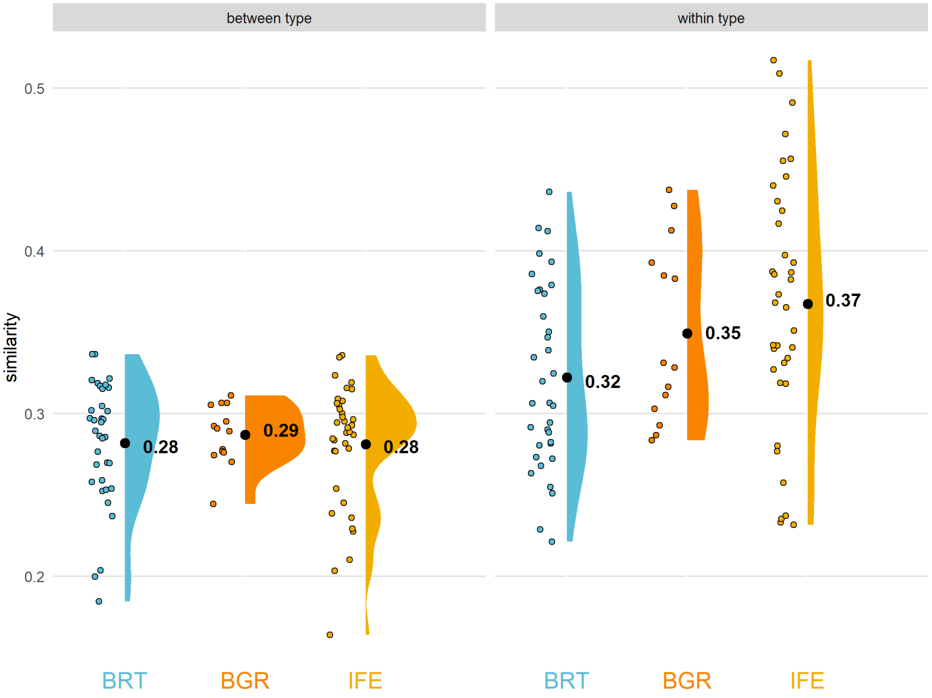

Figure 6.11: Similarity between and within types of the Broad River Types (BRT), Illies Freshwater Ecoregions (IFE) and the Biogeographic Regions (BGR). Density curves show the distribution of similarities which are shown as points. The black point within the density curve show the mean value which is also given as a number.

6.1.7 SM 7 - Typical communities

The figures 6.12 to 6.14 show the composition of typical communities for all three typologies. Lists of taxa are provided after the figures.

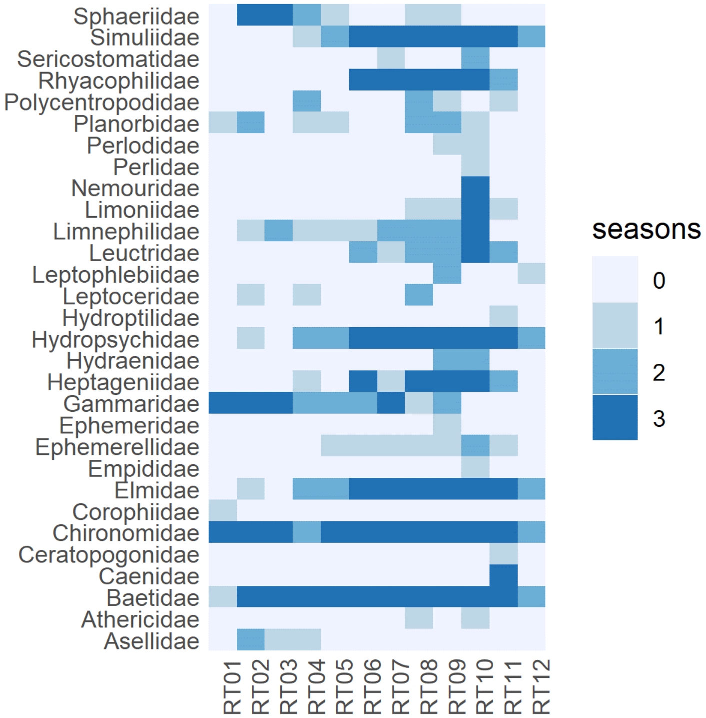

Figure 6.12: The composition of typical communities for the Broad River Types. The cell color indicates for how many seasons any given taxon is part of the typical community.

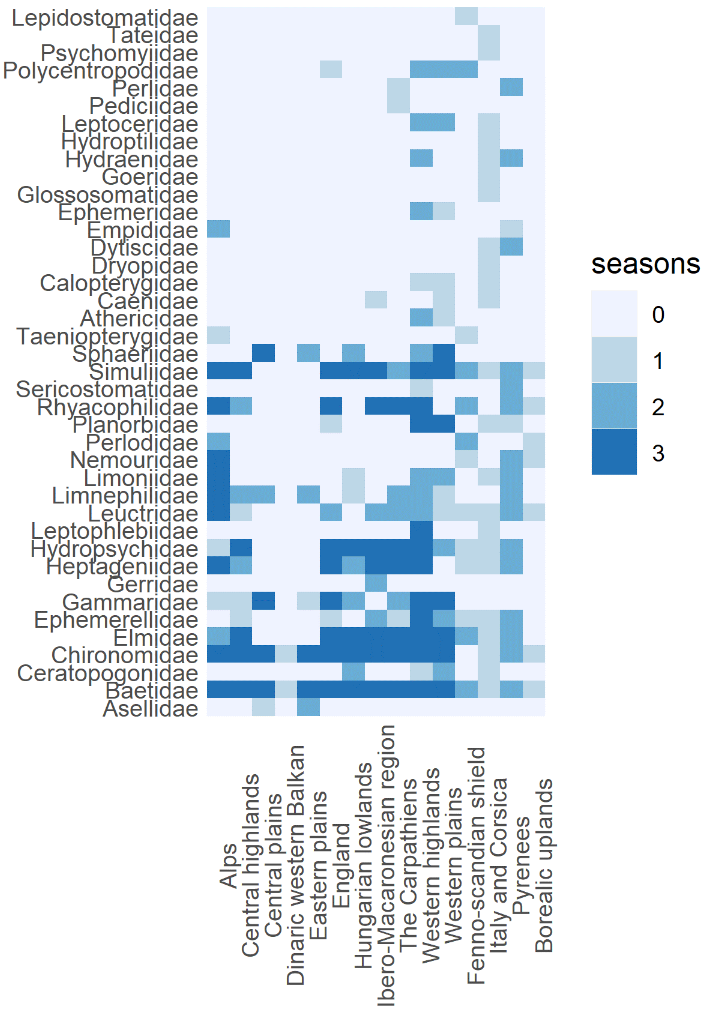

Figure 6.13: The composition of typical communities for Illies Freshwater Ecoregions. The cell color indicates for how many seasons any given taxon is part of the typical community.

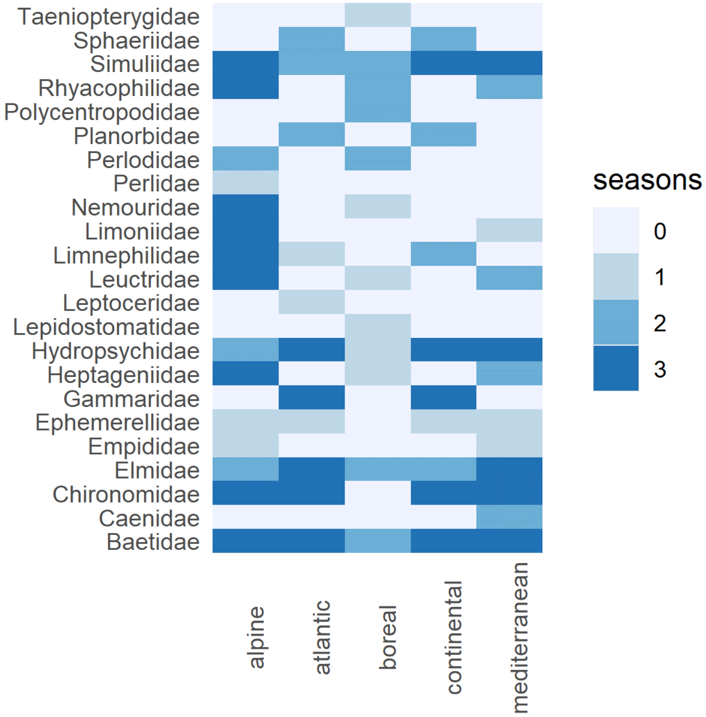

Figure 6.14: The composition of typical communities for the Biogeographic Regions. The cell color indicates for how many seasons any given taxon is part of the typical community.

6.1.7.1 Typical Taxa - Broad River Types

RT01 – Very large rivers

Spring

Chironomidae, Gammaridae

Summer

Chironomidae, Gammaridae, Planorbidae, Corophiidae

Autumn

Chironomidae, Gammaridae, Baetidae

RT02 – Lowland, calcareous or mixed, medium- large

Spring

Chironomidae, Baetidae, Sphaeriidae, Gammaridae, Asellidae, Limnephilidae

Summer

Chironomidae, Hydropsychidae, Baetidae, Gammaridae, Planorbidae, Leptoceridae, Sphaeriidae, Asellidae

Autumn

Chironomidae, Gammaridae, Baetidae, Elmidae, Planorbidae, Sphaeriidae

RT03 – Lowland, calcareous or mixed, very small - small

Spring

Chironomidae, Baetidae, Sphaeriidae, Gammaridae, Asellidae, Limnephilidae

Summer

Chironomidae, Baetidae, Limnephilidae, Gammaridae, Sphaeriidae

Autumn

Chironomidae, Gammaridae, Baetidae, Sphaeriidae

RT04 – Lowland, siliceous incl organic, medium - large

Spring

Chironomidae, Baetidae, Gammaridae, Limnephilidae

Summer

Chironomidae, Hydropsychidae, Elmidae, Baetidae, Gammaridae, Planorbidae, Leptoceridae, Sphaeriidae, Polycentropodidae, Asellidae

Autumn

Hydropsychidae, Baetidae, Simuliidae, Heptageniidae, Elmidae, Polycentropodidae, Sphaeriidae

RT05 - Lowland, siliceous incl organic, very small - small

Spring

Chironomidae, Baetidae, Gammaridae, Limnephilidae

Summer

Chironomidae, Hydropsychidae, Ephemerellidae, Elmidae, Baetidae, Gammaridae, Simuliidae, Planorbidae, Sphaeriidae

Autumn

Hydropsychidae, Chironomidae, Baetidae, Simuliidae, Elmidae

RT06 – Mid-altitude, calcareous, incl. organic, medium - large

Spring

Chironomidae, Baetidae, Hydropsychidae, Simuliidae, Heptageniidae, Rhyacophilidae, Elmidae, Limnephilidae

Summer

Chironomidae, Hydropsychidae, Leuctridae, Ephemerellidae, Elmidae, Baetidae, Heptageniidae, Gammaridae, Rhyacophilidae, Simuliidae

Autumn

Hydropsychidae, Chironomidae, Gammaridae, Baetidae, Simuliidae, Leuctridae, Heptageniidae, Rhyacophilidae, Elmidae

RT07 – Mid-altitude, calcareous, incl. organic, very small – small

Spring

Chironomidae, Baetidae, Hydropsychidae, Simuliidae, Rhyacophilidae, Elmidae, Gammaridae, Limnephilidae

Summer

Chironomidae, Hydropsychidae, Ephemerellidae, Elmidae, Baetidae, Limnephilidae, Gammaridae, Rhyacophilidae, Simuliidae

Autumn

Hydropsychidae, Chironomidae, Gammaridae, Baetidae, Simuliidae, Leuctridae, Heptageniidae, Rhyacophilidae, Elmidae, Sericostomatidae

RT08 – Mid-altitude, siliceous, incl. organic, medium - large

Spring

Chironomidae, Baetidae, Hydropsychidae, Simuliidae, Heptageniidae, Rhyacophilidae, Elmidae, Limnephilidae

Summer

Chironomidae, Limoniidae, Hydropsychidae, Leuctridae, Ephemerellidae, Elmidae, Baetidae, Athericidae, Limnephilidae, Heptageniidae, Gammaridae, Rhyacophilidae, Simuliidae, Planorbidae, Leptoceridae, Polycentropodidae

Autumn

Hydropsychidae, Chironomidae, Baetidae, Simuliidae, Leuctridae, Heptageniidae, Rhyacophilidae, Elmidae, Leptoceridae, Planorbidae, Polycentropodidae, Sphaeriidae

RT09 – Mid-altitude, siliceous, incl. organic, very small – small

Spring

Chironomidae, Baetidae, Hydropsychidae, Simuliidae, Heptageniidae, Perlodidae, Rhyacophilidae, Elmidae, Gammaridae, Limnephilidae

Summer

Chironomidae, Limoniidae, Hydropsychidae, Leuctridae, Ephemerellidae, Elmidae, Baetidae, Ephemeridae, Limnephilidae, Heptageniidae, Gammaridae, Rhyacophilidae, Leptophlebiidae, Simuliidae, Hydraenidae, Planorbidae, Sphaeriidae, Polycentropodidae

Autumn

Hydropsychidae, Chironomidae, Baetidae, Leptophlebiidae, Simuliidae, Leuctridae, Heptageniidae, Rhyacophilidae, Elmidae, Hydraenidae, Planorbidae

RT10 – Highland and glacial

Spring

Chironomidae, Baetidae, Hydropsychidae, Simuliidae, Heptageniidae, Leuctridae, Perlodidae, Rhyacophilidae, Nemouridae, Elmidae, Limoniidae, Limnephilidae

Summer

Chironomidae, Limoniidae, Hydropsychidae, Leuctridae, Ephemerellidae, Elmidae, Baetidae, Limnephilidae, Heptageniidae, Rhyacophilidae, Simuliidae, Hydraenidae, Sericostomatidae, Nemouridae

Autumn

Hydropsychidae, Limnephilidae, Empididae, Chironomidae, Baetidae, Limoniidae, Simuliidae, Leuctridae, Perlidae, Nemouridae, Heptageniidae, Rhyacophilidae, Athericidae, Ephemerellidae, Elmidae, Hydraenidae, Sericostomatidae, Planorbidae

RT11 – Mediterranean perennial

Spring

Chironomidae, Baetidae, Hydropsychidae, Simuliidae, Elmidae, Caenidae

Summer

Chironomidae, Limoniidae, Hydropsychidae, Leuctridae, Ephemerellidae, Elmidae, Baetidae, Caenidae, Heptageniidae, Rhyacophilidae, Ceratopogonidae, Simuliidae

Autumn

Hydropsychidae, Chironomidae, Baetidae, Simuliidae, Leuctridae, Heptageniidae, Rhyacophilidae, Caenidae, Elmidae, Hydroptilidae, Polycentropodidae

RT12 – Mediterranean temporary and very small

Spring

Chironomidae, Baetidae, Hydropsychidae, Simuliidae, Elmidae, Leptophlebiidae

Summer

Chironomidae, Hydropsychidae, Elmidae, Baetidae, Simuliidae

6.1.7.2 Typical Assemblages – Biogeographic Regions

Alpine

Spring

Chironomidae, Baetidae, Simuliidae, Heptageniidae, Leuctridae, Perlodidae, Rhyacophilidae, Nemouridae, Limoniidae, Limnephilidae

Summer

Empididae, Chironomidae, Limoniidae, Hydropsychidae, Leuctridae, Ephemerellidae, Elmidae, Baetidae, Limnephilidae, Heptageniidae, Rhyacophilidae, Simuliidae, Perlidae, Nemouridae

Autumn

Hydropsychidae, Limnephilidae, Chironomidae, Baetidae, Perlodidae, Limoniidae, Simuliidae, Leuctridae, Nemouridae, Heptageniidae, Rhyacophilidae, Elmidae

Atlantic

Spring

Chironomidae, Baetidae, Hydropsychidae, Elmidae, Gammaridae, Limnephilidae

Summer

Chironomidae, Hydropsychidae, Ephemerellidae, Elmidae, Baetidae, Gammaridae, Simuliidae, Planorbidae, Leptoceridae, Sphaeriidae

Autumn

Hydropsychidae, Chironomidae, Gammaridae, Baetidae, Simuliidae, Elmidae, Planorbidae, Sphaeriidae

Boreal

Summer

Leuctridae, Elmidae, Baetidae, Perlodidae, Rhyacophilidae, Simuliidae, Polycentropodidae

Autumn

Hydropsychidae, Baetidae, Perlodidae, Simuliidae, Nemouridae, Taeniopterygidae, Heptageniidae, Rhyacophilidae, Elmidae, Polycentropodidae, Lepidostomatidae

Continental

Spring

Chironomidae, Baetidae, Hydropsychidae, Simuliidae, Gammaridae, Limnephilidae

Summer

Chironomidae, Hydropsychidae, Ephemerellidae, Elmidae, Baetidae, Limnephilidae, Gammaridae, Simuliidae, Planorbidae, Sphaeriidae

Autumn

Hydropsychidae, Chironomidae, Gammaridae, Baetidae, Simuliidae, Elmidae, Planorbidae, Sphaeriidae

Mediterranean

Spring

Chironomidae, Baetidae, Hydropsychidae, Simuliidae, Elmidae

Summer

Chironomidae, Limoniidae, Hydropsychidae, Leuctridae, Ephemerellidae, Elmidae, Baetidae, Caenidae, Heptageniidae, Rhyacophilidae, Simuliidae

Autumn

Hydropsychidae, Empididae, Chironomidae, Baetidae, Simuliidae, Leuctridae, Heptageniidae, Rhyacophilidae, Caenidae, Elmidae

6.1.7.3 Typical Assemblages – Illies Freshwater Ecoregions

Alps

Spring

Chironomidae, Baetidae, Simuliidae, Heptageniidae, Leuctridae, Perlodidae, Taeniopterygidae, Rhyacophilidae, Nemouridae, Limoniidae, Limnephilidae

Summer

Empididae, Chironomidae, Limoniidae, Leuctridae, Elmidae, Baetidae, Limnephilidae, Heptageniidae, Rhyacophilidae, Simuliidae, Nemouridae

Autumn

Hydropsychidae, Limnephilidae, Empididae, Chironomidae, Gammaridae, Baetidae, Perlodidae, Limoniidae, Simuliidae, Leuctridae, Nemouridae, Heptageniidae, Rhyacophilidae, Elmidae

Borealic uplands

Autumn

Chironomidae, Baetidae, Perlodidae, Simuliidae, Leuctridae, Nemouridae, Rhyacophilidae

Central highlands

Spring

Chironomidae, Baetidae, Hydropsychidae, Simuliidae, Heptageniidae, Rhyacophilidae, Elmidae, Limnephilidae

Summer

Chironomidae, Hydropsychidae, Leuctridae, Ephemerellidae, Elmidae, Baetidae, Limnephilidae, Gammaridae, Rhyacophilidae, Simuliidae

Autumn

Hydropsychidae, Chironomidae, Baetidae, Simuliidae, Heptageniidae, Elmidae

Central plains

Spring

Chironomidae, Baetidae, Sphaeriidae, Gammaridae, Asellidae, Limnephilidae

Summer

Chironomidae, Baetidae, Limnephilidae, Gammaridae, Sphaeriidae

Autumn

Chironomidae, Gammaridae, Baetidae, Sphaeriidae

Dinaric Western Balkan *Spring*

Chironomidae, Baetidae

Eastern plains

Spring

Chironomidae, Baetidae, Sphaeriidae, Asellidae, Limnephilidae

Summer

Chironomidae, Baetidae, Limnephilidae, Sphaeriidae, Asellidae

Autumn

Chironomidae, Gammaridae, Baetidae

England

Spring

Chironomidae, Baetidae, Hydropsychidae, Simuliidae, Heptageniidae, Leuctridae, Rhyacophilidae, Elmidae, Gammaridae

Summer

Chironomidae, Hydropsychidae, Leuctridae, Ephemerellidae, Elmidae, Baetidae, Heptageniidae, Gammaridae, Rhyacophilidae, Simuliidae, Planorbidae, Polycentropodidae

Autumn

Hydropsychidae, Chironomidae, Gammaridae, Baetidae, Simuliidae, Heptageniidae, Rhyacophilidae, Elmidae

Fenno-scandian shield

Summer

Leuctridae, Elmidae, Baetidae, Perlodidae, Rhyacophilidae, Simuliidae, Polycentropodidae

Autumn

Hydropsychidae, Baetidae, Perlodidae, Simuliidae, Nemouridae, Taeniopterygidae, Heptageniidae, Rhyacophilidae, Ephemerellidae, Elmidae, Polycentropodidae, Lepidostomatidae

Hungarian lowlands

Spring

Chironomidae, Baetidae, Hydropsychidae, Simuliidae, Heptageniidae, Ceratopogonidae, Elmidae, Sphaeriidae, Gammaridae, Limnephilidae

Summer

Chironomidae, Limoniidae, Hydropsychidae, Elmidae, Baetidae, Heptageniidae, Gammaridae, Simuliidae

Autumn

Hydropsychidae, Chironomidae, Baetidae, Simuliidae, Elmidae, Ceratopogonidae, Sphaeriidae

Ibero-Macaronesian region

Spring

Chironomidae, Baetidae, Hydropsychidae, Simuliidae, Heptageniidae, Rhyacophilidae, Elmidae, Ephemerellidae, Gerridae

Summer

Chironomidae, Hydropsychidae, Leuctridae, Ephemerellidae, Elmidae, Baetidae, Heptageniidae, Rhyacophilidae, Simuliidae

Autumn

Hydropsychidae, Chironomidae, Baetidae, Simuliidae, Leuctridae, Heptageniidae, Rhyacophilidae, Caenidae, Elmidae, Gerridae

Italy and Corsica

Summer

Chironomidae, Limoniidae, Hydropsychidae, Leuctridae, Ephemerellidae, Elmidae, Baetidae, Caenidae, Hydroptilidae, Heptageniidae, Psychomyiidae, Ceratopogonidae, Leptophlebiidae, Simuliidae, Hydraenidae, Goeridae, Calopterygidae, Planorbidae, Leptoceridae, Dytiscidae, Glossosomatidae, Dryopidae, Tateidae

Pyrenees

Summer

Chironomidae, Limoniidae, Hydropsychidae, Leuctridae, Ephemerellidae, Elmidae, Baetidae, Limnephilidae, Heptageniidae, Rhyacophilidae, Simuliidae, Perlidae, Hydraenidae, Sericostomatidae, Nemouridae, Dytiscidae

Autumn

Hydropsychidae, Limnephilidae, Empididae, Chironomidae, Baetidae, Limoniidae, Simuliidae, Leuctridae, Perlidae, Nemouridae, Heptageniidae, Rhyacophilidae, Ephemerellidae, Elmidae, Hydraenidae, Sericostomatidae, Planorbidae, Dytiscidae

The Carpathiens

Spring

Chironomidae, Baetidae, Hydropsychidae, Simuliidae, Heptageniidae, Rhyacophilidae, Elmidae, Limnephilidae

Summer

Chironomidae, Hydropsychidae, Pediciidae, Leuctridae, Ephemerellidae, Elmidae, Baetidae, Limnephilidae, Heptageniidae, Gammaridae, Rhyacophilidae, Simuliidae, Perlidae

Autumn

Hydropsychidae, Chironomidae, Gammaridae, Baetidae, Leuctridae, Heptageniidae, Rhyacophilidae, Elmidae

Western highlands

Spring

Chironomidae, Baetidae, Hydropsychidae, Simuliidae, Heptageniidae, Rhyacophilidae, Elmidae, Ephemerellidae, Gammaridae, Planorbidae, Leptophlebiidae, Sericostomatidae, Limnephilidae

Summer

Chironomidae, Limoniidae, Hydropsychidae, Leuctridae, Ephemerellidae, Elmidae, Baetidae, Athericidae, Ephemeridae, Limnephilidae, Heptageniidae, Gammaridae, Rhyacophilidae, Leptophlebiidae, Simuliidae, Hydraenidae, Planorbidae, Leptoceridae, Sphaeriidae, Polycentropodidae

Autumn

Hydropsychidae, Chironomidae, Gammaridae, Baetidae, Limoniidae, Leptophlebiidae, Simuliidae, Leuctridae, Heptageniidae, Rhyacophilidae, Athericidae, Ephemerellidae, Elmidae, Hydraenidae, Leptoceridae, Ephemeridae, Ceratopogonidae, Planorbidae, Calopterygidae, Polycentropodidae, Sphaeriidae

Western plains

Spring

Chironomidae, Baetidae, Simuliidae, Ceratopogonidae, Elmidae, Ephemerellidae, Sphaeriidae, Gammaridae, Planorbidae, Limnephilidae

Summer

Chironomidae, Limoniidae, Hydropsychidae, Ephemerellidae, Elmidae, Baetidae, Gammaridae, Simuliidae, Planorbidae, Leptoceridae, Sphaeriidae, Polycentropodidae

Autumn

Hydropsychidae, Chironomidae, Gammaridae, Baetidae, Limoniidae, Simuliidae, Leuctridae, Athericidae, Caenidae, Elmidae, Leptoceridae, Ephemeridae, Ceratopogonidae, Planorbidae, Calopterygidae, Polycentropodidae, Sphaeriidae

6.1.8 SM 8 - Algorithm to compute Classification Strength

```r
#' Compute classification strength
#'
#' @param dist A distance matrix
#' @param grouping character vector with group membership of sites
#' @param season character, for which season is the run?
#' The value is supplied as value for the output table.
#' @param typology character, for this typology is this
#'  test run? The value is supplied as value for the output table.
#'
#' @return data.table
#' @export
#'
#' @examples
compute_cs <- function(dist, grouping, season, typology){

                 #- unique types
                grouping.u <- unique(grouping)
                #- transform to matrix
                dist2 <- as.matrix(dist)
                dist2 <- 1 - dist2
                # ---> for every type: how similar are observations
                # within types and between types
                for (k in seq_along(grouping.u)) {

                        if (k == 1) wts <- bts <- c()
                        k.id1    <- which(grouping == grouping.u[k])
                        k.id.n1  <- which(grouping != grouping.u[k])
                        k.sim1   <- dist2[k.id1, k.id1]
                        k.sim.n1 <- dist2[k.id1, k.id.n1]
                        k.ut     <- k.sim1[upper.tri(k.sim1)]
                        k.lt     <- k.sim1[lower.tri(k.sim1)]
                        k.ut.n   <- k.sim.n1[upper.tri(k.sim.n1)]
                        k.lt.n   <- k.sim.n1[lower.tri(k.sim.n1)]
```

```
         wts[k] <-  mean(append(k.ut, k.lt), na.rm = T)
         bts[k] <-  mean(append(k.ut.n, k.lt.n), na.rm = T)

         rm(list = ls()[grepl(x = ls(), pattern = "^k\\.")])
         rm(k)

 }
 #- Relative frequencies of types
 props <- grouping |>
         table() |>
         proportions() |>
         round(2)
 props <- data.frame(type = names(props),
                     proportion = c(props))
 #- collect loop results in table
 csj <- data.frame(
         within_type = wts,
         between_type = bts,
         type = grouping.u,
         typlogy = typology,
         season = season
 )
 #- combine loop results with relative frequencies
 csj <- dplyr::left_join(x = csj,
                         y = props,
                         by = "type")
 csj <-
         csj |>
         dplyr::mutate(within_weighted = within_type * proportion,
                       between_type_mean = mean(csj$between_type)) |>
         dplyr::mutate(within_weighted_sum = sum(within_weighted)) |>
         dplyr::mutate(classification_strength =
                               within_weighted_sum - between_type_mean)

return(csj)
```

```
}
```

6.2 Supplementary Materials for *European river typologies fail to capture diatom, fish, and macrophyte community composition*

6.2.1 SM 1 - Reference typologies

lllies’ Freshwater ecoregions (IFE, Fig. 6.15) are a region-based typology system presented in Illies (1978). The regions were derived from the distribution of 75 freshwater taxa (mostly invertebrates) and political borders (Economou *et al.*, 2004). We used the slightly modified version, which is used in the WFD as an ecoregion variable under System A and is available under https://www.eea.europa.eu/data-and-maps/data/ecoregions-for-rivers-and-lakes.

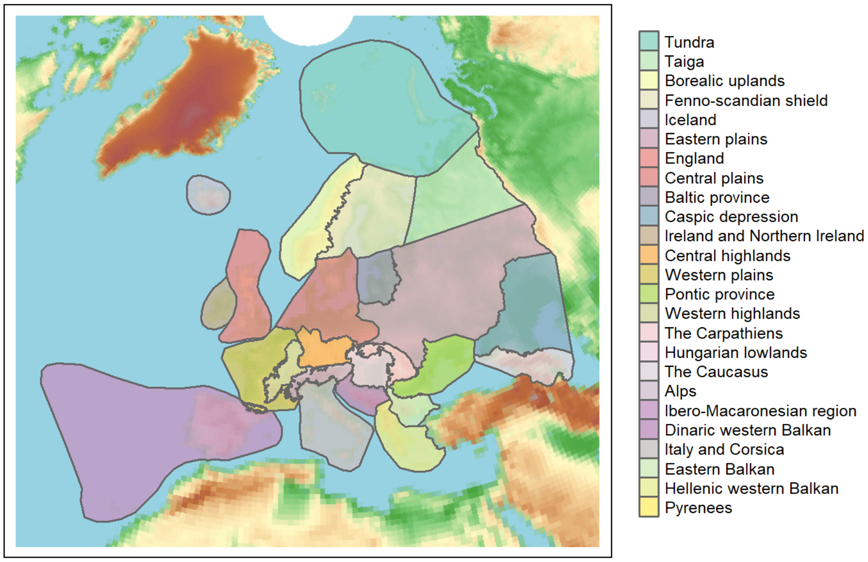

Figure 6.15: Illies Freshwater Ecoregions.

The European Biogeographic Regions (BGR, Fig. 6.16) designate 12 regions based on the distribution of potential natural vegetation (Noirfalse, 1987) and are employed by the European Habitats and the Birds Directive. The five initial regions (Alpine, Atlantic, Continental, Macaronesian and Mediterranean) were expanded by six new regions (Arctic, Boreal, Anatolian, Black Sea, Pannonian and Steppic) with extensions of the European Union. We used the version available under https://www.eea.europa.eu/data-and-maps/data/biogeographical-regions-europe-3.

The Freshwater Ecoregions of the World (FEoW, Fig. 6.17) use catchments as their basic mapping units

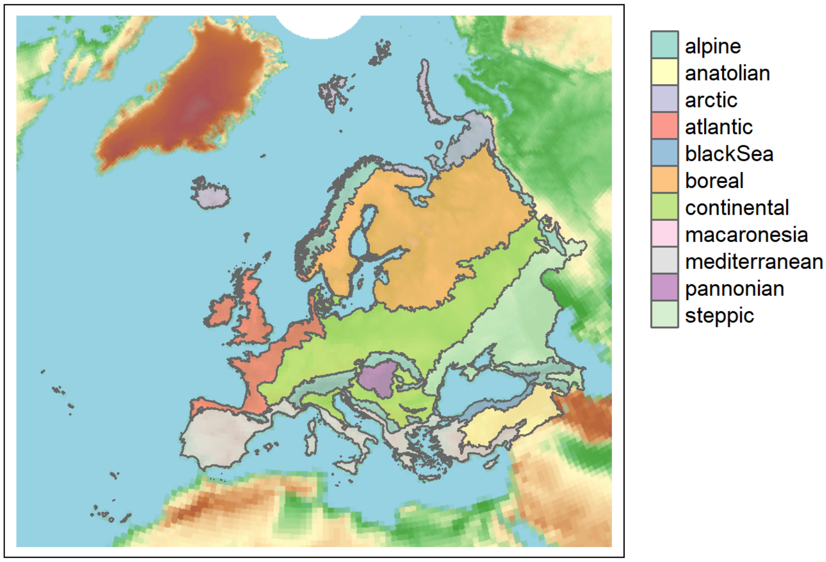

Figure 6.16: The Biogeographic Regions.

(Abell *et al.*, 2008). The catchments were combined or further separated into sub-catchment units based on the distribution of fish species and expert opinion. The FEoW are a global typology system dividing all land areas into 426 regions. Of these, 33 occur in Europe and we consider these as a pan-European typology system (see section 6.2.3 for the selection of analyzed types). We used the version available at https://www.feow.org/download.

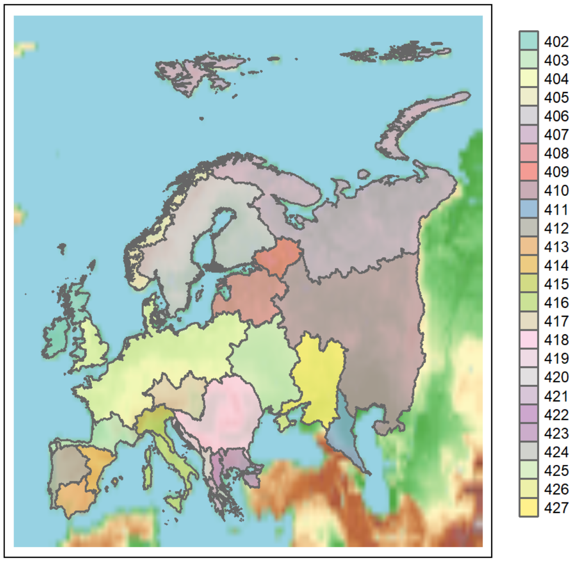

Figure 6.17: Freshwater Ecoregions of the World.

The Environmental Zones of Europe (EnZ, Fig. 6.18) are based on three principal components derived from

20 environmental variables capturing climate, geomorphology, oceanicity, northing, geology, and soil on a 1 km raster of the greater European window. Using the clustering algorithm Iterative Self-Organizing Data (Tou & Gonzalez, 1974) on the PCA scores, Metzger *et al.* (2005) identified 84 groups (so-called *strata*). They further aggregated these 84 groups into 13 environmental zones based on arbitrarily chosen divisions of the first principal component. The environmental zones data are available under https://datashare.ed.ac.uk/handle/10283/3091.

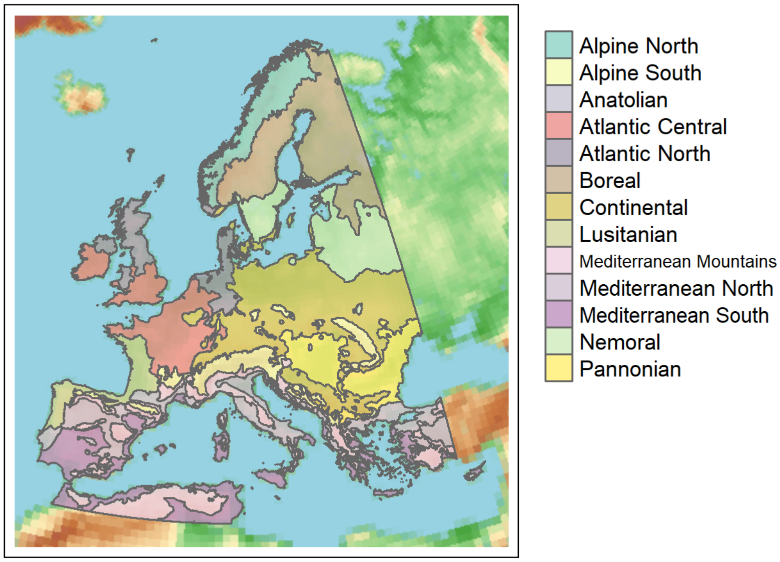

Figure 6.18: Environmental Zones.

The following map (Fig. 6.19) shows the additional spatial autocorrelation (SA) classifications.

6.2.2 SM 2 - Data Sets

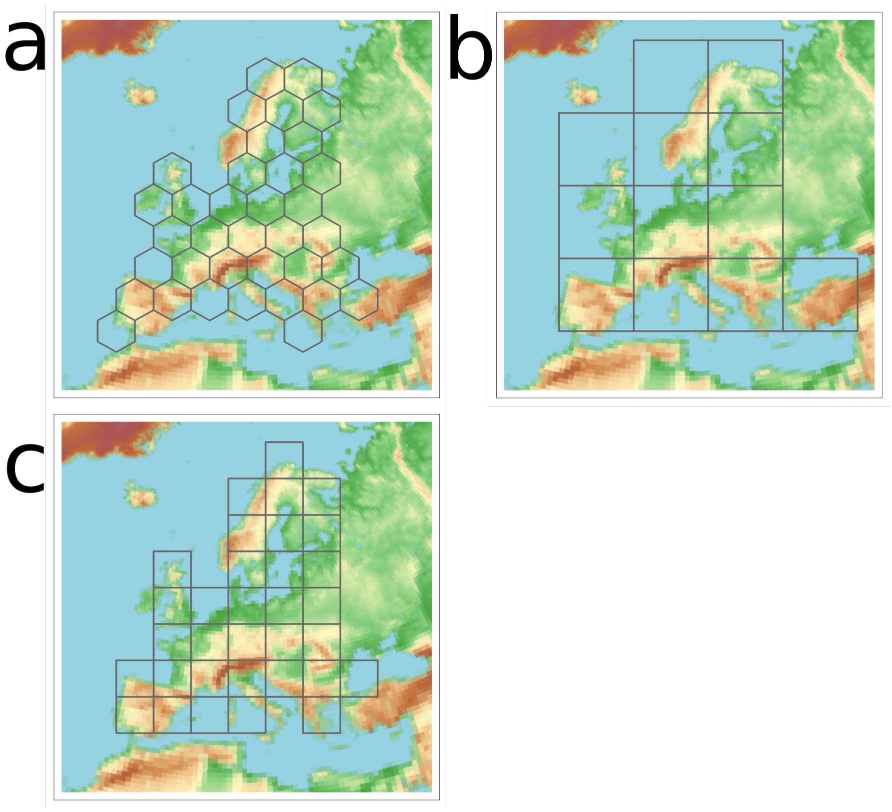

Figure 6.19: The additional spatial autocorrelation classifications. a) The 36-type hexagonal spatial autocorrelation classification. b) The 12-type square spatial autocorrelation classification. c) The 33-type square spatial autocorrelation classification

Table 6.6: Diatom data sets. The numbers indicate the original number and finally used number in brackets. EN 13946 refers to the European Norm: “Guidance for the routine sampling and preparation of benthic diatoms from rivers and lakes” and EN 14407 refers to the European Standard „Water quality - Guidance standard for the identification, enumeration and interpretation of benthic diatom samples from running waters“.

Data Set	Samples	Sites	Sampling method
National Monitoring Croatia	273 (32)	273 (32)	EN 13946 and EN 14407
National Monitoring Czech Republic	8462 (218)	1634 (218)	EN 13946 and EN 14407
Study from Finland I	105 (19)	105 (19)	See (Soininen & Kokocinski, 2006)
Study from Finland II	105 (3)	105 (3)	See (Jyrkankallio-Mikkola et al., 2017)
National Monitoring Finland	3105 (341)	1580 (341)	EN 13946 and EN 14407
IRSTEA data France	2207 (449)	2207 (449)	EN 13946 and EN 14407
National Monitoring France	40622 (1669)	8459 (1669)	EN 13946 and EN 14407
Federal Monitoring Baden-Wurttemberg, Germany	611 (91)	611 (91)	EN 13946 and EN 14407
Federal Monitoring Brandenburg, Germany	819 (66)	670 (66)	EN 13946 and EN 14407
Federal Monitoring Hesse, Germany	1291 (24)	689 (24)	EN 13946 and EN 14407
National Monitoring Germany	319 (19)	233 (19)	EN 13946 and EN 14407
Federal Monitoring Lower Saxony, Germany	4731 (93)	1875 (93)	EN 13946 and EN 14407
Federal Monitoring Saxony, Germany	547 (51)	547 (51)	EN 13946 and EN 14407
National monitoring Poland	4090 (196)	3148 (196)	EN 13946 and EN 14407
National monitoring Portugal	199 (38)	199 (38)	EN 13946 and EN 14407

Data Set	Samples	Sites	Sampling method
National monitoring Slovakia	294 (27)	235 (27)	EN 13946 and EN 14407
Federal monitoring, Duero basin, Spain	1347 (83)	600 (83)	EN 13946 and EN 14407
Federal monitoring, Ebro basin, Spain	1502 (95)	392 (95)	EN 13946 and EN 14407
Project AQEM Sweden	75 (3)	75 (3)	See (Kovas et al., 2006)
National monitoring Sweden	1912 (197)	1097 (197)	EN 13946 and EN 14407
National Monitoring UK	14419 (469)	4682 (469)	EN 13946 and EN 14407

Table 6.7: Fish data sets. The numbers indicate the original number and finally used number in brackets. All datasets sampled according to EN 141011 “Water Quality - Sampling of Fish with Electricity”.

Data set	Samples	Sites
National Monitoring Czech Republic	977 (93)	474 (93)
National Monitoring Finland	2137 (150)	947 (150)
National Monitoring France	15889 (418)	2905 (418)
Federal Monitoring Brandenburg, Germany	488 (49)	354 (49)
Federal Monitoring Hesse, Germany	2278 (39)	994 (39)
Federal Monitoring Lower Saxony, Germany	731 (41)	576 (41)
Federal Monitoring Mecklenburg-Vorpommern, Germany	151 (27)	124 (27)
Federal Monitoring North Rhine-Westphalia, Germany	1071 (17)	983 (17)
Federal Monitoring Saxony-Anhalt, Germany	1568 (27)	451 (27)

Data set	Samples	Sites
Federal Monitoring Schleswig-Holstein, Germany	1528 (36)	817 (36)
Data base from the WFD intercalibration	1722 (208)	1722 (208)
National Monitoring Netherlands	664 (4)	318 (4)
National Monitoring Poland	3574 (476)	3124 (476)
National Monitoring Portugal	196 (19)	194 (19)
Federal monitoring, Duero basin, Spain	335 (12)	313 (12)
Project STAR, Sweden	28 (9)	28 (9)
National Monitoring UK	5284 (378)	3130 (378)

Table 6.8: Aquatic Macrophyte data sets. The numbers indicate the original number and finally used number in brackets. EN 14185 refers to the European Norm: “Water quality Guidance standard for the surveying of aquatic macrophytes in running waters”.

Data set	Samples	Sites	Sampling Method
National Monitoring Austria	85 (17)	85 (17)	EN 14184
National Monitoring Czech Republic	1444 (42)	596 (42)	EN 14184
National Monitoring Finland	188 (34)	188 (34)	EN 14184
National Monitoring France	6496 (409)	1655 (409)	EN 14184
Federal Monitoring Baden-Wurttemberg, Germany	594 (87)	594 (87)	EN 14184
Federal Monitoring, Bavaria, Germany	1567 (103)	865 (103)	EN 14184

Data set	Samples	Sites	Sampling Method
Federal Monitoring, Brandenburg, Germany	748 (64)	707 (64)	EN 14184
Federal Monitoring, Lower Saxony, Germany	4297 (82)	1627 (82)	EN 14184
Federal Monitoring, Mecklenburg-Vorpommern, Germany	318 (56)	201 (56)	EN 14184
Federal Monitoring, Saxony, Germany	536 (47)	536 (47)	EN 14184
Federal Monitoring, Schleswig-Holstein, Germany	520 (36)	414 (36)	EN 14184
National Monitoring Netherlands	4028 (21)	1688 (21)	EN 14184
National Monitoring Poland	2056 (412)	1973 (412)	EN 14184
National Monitoring Portugal	41 (16)	41 (16)	EN 14184
Federal monitoring, Duero basin, Spain	1162 (112)	560 (112)	EN 14184
Federal monitoring, Ebro basin, Spain	1438 (84)	367 (84)	EN 14184
National Monitoring Slovakia	364 (12)	364 (12)	EN 14184
Project STAR, Sweden	27 (9)	27 (9)	See (Hering et al., 2006)
National Monitoring UK	3454 (172)	2434 (172)	EN 14184

6.2.3 SM 3 - The effect of temporal changes on typology system performance

6.2.3.1 Analysis of five-year groups

The taxonomic composition of many ecological communities is and has been changing. Tison-Rosebery *et al.* (2022) have shown considerable taxonomic differences between samples of macroinvertebrates, diatoms, and fishes from the later 1990s and the early 2010s. When we evaluate the similarity of communities within types over a larger time span, these changes can decrease the similarity and thus decrease classification performance. However, these temporal trends will also affect the similarity of communities among types and it will probably affect all typology systems similarly. Nonetheless, we evaluated whether the typologies' performances would differ strongly when we considered only samples from smaller time intervals. We split the data sets into intervals of five years and evaluated the geographical spread of these subsets visually (Fig. 6.20 to 6.22).

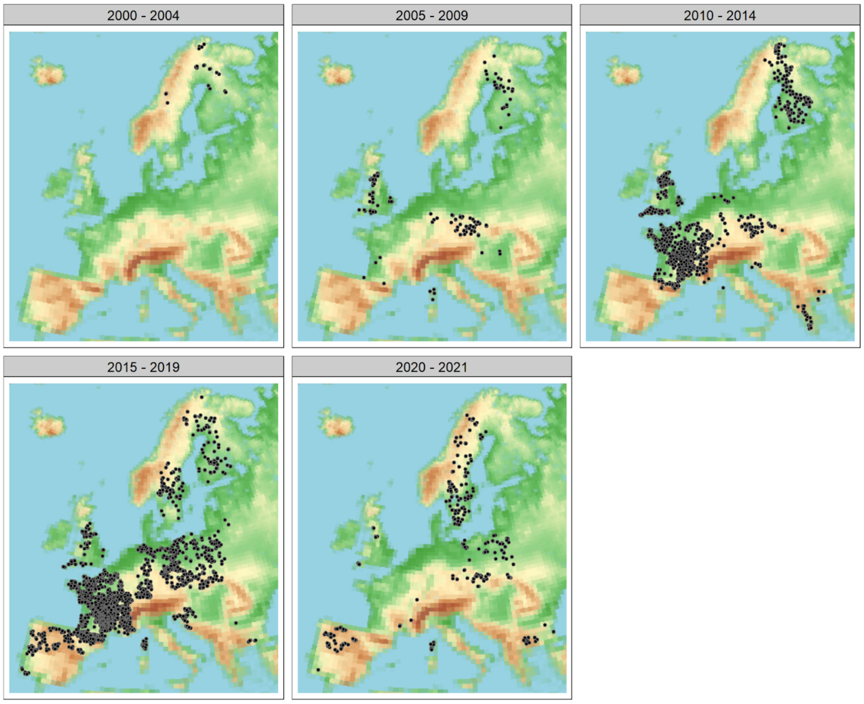

Figure 6.20: Spatial distribution of diatom samples within five-year time intervals. As the total number of years was not divisible by five, the last two years form a separate group. The two groups 2010-2014 and 2015-2019 have the largest geographic span and include the highest proportion of ecosystem types.

For diatoms, we analyzed the two intervals 2010 - 2014 and 2015 - 2019. For fish, we analyzed the two intervals 2005 - 2009 and 2015 - 2019. For macrophytes, only the interval 2015 -2019 included sufficient data to merit analysis. As in the main analysis, we omitted types for which we had less than 20 samples. For the fish analysis, we had to reduce this threshold to 10 to include more than one type per typology system. With the resulting data sets we conducted the same analyses as in the main analysis.

The results of the ANOSIM differ strongly but not systematically between the different data sets (Fig. 6.23). For diatoms, all typologies perform better for the early interval than for the complete data set, but worse for the latter. For fish, the results vary more strongly between typology systems, but the shorter intervals usually perform better. Especially, the FEoW increases its performance markedly for the early interval. In macrophytes, we see a strong decrease in performance from the complete data set to the interval data.

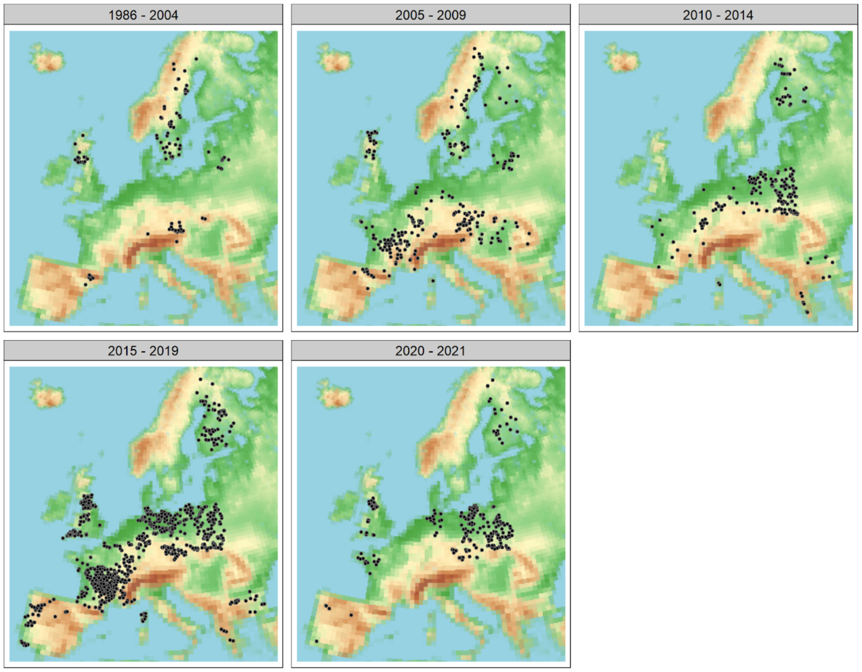

Figure 6.21: Spatial distribution of fish samples within five-year time intervals. As the total number of years was not divisible by five, the last two years form a separate group. Our data set included a few samples from the 20th century. For convenience, we grouped them with the earliest five-year interval. As the number of samples was low regardless, they were not analyzed here. The two groups 2005-2009 and 2015-2019 have the largest geographic span and include the highest proportion of ecosystem types.

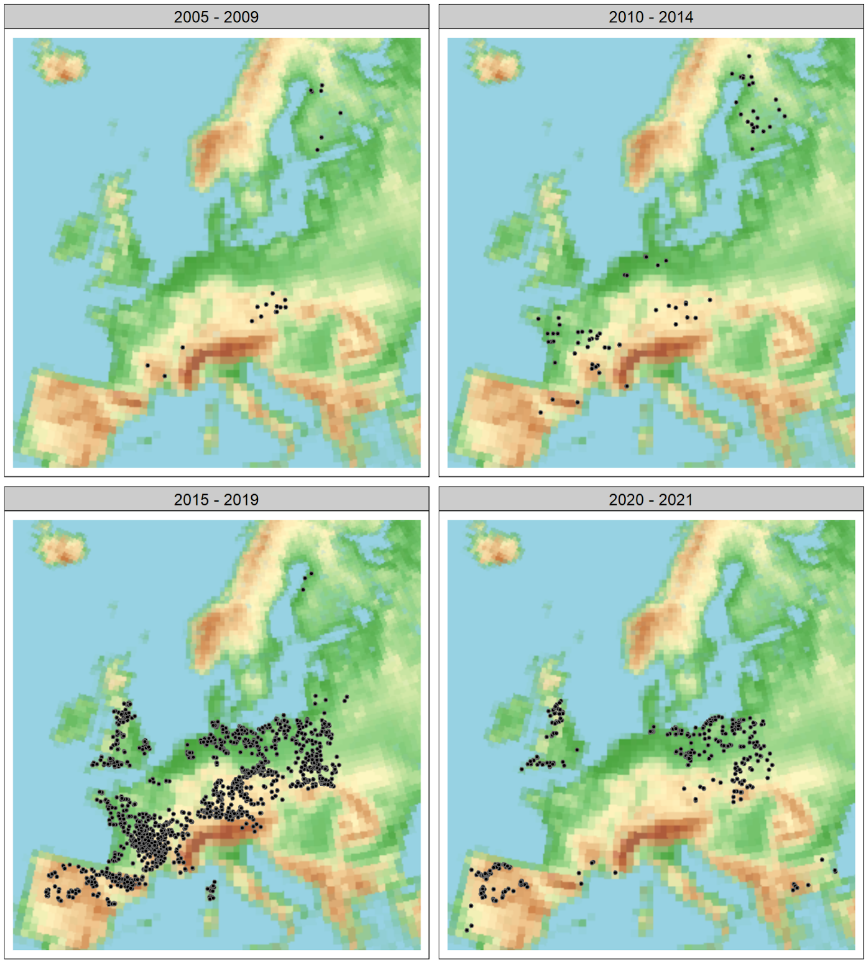

Figure 6.22: Spatial distribution of macrophyte samples within five-year time intervals. As the total number of years was not divisible by five, the last two years form a separate group. Only the interval between 2015 and 2019 included sufficient samples to merit an analysis

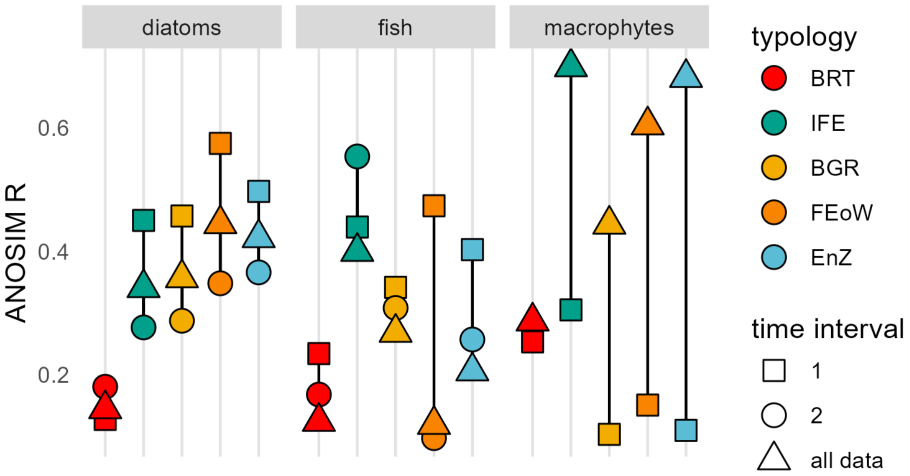

Figure 6.23: Results of the ANOSIM analysis of the five-year interval data. The typology system is given by the color and the shape of symbols indicates the data set. The first time-interval is always the chronologically former. The exact years differ between taxa. The triangle shows the result of the main analysis (i.e., the complete data set) as a comparison. The black line between the respectively highest and lowest values illustrates the variation between results.

For diatoms, classification strength increased markedly for the early time interval but decreased slightly for the later interval (Fig 6.24). For fish, the time intervals also show higher classification strengths, especially the FEoW for the first interval. For macrophytes, the five-year interval has almost the same classification strength as the complete data set.

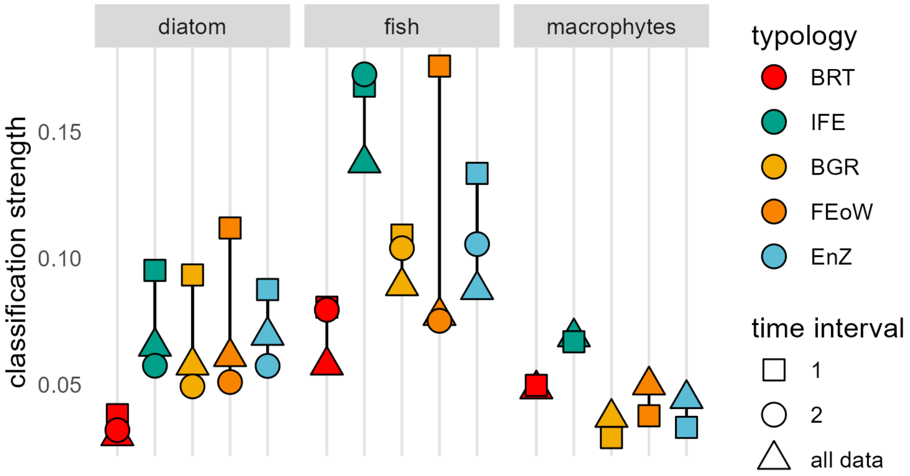

Figure 6.24: Classification strength of the five-year interval data. The typology system is given by the color and the shape of symbols indicates the data set. The first time-interval is always the chronologically former. The exact years differ between taxa. The triangle shows the result of the main analysis (i.e., the complete data set) as a comparison. The black line between the respectively highest and lowest values illustrates the variation between results.

The dissimilarity of typical communities is typically higher for the five-year interval data (Fig. 6.25). This difference is typically least pronounced for the BRT.

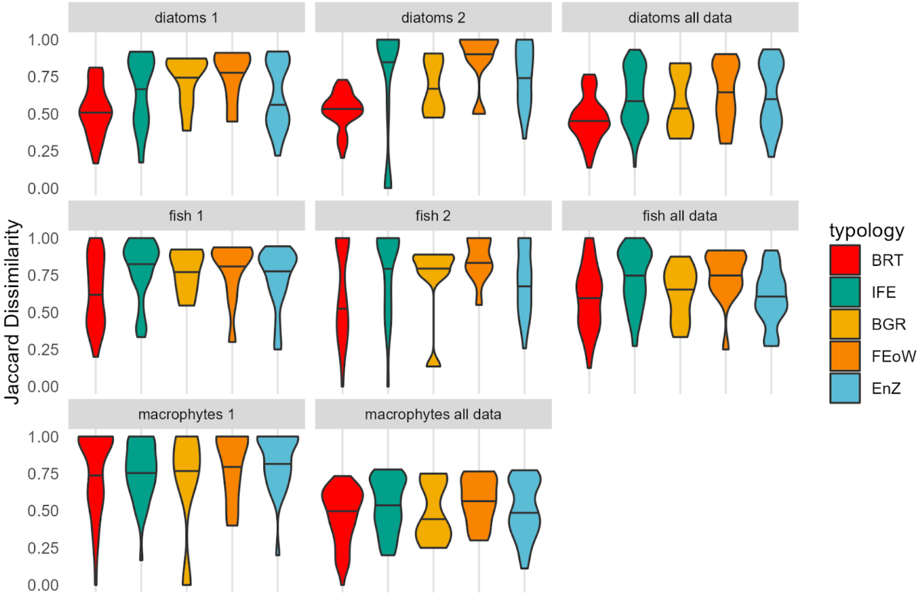

Figure 6.25: Jaccard dissimilarity of typical communities. The color of the violin plots indicates the typology system and the black bar is the median similarity. The first row shows results for diatoms, the second for fish and the third for macrophytes. The numbers in the facet titles are the interval numbers. The first time-interval is always the chronologically former. The exact years differ between taxa.

In concordance with the previous results, the area under the zeta diversity decline curve ($AUC\zeta$) increased for some five-year interval data but not for others (Fig. 6.26). We observe no consistent patterns of increase or decrease for any particular typology system.

The five-year interval data sets do not only restrict the data sets temporally but also spatially. For diatoms for example, much of the Mediterranean, Swedish and Polish data is missing from the early interval. Therefore, the better performance of this data set might be a sign of temporal changes but might also indicate that these areas are where the typology systems are weakest. Our data set prohibits us from discriminating between these effects. However, this analysis indicates that shorter time spans potentially would show a better performance for some of the typology systems and taxa. This does not affect our answers to two research questions since (i) the BRT still below the a priori thresholds for ANOSIM and classification strength and (ii) the other typology systems still perform better in most settings.

6.2.3.2 Analysis of one-year groups

Diatoms have the shortest generation time among the three taxonomic groups investigated in this study. Therefore, they should show the fastest changes in community composition and would consequently be the most heavily affected taxon when using a dataset that spans a long time span. Therefore, we also repeated

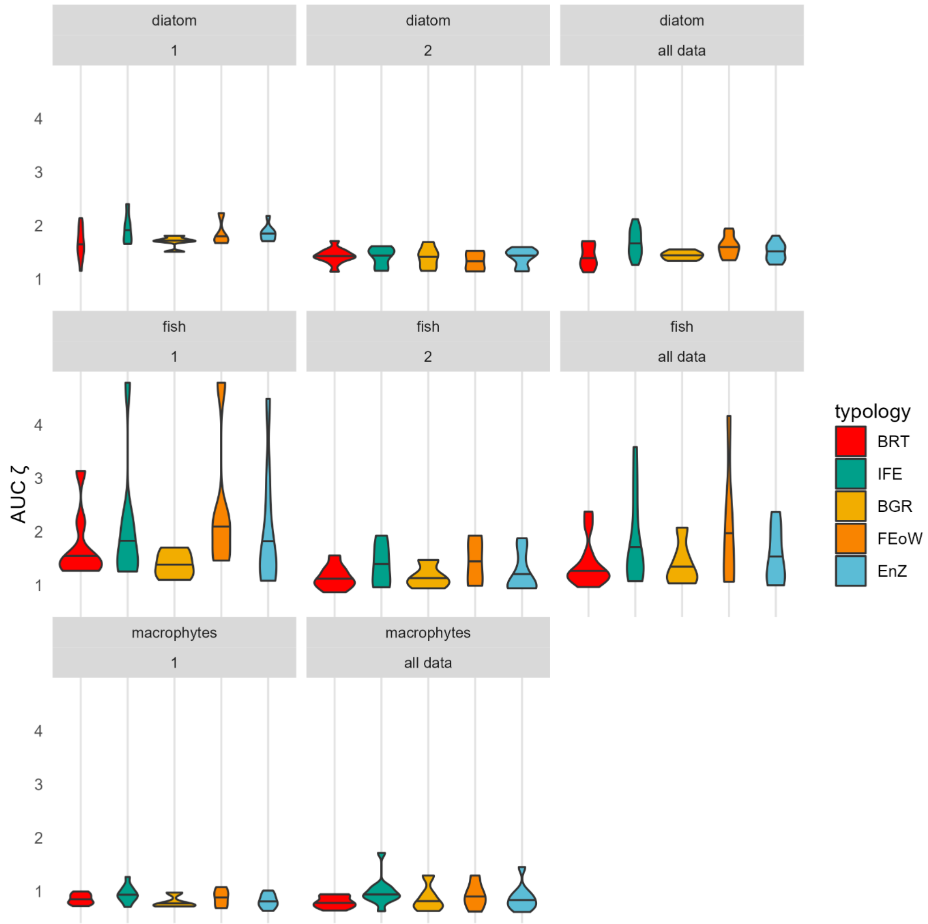

Figure 6.26: Area under the zeta diversity decline curve for diatoms, fishes, and macrophytes. The colors indicate the different typology systems and the facets data sets. The first time-interval is always the chronologically former. The exact years differ between taxa. The black lines inside the violin plots show the median.

our analysis for a set of single year intervals for diatoms. For this analysis, we relied on the data sets that included all the years for which we had the most samples, namely 2011 to 2017. These data sets were the national monitoring from the Czech Republic, France, Finland, England, and the federal monitoring from the German states Lower Saxony and Hesse (Fig. 6.27).

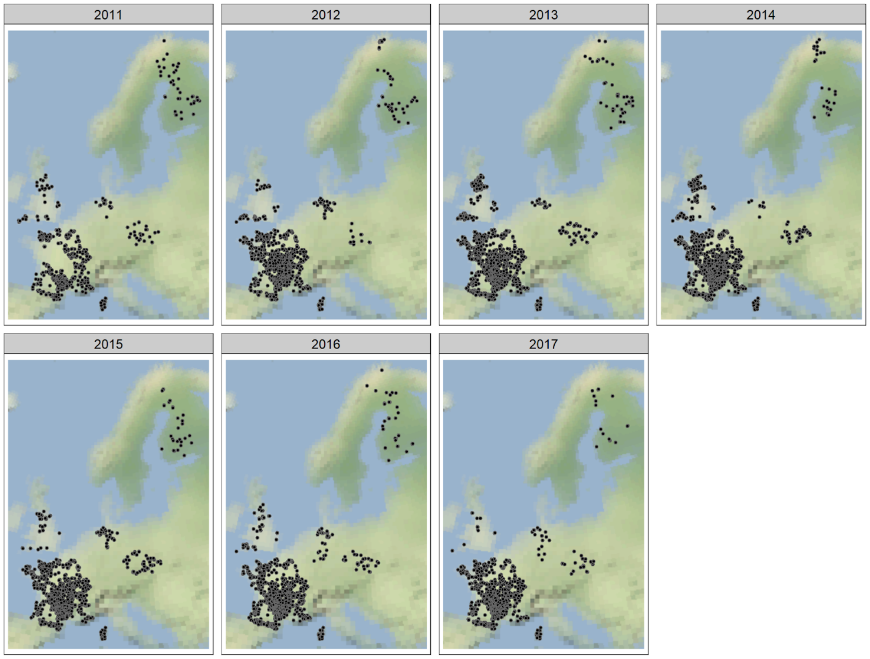

Figure 6.27: Map of sampling sites for the yearly data. Each black dot represents a sampling site. The windows are the different sampling years.

We repeated the ANOSIM and the classification strength analysis for these seven data sets as well as for a combined data set from all seven years. Prior to the analysis, the data sets were reduced to sampling sites from types that were present in at least six of the seven years and had at least five samples each year. If the performance of typology systems as means to create site groups with similar community composition would be strongly affected by temporal variation in community composition, we would expect a lower ANOSIM R statistic and a lower classification strength for the seven year data set relative to the seven one year data sets.

For each typology system, the ANOSIM R and classification strength for the seven-year dataset was lower than the median value for the one-year datasets but just slightly (Figure 6.28 and 6.29). None of the one-year data sets exceeded the predetermined thresholds of 0.5 for ANOSIM or 0.1 for classification strength. The classification strength of the EnZ for the seven-year data set is the only instance where the seven-year data obtained a lower test statistic than any of the one-year data sets.

The results agree with those of Tison-Rosebery *et al.* (2022). On average, classification performance was

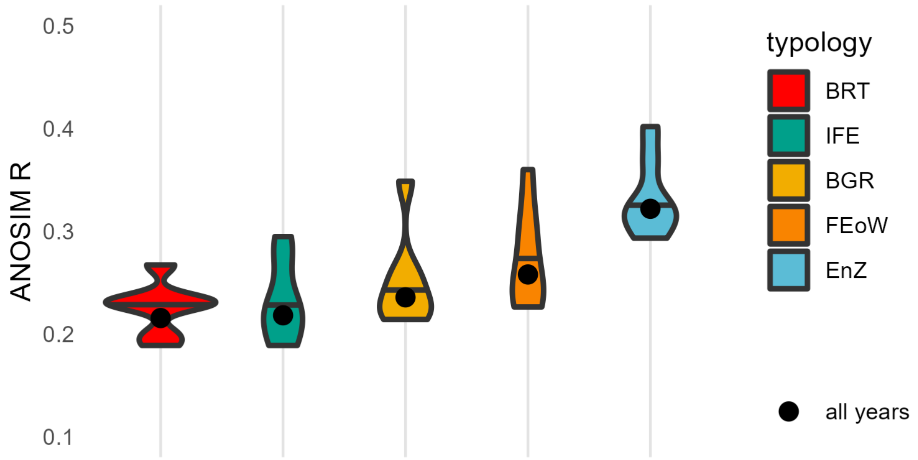

Figure 6.28: Similarity of community composition in one-year datasets compared with Analysis of Similarity (ANOSIM) of the Broad River Types (BRT), Illies Freshwater Ecoregions (IFE), Biogeographic Regions (BGR), Freshwater Ecoregions of the World (FEoW), and Environmental Zones (EnZ) across diatoms, fishes, and macrophytes. An R of 1 corresponds to a perfect classification where within-time similarities exceed among-type similarities. The black dots are the ANOSIM R for the dataset that combined all seven years.

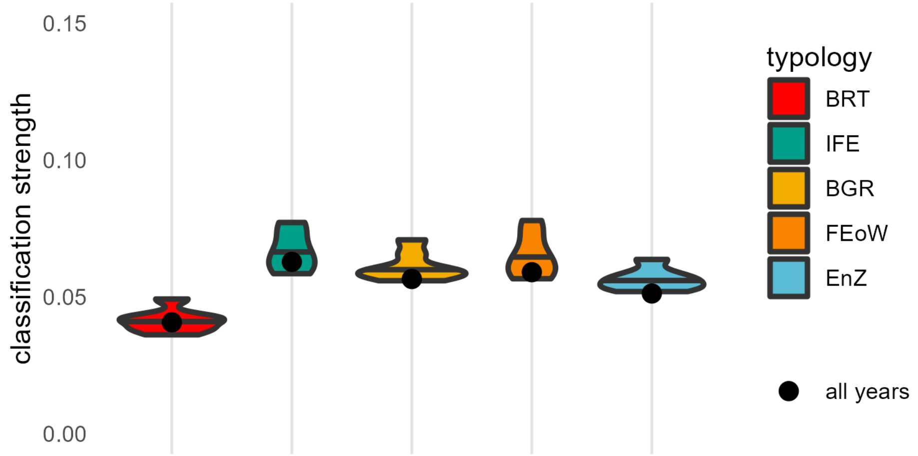

Figure 6.29: Similarity of community composition in one-year datasets compared with Classification Strength (CS) analysis of the Broad River Types (BRT), Illies Freshwater Ecoregions (IFE), Biogeographic Regions (BGR), Freshwater Ecoregions of the World (FEoW), and Environmental Zones (EnZ) across diatoms, fishes, and macrophytes. A CS of 1 indicates a perfect classification where all communities within a type are identical and share no species with communities from other types. The black dots are the ANOSIM R for the dataset that combined all seven years.

higher for the one-year datasets than for the seven-year dataset. However, the actual differences were small. Therefore, our results also indicate that the results of our main analysis would not change qualitatively if they would extend over a smaller temporal span. While the complete datasets for the three taxonomic groups span larger time intervals, 73 %, 71 %, and 92 % of samples for diatoms, fishes, and macrophytes, respectively, lie within seven-year intervals.

6.2.4 SM 4 - Designation of least disturbed sites

We used the stressor database published by Lemm *et al.* (2021) to classify sub-catchment units (FEC) into the two groups disturbed and least disturbed. For this classification we considered all seven stressors contained in the database. Each catchment where the value of one of the stressors was above the 24 % percentile for the respective stressor and Broad River Type, was considered disturbed. To determine the optimal threshold (24 %), we used the Water Framework Directive ecological status assessment for each FEC. This information is also contained in the database of Lemm *et al.* (2021). We calculated the percentage of FECs with high or good ecological status (henceforth good) and the percentage of FECs with moderate, poor, or bad (henceforth bad) ecological status at threshold values ranging from 0.05 to 1 (Fig. 6.30).

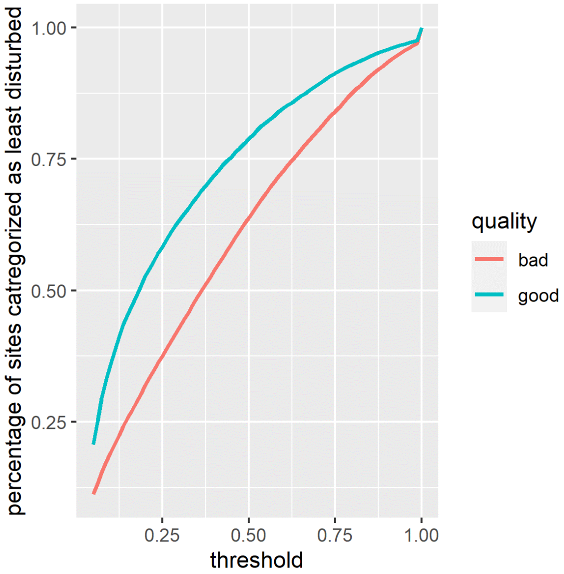

Figure 6.30: Percentage of sites with good or high (good) or moderate, poor, and bad ecological status (bad) that were classified as least disturbed as a function of the delineation threshold.

The percentage of good and bad FECs increased with an increasing threshold value. For low threshold values (approximately < 0.3), the percentage of good FECs increased faster than that of bad FECs. The difference between them was maximized at a threshold of 0.24 (Fig. 6.31).

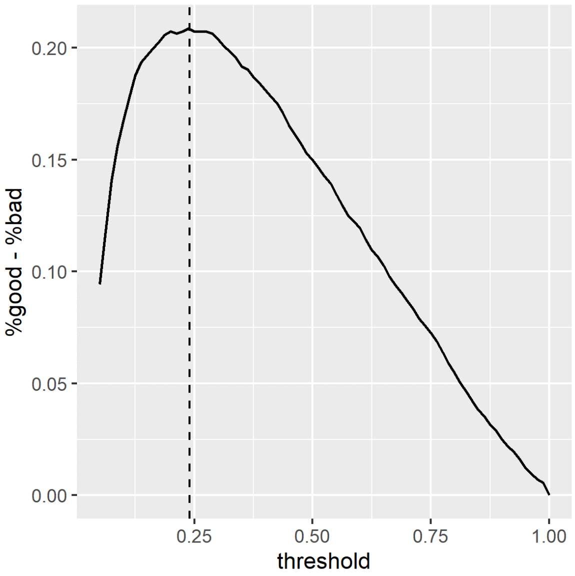

Figure 6.31: Difference between the percentage of FECs with good or high (good) and FECs with moderate, poor, or bad ecological status (bad) as a function of the delineation threshold. A dashed line marks the curve's maximum at a threshold of 0.24.

6.2.5 SM 5 - Representation of ecosystem types

We did not analyze all types of the tested ecosystem typology systems. The Freshwater Ecosystem of the World (FEoW) typology system extends beyond Europe and all non-European types were removed before analyses. The European selection of FEoW types included the types 401 to 425, as well as 436, 437, 440, and 442 (Appendix, Fig. 6.33). Further, we removed all types for which we had < 20 samples. For the Broad River Types, we analyzed all twelve types for diatoms and macrophytes. For fishes we analyzed all BRT types, except for Mediterranean temporary and very small rivers (RT12). For the Biogeographic regions, we included the types alpine, atlantic, boreal, continental, and mediterranean for all three taxonomic groups. For Illies Freshwater Ecoregions, the Freshwater Ecoregions of the world, and the Environmental Zones the analyzed types differed more strongly between taxa and are shown in Figure 6.32 to 6.34.

The number of samples we analyzed per type was not balanced. The percentage of samples belonging to each type for each typology system and taxonomic group is shown in Fig. 6.35.

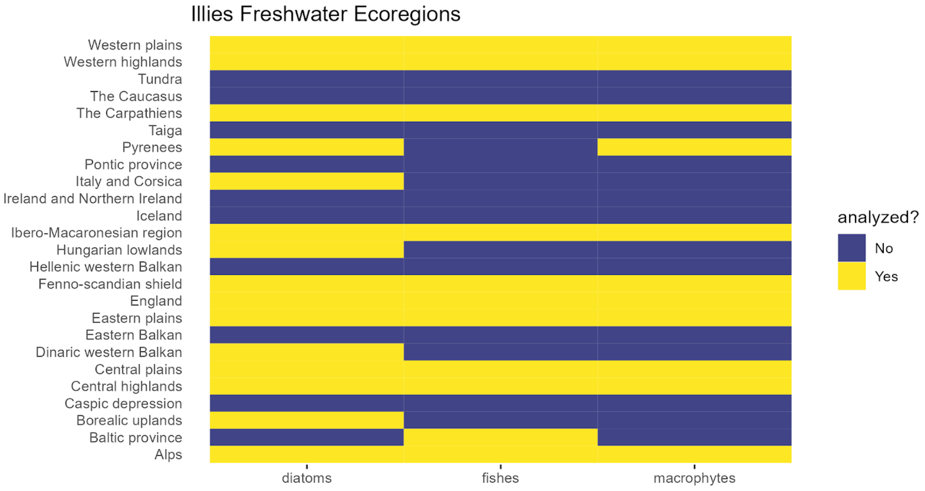

Figure 6.32: Which types from Illies Freshwater Ecoregions were analyzed for which taxon? A yellow box indicates that the type was analyzed for the respective taxon and a blue box indicates the opposite.

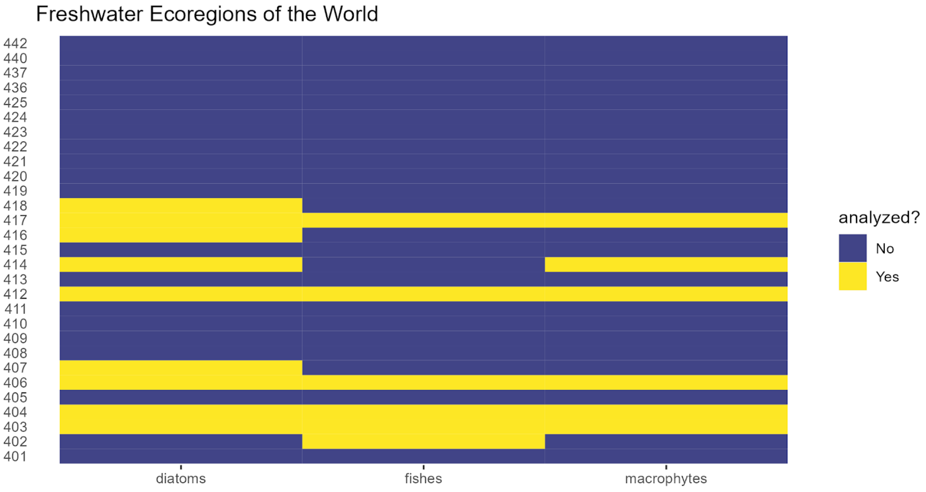

Figure 6.33: Which types from the Freshwater Ecoregions of the World were analyzed for which taxon? A yellow box indicates that the type was analyzed for the respective taxon and a blue box indicates the opposite.

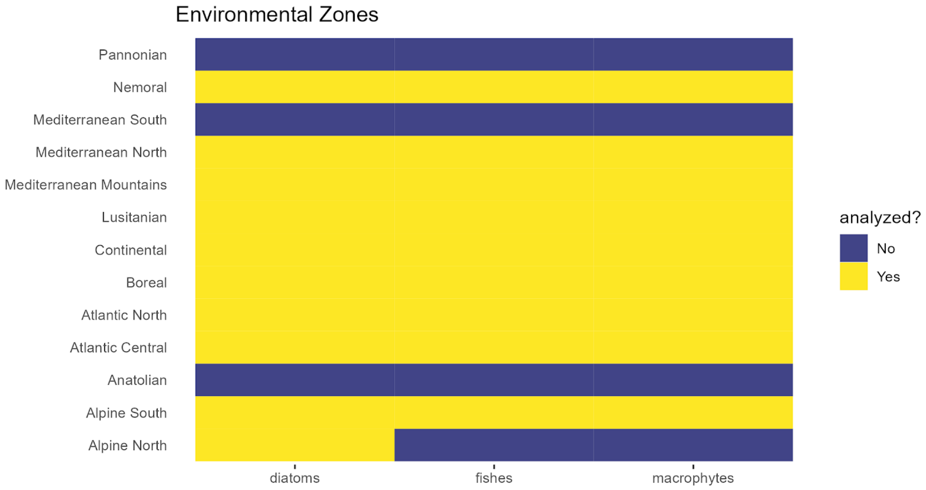

Figure 6.34: Which types from the Environmental Zones were analyzed for which taxon? A yellow box indicates that the type was analyzed for the respective taxon and a blue box indicates the opposite.

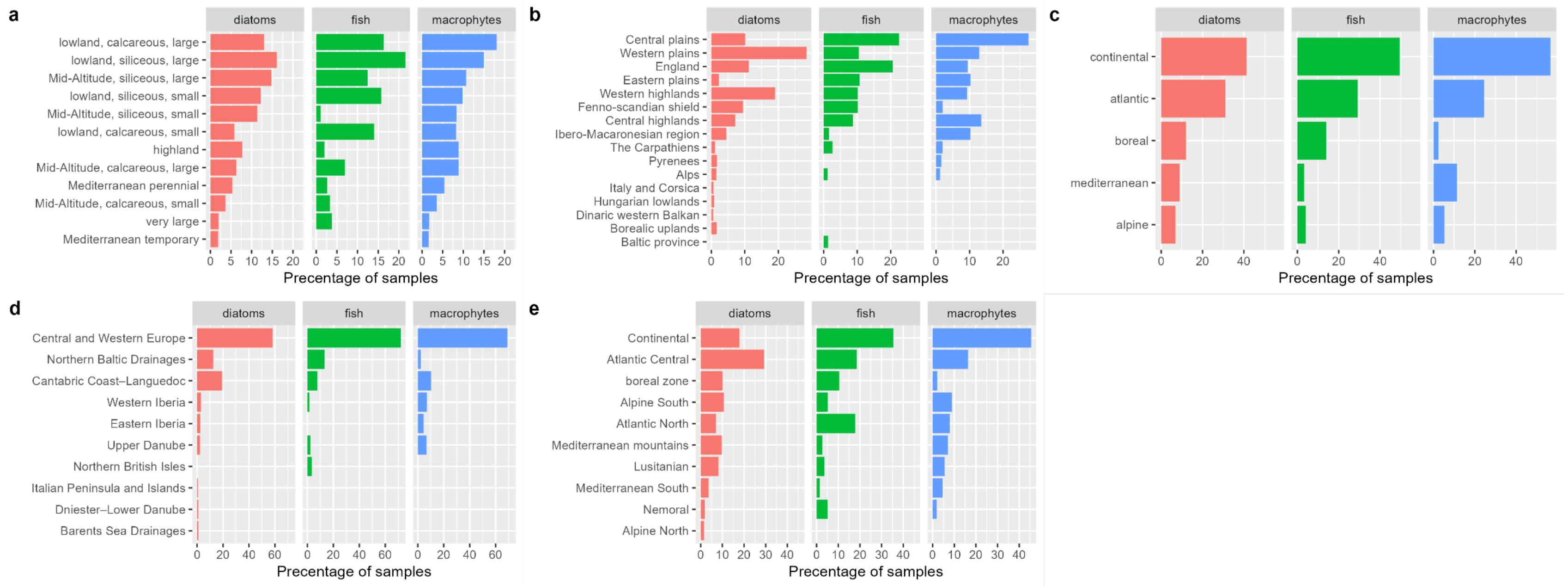

Figure 6.35: Percentage of analyzed samples belonging to the different types of the a) Broad River Types, b) Illies Freshwater Ecoregions, c) Biogeographic Regions, d) Freshwater Ecoregions of the World, e) Environmental Zones.

6.2.6 SM 6 - Results for all spatial autocorrelation models

In the following, we show the results for all four SA classifications with the BRT as a frame of reference. In the ANOSIM, the SA classifications with many types (i.e., small cells and large number of types) performed better than those with fewer types (Fig. 6.36). The hexagonal SA classification with large types is the worst for diatoms but approximately average for fish and macrophytes. There is no systematic performance difference between hexagons and squares.

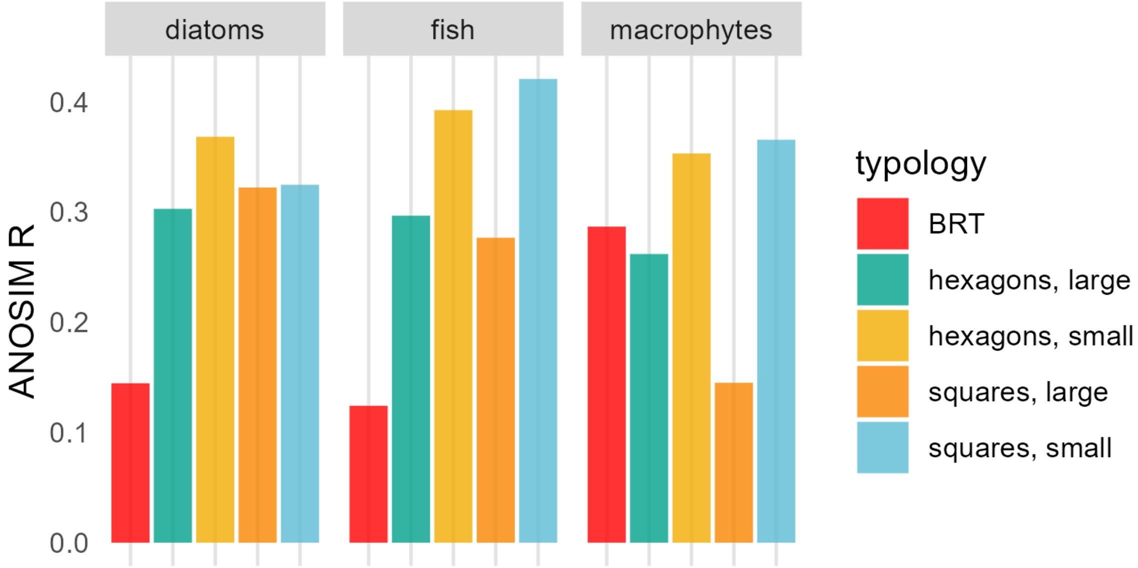

Figure 6.36: Results of ANOSIM analysis of multiple spatial autocorrelation classifications.

The classification strengths of most SA classifications exceed that of the BRT (Fig. 6.37). As with the ANOSIM, SA classifications with smaller mapping units outperform those with larger ones but we observed no systematic differences between geometric forms of mapping units.

The median dissimilarity between typical communities was higher in each of the four SA classifications than in the Broad River Types (Fig. 6.38). The SA classifications with smaller mapping units had more dissimilar typical communities of diatoms and fishes than the SA classifications with larger mapping units. The typical communities of macrophyte had a high dissimilarity in all SA classifications.

The Area under the zeta diversity decline curve ($AUC\zeta s$) shows several outliers, most of which have large $AUC\zeta s$ and occur for fish (Fig. 6.39). The variation within SA classifications typically exceeds that between them. Typology systems with smaller types tend to have a higher $AUC\zeta$ than those with larger types but differences are small. The BRTs typically have the lowest $AUC\zeta$.

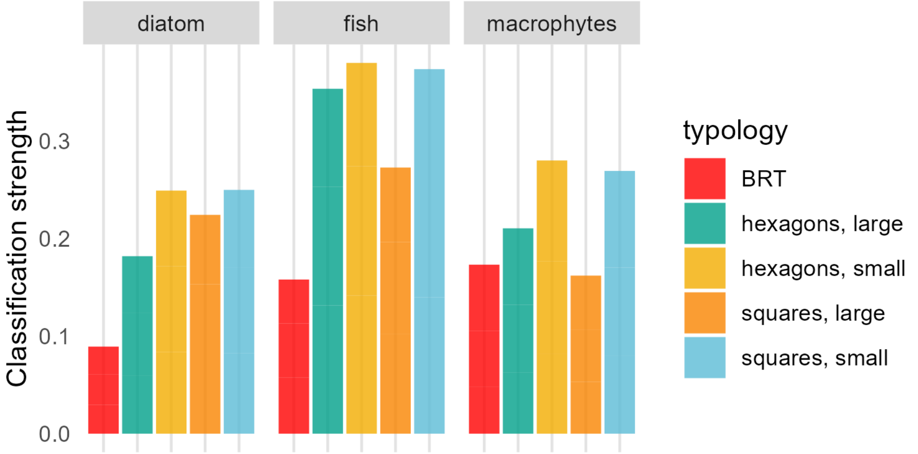

Figure 6.37: Classification strength for all spatial autocorrelation classifications and the Broad River Types. Typology system is indicated by color.

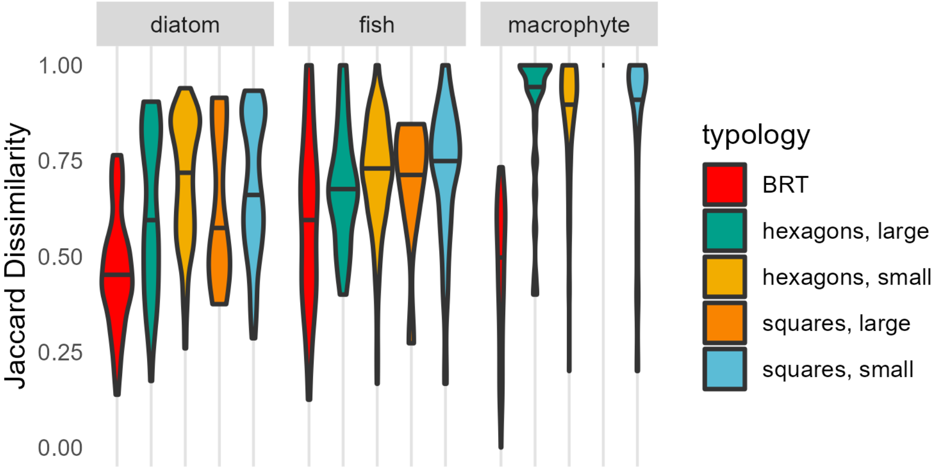

Figure 6.38: Jaccard dissimilarity between typical communities of all spatial autocorrelation classifications and the Broad River Types (BRT). The typology system is indicated by the color. Black bars inside the violins indicate the median similarity

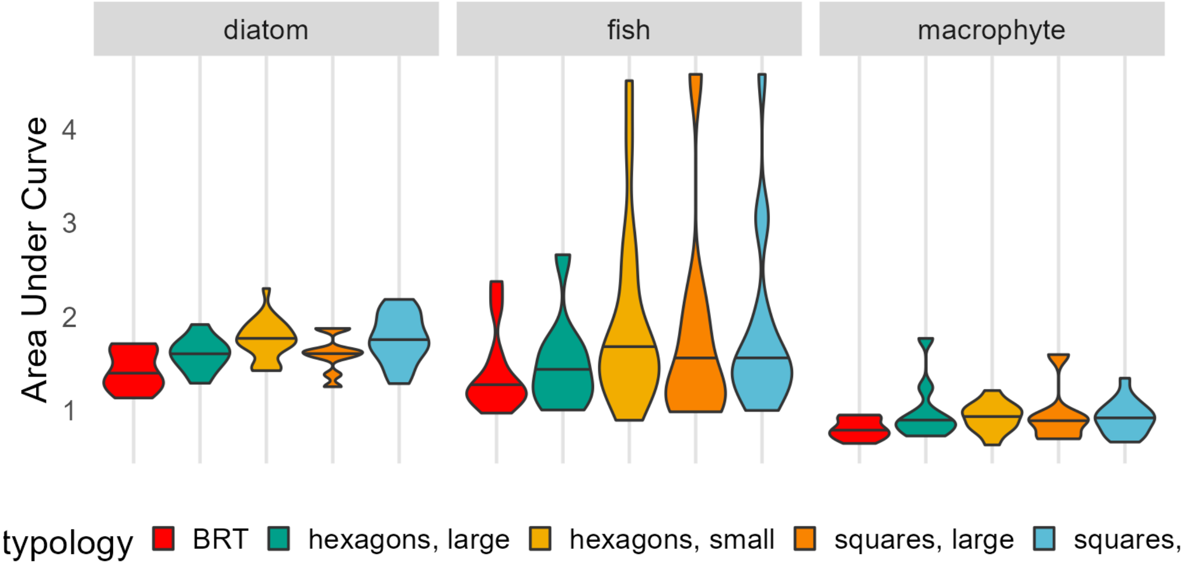

Figure 6.39: Area under the zeta-diversity decline curves for all four SA classifications and the Broad River Types (BRT). The color indicates the typology system.

6.2.7 SM 8 - Harmonization tables

The harmonization tables are available in the Zenodo Folder https://zenodo.org/records/7751344

6.2.8 SM 9 - Typical communities

The typical communities are available in the Zenodo Folder https://zenodo.org/records/7751344

6.3 Supplementary Materials for *Sensitivity of European macroinvertebrate assemblages toward three pesticides across river types*

6.3.1 SM 1 - Overview of Datasets

The following section gives additional details on our database's individual datasets. Table 6.9 provides a general overview.

Table 6.9: Overview of individual datasets making up the macroinvertebrate assemblage database.The table provides each dataset's start and end year and the number (#) of all sites and least disturbed sites.

Dataset	Start Date	End Date	# Sites	# Least Impaired Sites
Monitoring data, Flanders, Belgium	2005	2019	362	31
Monitoring data, Croatia	2017	2017	19	8
Monitoring data, Netherlands	2005	2017	246	46
Monitoring data, Finland	2007	2017	132	100
Monitoring data, France	2005	2020	4,193	1,492
Monitoring data, Germany	2005	2013	4,336	710
Monitoring data, Greece	2005	2013	87	13
Ecosurv Project, Hungary	2005	2005	239	21
Monitoring data, Norway	2017	2018	6	6
Monitoring data, Poland	2009	2019	759	318
Monitoring data, Portugal	2017	2019	194	53
Monitoring, Ebro Catchment, Spain	2006	2020	457	137
Monitoring data, Spain	2013	2017	772	252
Monitoring data, Sweden	2018	2021	99	60
Monitoring data, United Kingdom	2016	2021	1,662	340
Biodrought Project, Czech Republic	2012	2014	5	0
Monitoring, Slovakia	2008	2018	30	0

Of these data sets, some are openly available. Monitoring data, Flanders, Belgium (Vannevel *et al.*, 2022) are available on GBIF at https://www.gbif.org/dataset/5ca32e22-1f1b-4478-ba7f-1916c4e88d67. Monitoring data, France is available at https://naiades.eaufrance.fr/. Monitoring data, Ebro Catchment, Spain is available at http://www.datossuperficiales.chebro.es:81/WCASF/. Monitoring data, Sweden is available at https://miljodata.slu.se/MVM/Search. Monitoring data, United Kingdom is available at https://environment.data.gov.uk/ecology/explorer/how-to-use/.

6.3.2 SM 2 - Lists of taxa used to train the models

The following taxa were used to train the Athrazine model:
Acroneuria sp., Asellus aquaticus, Biomphalaria alexandrina, Brachionus calyciflorus, Ceriodaphnia reticulata, Ceriodaphnia silvestrii, Chironomus riparius, Chironomus tentans, Daphnia carinata, Daphnia magna, Daphnia pulex, Deleatidium sp., Echinogammarus tibaldii, Eurytemora affinis, Gammarus fasciatus, Gammarus fossarum, Gammarus italicus, Gammarus pulex, Hyalella azteca, Macrothrix flabelligera, Mesocyclops longisetus, Pacifastacus leniusculus, Palaemonetes argentinus, Pseudosida ramosa, Sigara arguta, Thamnocephalus platyurus, and *Utterbackia imbecillis*

The following taxa were used to train the Copper model:

Acroneuria lycorias, Alona affinis, Amnicola sp., Asellus aquaticus, Campeloma decisum, Ceriodaphnia dubia, Ceriodaphnia reticulata, Cherax destructor, Chironomus decorus, Chironomus javanus, Chironomus riparius, Chironomus tentans, Corbicula malinensis, Corbicula australis, Crangonyx pseudogracilis, Cypris subglobosa, Culex sp., Daphnia ambigua, Daphnia carinata, Daphnia magna, Daphnia parvula, Daphnia pulex, Daphnia pulicaria, Daphnia rosea, Ecdyonurus torrentis, Echinogammarus berilloni, Erpobdella testacea, Gammarus pseudolimnaeus, Gammarus pulex, Goniobasis livescens, Juga livescens, Gyraulus circumstriatus, Limnodrilus hoffmeisteri, Lophopodella carteri, Lumbriculus variegatus, Lymnaea stagnalis, Macrobrachium sp., Macrobrachium lanchesteri, Melanoides tuberculata, Moina dubia, Nais sp., Nais elinguis, Orconectes rusticus, Paratya australensis, Pectinatella magnifica, Philodina acuticornis, Physa heterostropha, Physa integra, Plumatella emarginata, Procambarus clarkii, Rhithrogena semicolorata, Sericostoma personatum, Simocephalus serrulatus, Siphlonurus armatus, Stenocypris major, Tropocyclops prasinus mexicanus, Tubifex tubifex, Unio angasi, and *Utterbackia imbecilis*.

The following taxa were used to train the Imidacloprid model:

Aedes sp., Asellus aquaticus, Caecidotea sp., Caenis horaria, Caenis sp., Ceriodaphnia dubia, Chaetopteryx villosa, Chaoborus obscuripes, Cheumatopsyche sp., Chironomus dilutus, Chironomus tentans, Cloeon dipterum, Cloeon sp., Coenagrion sp., Daphnia magna, Gammarus pulex, Deleatidium sp., Epeorus longimanus, Ephemerella sp., Gyrinus sp., Heptageniidae, Hexagenia sp., Hyalella azteca, Isonychia bicolor, Lampsilis fasciola, Lumbriculus variegatus, Maccaffertium sp., Micrasema sp., Neocloeon triangulifer, Plea minutissima, Simulium vittatum, Stenelmis sp., and *Trichocorixa sp.* .

6.3.3 SM 3 - Predicted EC50 values

The predicted EC_{50} values are available under: https://seafile.rlp.net/d/899eb07c6f8140628fa5/

6.3.4 SM4 - How many samples/taxa were analyzed for each type?

Table 6.10: Number of samples from least impacted sites, where at least 75% of taxa had converging Markov chains and that were inside the 95% highest density interval, analyzed for each combination of river type and chemical.

Broad River Type	Samples Athrazine	Samples Copper	Samples Imidacloprid
RT1	61	74	70
RT2	503	516	502
RT3	255	261	254
RT4	426	374	408
RT5	361	366	362
RT6	198	190	198
RT7	115	114	117
RT8	457	421	451
RT9	364	344	359
RT10	336	275	333
RT11	279	230	275
RT12	99	77	103

Table 6.11: Number of taxa from least impacted sites, where at least 75% of taxa had converging Markov chains and that were inside the 95% highest density interval, analyzed for each combination of river type and chemical.

Broad River Type	Taxa Atrazine	Taxa Copper	Taxa Imidacloprid
RT1	428	449	447
RT2	1,069	1,087	1,071
RT3	850	851	838
RT4	916	912	889
RT5	789	790	783
RT6	604	593	604
RT7	473	464	473
RT8	739	727	739
RT9	692	690	693
RT10	365	351	365
RT11	374	366	374
RT12	265	246	265

6.3.5 SM 5 Results for Alternative Typology Systems

Here, we report the results obtained for two additional typology systems: Illies Freshwater Ecoregions (IFE, Illies, 1978) and the European Environmental Zones (ENZ, Metzger *et al.*, 2005). Both typology systems differ from the Broad River Types in that they classify contiguous areas instead of river segments. Therefore, they are potentially superior in capturing broad-scale patterns in organisms' distribution but fail to integrate longitudinal changes along the river. We chose IFE because previous studies suggest they capture patterns in macroinvertebrate assemblage composition better than alternative systems (Jupke *et al.*, 2022). We chose ENZ because previous studies have suggested combining the Broad River Types with them; hence their performance here is of interest (Watson *et al.*, 2021).

The variation among IFE and ENZ types was similar to than that among the Broad River Types (Fig 6.40). Again, we observed the largest range for copper. In IFE, the median scaled HC_5 of the Central plains is -0.21, i.e., at approximately 61 % of the overall median HC_5 for copper. In the Fenno-Scandian shield it is at 0.22, i.e., approximately 1.7 times the overall median for copper. In ENZ, the lowest scaled HC_5 was observed for the Pannonian regions (-$,$0.29), indicating a difference in river-type-specific HC_5 median that is approximately half the overall median and the highest scaled HC_5 was observed for Atlantic North (0.21), i.e., it is approximately 1.6 times the overall median for copper.

The Cliff's d analysis indicated the difference between types of IFE and ENZ (Fig 6.41). Again, we observed the largest differences for copper, where most types differed for IFE and ENZ. For Atrazine, especially, the IFE types *Alps and Pyrenees* and the ENZ type *Atlantic North* showed the most pronounced differences. For Imidacloprid, the IFE types *Alps* and *Hungarian Lowland* and the ENZ types *Atlantic North* and *Pannonian region* showed the most pronounced responses.

Despite the prevalence of among-type differences, the magnitudes of these differences were similar to those observed for the Broad River Types (Fig 6.42). None of the differences was larger than one order of magnitude, and, except for Atrazine, inter-test variation exceeded the variation between types.

6.3.6 SM 6 - Results for all samples

The following sections show the results for all sampling sites, including disturbed and least disturbed ones. Figure 6.43 shows the variation between and within river types for all available sampling sites, including values outside the 95 % HDI. Including samples from disturbed sites and with HC_5 values outside the 95 % HDI only minimally alters the distribution of HC_5 values. The most notable difference to the distribution of the least disturbed sites are the outliers with high HC_5 values for Atrazine and Imidacloprid.

For Atrazine, the distributions of HC5 values are more similar when we included all sites in the analysis than when we included only the least disturbed sites (Fig. 6.44). The only noticeable differences are between lowland calcareous rivers (RT2,3) and highland rivers (RT10). The differences between RT3 and RT1, 7, 12, and between RT2 and RT12, which crossed the predetermined threshold in the analysis of least disturbed sites, were not confirmed in the analysis of all sites. Copper shows the most marked differences, which were still lower than in the analysis of only the least disturbed sites. No notable differences were found in the analysis of Imidacloprid.

The range of quotients between median river type HC_5 values for all samples (6.45) is similar, though smaller, to that for only the least disturbed samples (cf. Figure 4.6).

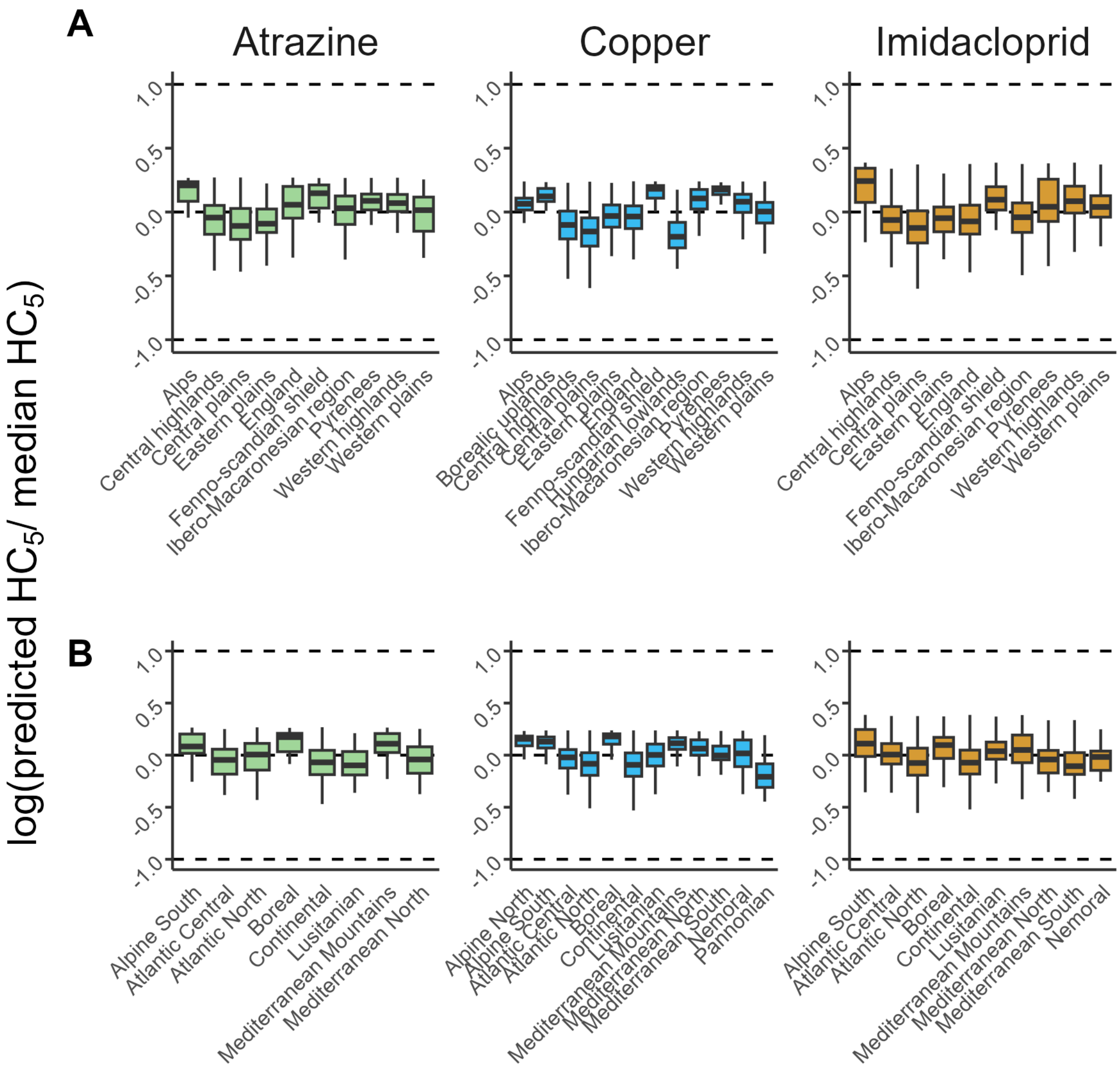

Figure 6.40: Density distribution of scaled hazard concentration 5 (HC5) values for each chemical and (A) Ecoregions or (B) Environmental Zones for which we had more than 20 samples. Scaling was achieved by dividing HC5 values by the median HC5 for the chemical across types and taking the decadal logarithm of this quotient. Values of zero thus imply that the value is equal to the chemical's overall median and values of one indicate that the value is one order of magnitude greater than the overall median. Horizontal lines within the density curves are medians. This plot shows only the least disturbed sites and values within the 95 percent highest density interval.

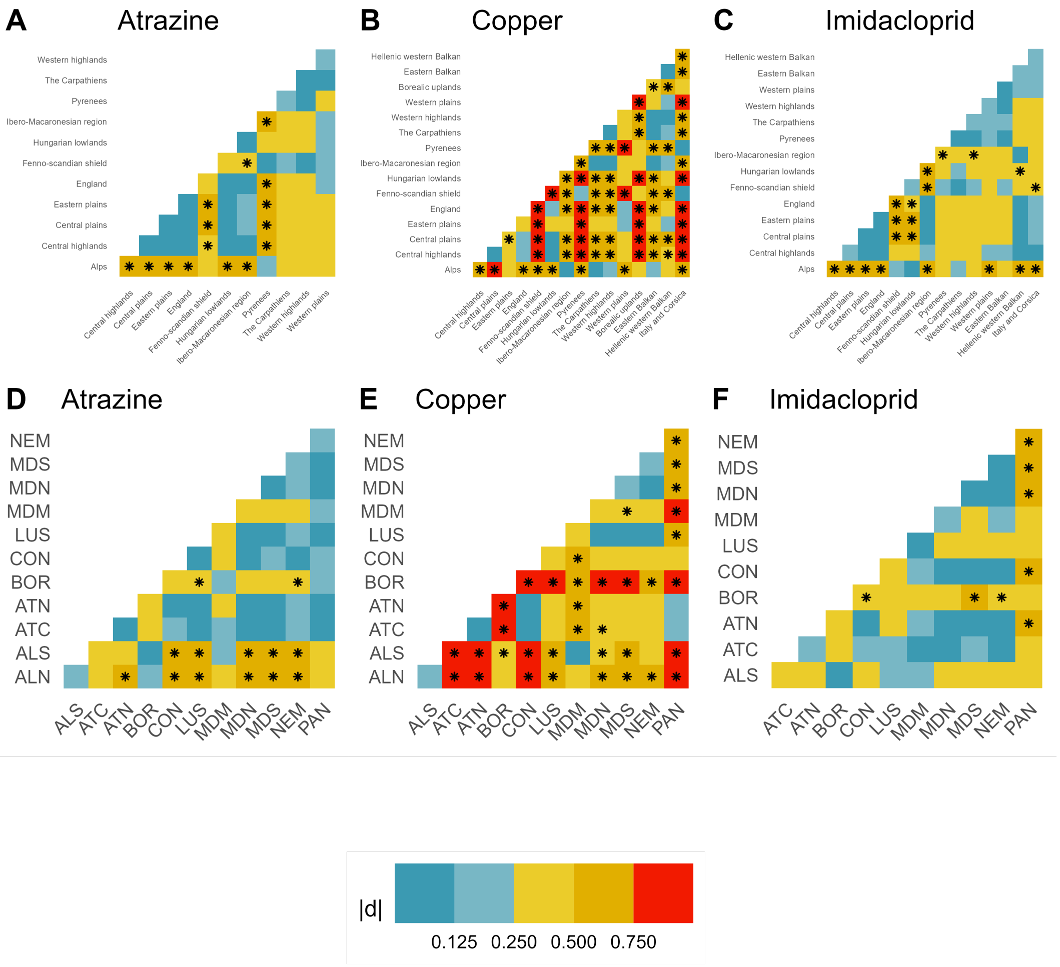

Figure 6.41: Differences between the assemblage hazard concentration 5 (HC5) values of different ecoregions (A-C) and environmental zones (D-F) expressed as the absolute value of Cliff's d. Dark blue cells indicate small differences, and dark yellow cells mark the largest observed differences. An asterisk marks Cliff's d values exceeding the 0.47 threshold. Values are based on the least disturbed sites only.

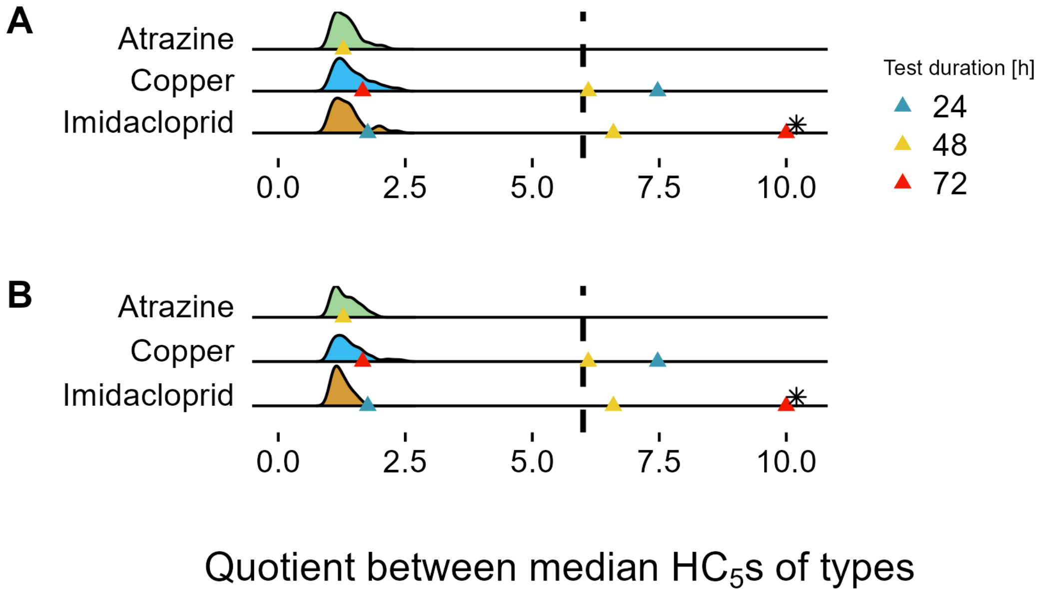

Figure 6.42: Factor of variation between median hazard concentrations 5 (HC5s) of Ecoregions (A) and Environmental Zones (B). The triangles show the variation in sensitivity (LC50) from single-species toxicity tests. Their color indicates the test duration in hours [h]. The triangle marked with an asterisk for Imidacloprid signifies a value that exceeds 10 (31). For the sake of legibility, the x-axis scale was kept at 10. The black dashed vertical line marks a difference of a factor of six.

6.3.7 SM 7 - Is there a systematic difference in the sensitivity of taxa with non-stationary Markov chains?

We excluded taxa for which the Markov chains did not converge to stationarity (henceforth non-stationary taxa), as indicated by the Heidelberg-Welch statistic. This removal can bias the results if these taxa skew toward high or low sensitivities. To evaluate the risk of this bias, we compared the predicted $\log(EC_{50})$ values of the non-stationary taxa with those of stationary taxa. While our low confidence in the predicted sensitivity values for non-stationary taxa lead us to remove them from the final analyses, they are the best indicators of their sensitivity available to us. There are no systematic differences between the sensitivities we predicted for stationary and non-stationary taxa (Figure 6.46).

6.3.8 SM 8 - Alternative version of Figure 3.2

Figure 6.47 shows the density distribution of Hazard Concentration 5 (HC5) values for each chemical and river type. It is an alternative version of Figure 3.2. The latter has a scaled y-axis, which might distort the results but is not.

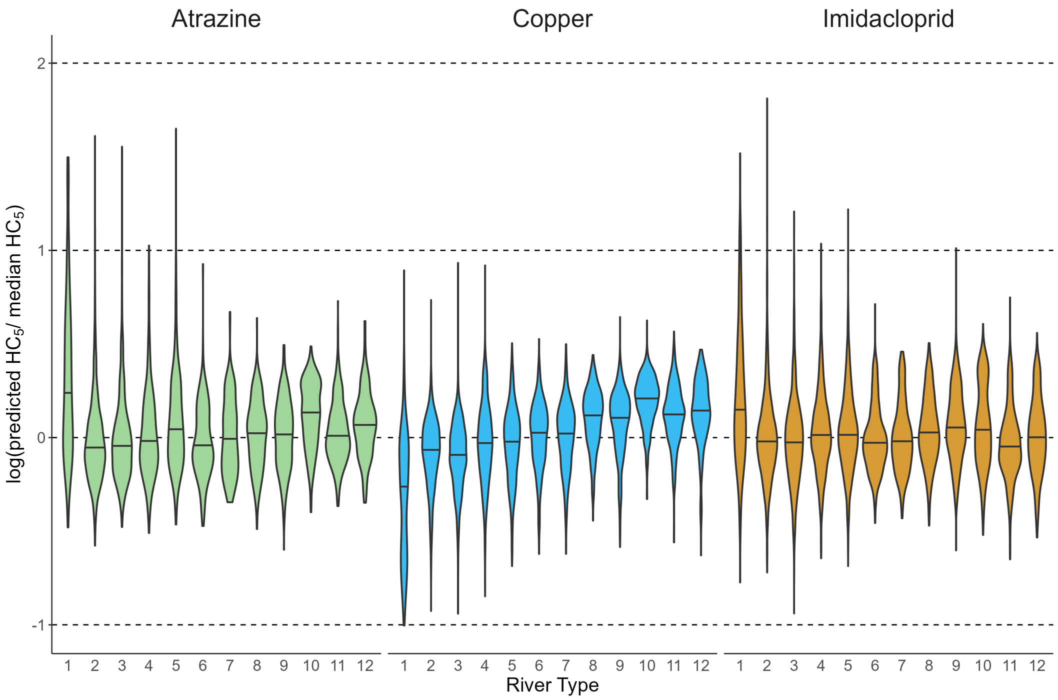

Figure 6.43: Variation in median hazard concentration 5 (HC5) values across river types. This plot shows the density distribution of scaled HC5 values for each chemical and river type. Scaling was achieved by dividing HC5 values by the median HC5 for the chemical across river types and are shown on a log10 scale. Values of zero thus imply that the value is equal to the chemical's overall median and values of one indicate that the value is an order of magnitude greater than the overall median. For an explanation of river types, see the method section. Horizontal lines within the density curves are medians. This plot shows all available sampling sites.

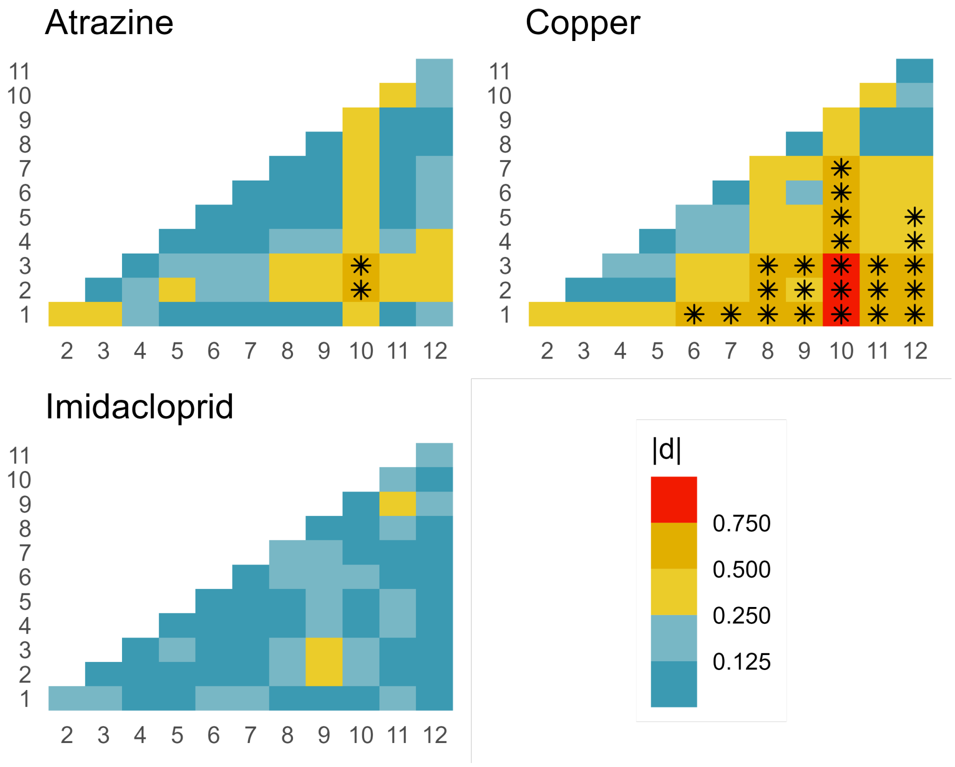

Figure 6.44: Differences between the assemblage hazard concentration 5 (HC5) values of different river types expressed as the absolute value of Cliff's d. Dark blue cells indicate small differences, and dark yellow cells mark the largest observed differences. An asterisk marks Cliff's d values that exceed the 0.47 threshold. Values are based on all available sampling sites.

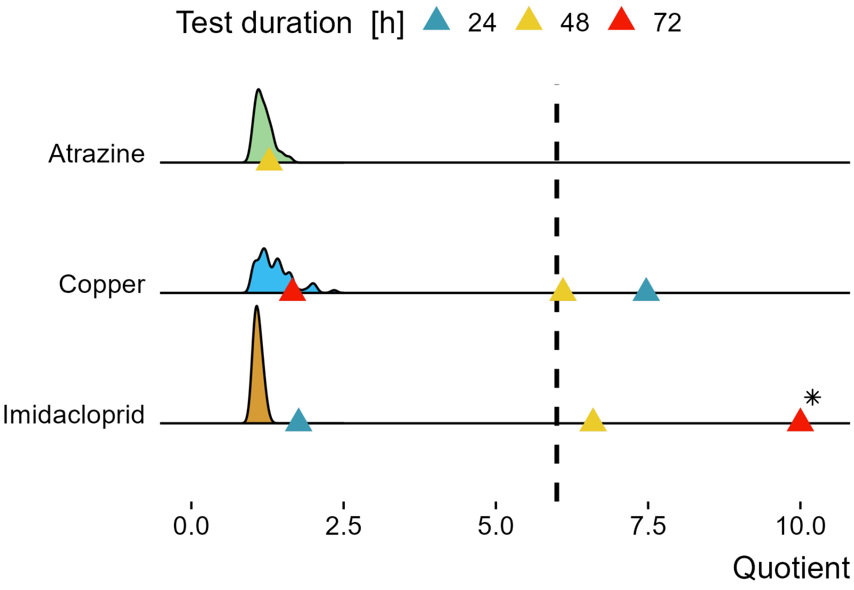

Figure 6.45: Factor of variation between median hazard concentrations 5 (HC5s) for all sites, i.e., including disturbed sites and sites outside the 95 percent highest density interval. The triangles show the variation in sensitivity (LC50) from single-species toxicity tests. Their color indicates the test duration in hours [h]. The triangle marked with an asterisk for Imidacloprid marks a value that exceeds 10 (31). For the sake of legibility, the x-axis scale was kept at 10. The black dashed vertical line marks a difference of a factor of six.

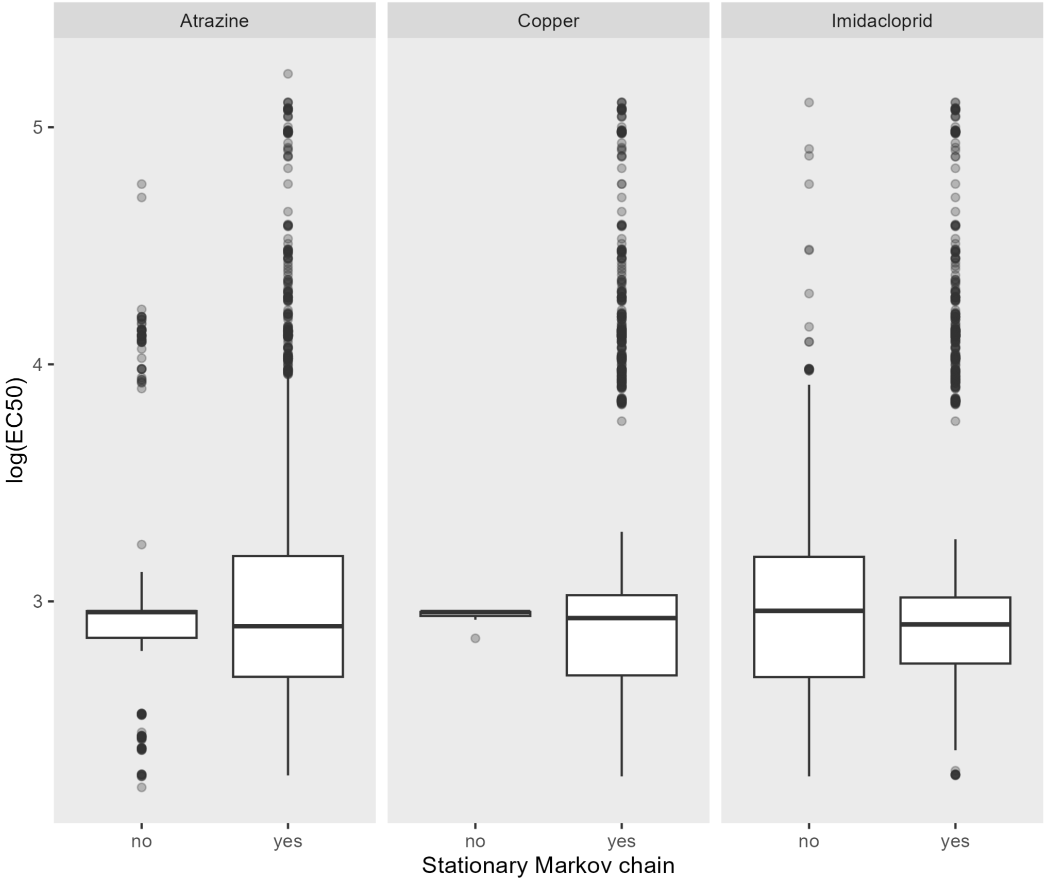

Figure 6.46: Predicted log(EC50) values for taxa with stationary and non-stationary posterior distributions.

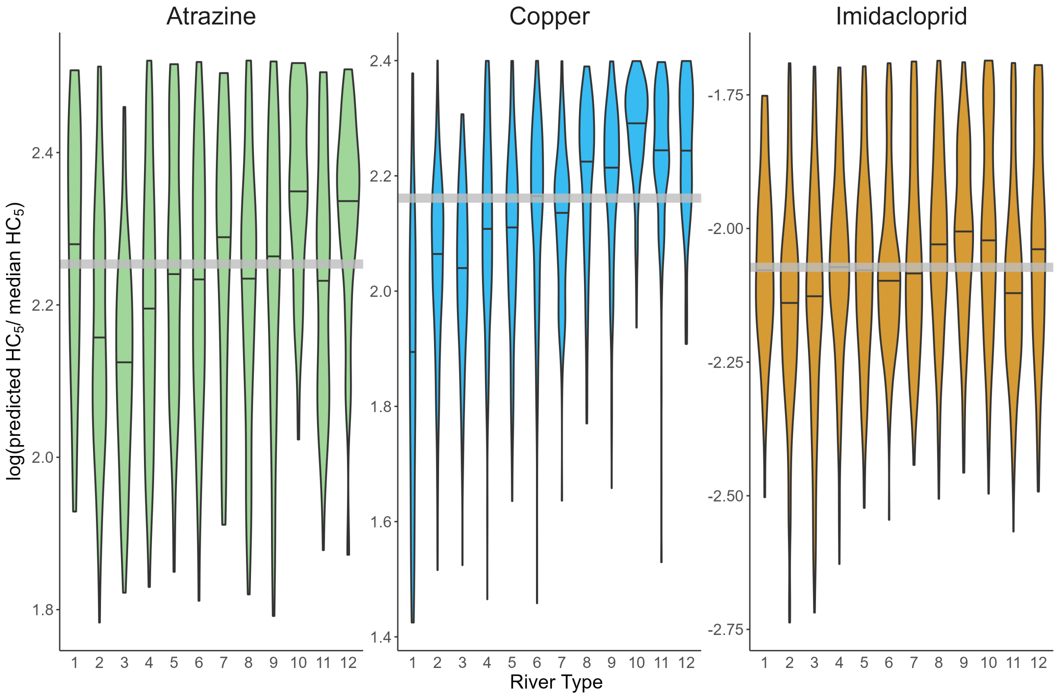

Figure 6.47: Density distribution of Hazard concentration 5 (HC5) values for each chemical and river type. Horizontal lines within the density curves are medians. The gray horizontal line shows the overall median of the respective chemical. The plot shows values from the least disturbed sites within the 95 percent highest density interval.

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Authors contributions

Article I

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

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Status: Published in Science of The Total Environment 842 156689

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Article II

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Article III

Title: Sensitivity of European macroinvertebrate assemblages toward three pesticides across river types

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I, the author of this work, certify that this work contains no material that has been accepted or submitted for the award of any other degree at any university or other tertiary institution. I prepared the work without the help of paid consultancy. All aids and sources are specified, other authors' contributions are documented, and a reference list is given. I know that violating any of these declarations can lead to my doctor's degree revocation.

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Jonathan Frederik Jupke

Declaration on the use of generative AI

I used generative AI in a supportive fashion during the writing of Jupke *et al.* 2023, Jupke *et al. in prep,* and the texts exclusive to this thesis (introduction and general discussion). I accessed the Large Language Model GPT 3.5 through the ChatGPT website (https://chat.openai.com/) and used the model to improve the texts linguistically, such as active versions of hitherto passive sentences or synonyms. I did not use whole sentences from the model or use the model to make content suggestions.

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Research Publications

Journal Articles

① N. Röder, V. S. Stoll, J. F. Jupke, *et al.*, “How non-target chironomid communities respond to mosquito control: Integrating DNA metabarcoding and joint species distribution modelling,” en, *Science of The Total Environment*, vol. 913, p. 169 735, Feb. 2024, ISSN: 00489697. DOI: `10.1016/j.scitotenv.2023.169735`.

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