

**Explaining the distribution of riverine
macroinvertebrates:
from autecological preferences to a
catchment-wide perspective**

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Chihiro: *Haku, listen. I just remembered something from a long time ago, I think it may help you. Once, when I was little, I dropped my shoe into a river. When I tried to get it back I fell in. I thought I'd drown but the water carried me to shore. It finally came back to me. The river's name was the Kahaku river. I think that was you, and your real name is Kahaku river.*

Haku: You did it, Chihiro! I remember! I was the spirit of the Kahaku river.

Chihiro: *A river spirit?*

Haku: My name is the Kahaku river.

Chihiro: *They filled in that river, it's all apartments now.*

Haku: That must be why I can't find my way home, Chihiro, I remember you falling into the river, and I remember your little pink shoe.

Chihiro: *So, you're the one who carried me back to shallow water, you saved me... I knew you were good!*

(Spirited Away, 2001)

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Abbreviations

ANOSIM Analysis of Similarity

ANOVA Analysis of Variance

BRT Boosted Regression Tree

CA Correspondence Analysis

CASiMiR Computer Aided Simulation Model for Instream Flow and Riparia

CV Cross Validation

EC Electrical Conductivity

ELWAS Elektronisches wasserwirtschaftliches Verbundsystem für die Wasserverwaltung in NRW

FDR False Discovery Rate

HET Habitat Evaluation Tool

HSC Habitat Sensitivity Class

IMPACT Developing an integrated model to predict abiotic habitat conditions and biota of rivers for application in climate change research and water management

LLUR Landesamt für Landwirtschaft, Umwelt und ländliche Räume

MHS Multi-Habitat-Sampling

nCPA Nonparametric Changepoint Analysis

NMDS Non-Metric Multidimensional Scaling

PCA Principal Component Analysis

PHABSIM Physical Habitat Simulation System

ROC Receiver Operating Characteristic

SDM Species Distribution Model

TITAN Threshold Indicator Taxa Analysis

WFD Water Framework Directive

WUA Weighted Usable Area

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1 Introduction

The explanation of distributional patterns of riverine macroinvertebrates remains one of the major challenges in aquatic ecology. In addition to natural drivers such as geology, geomorphology and ecoregion influencing river characteristics and the composition of their communities, freshwaters are nowadays heavily impacted by various anthropogenic stressors operating on different spatial scales (Feld and Hering 2007, Figure 1).

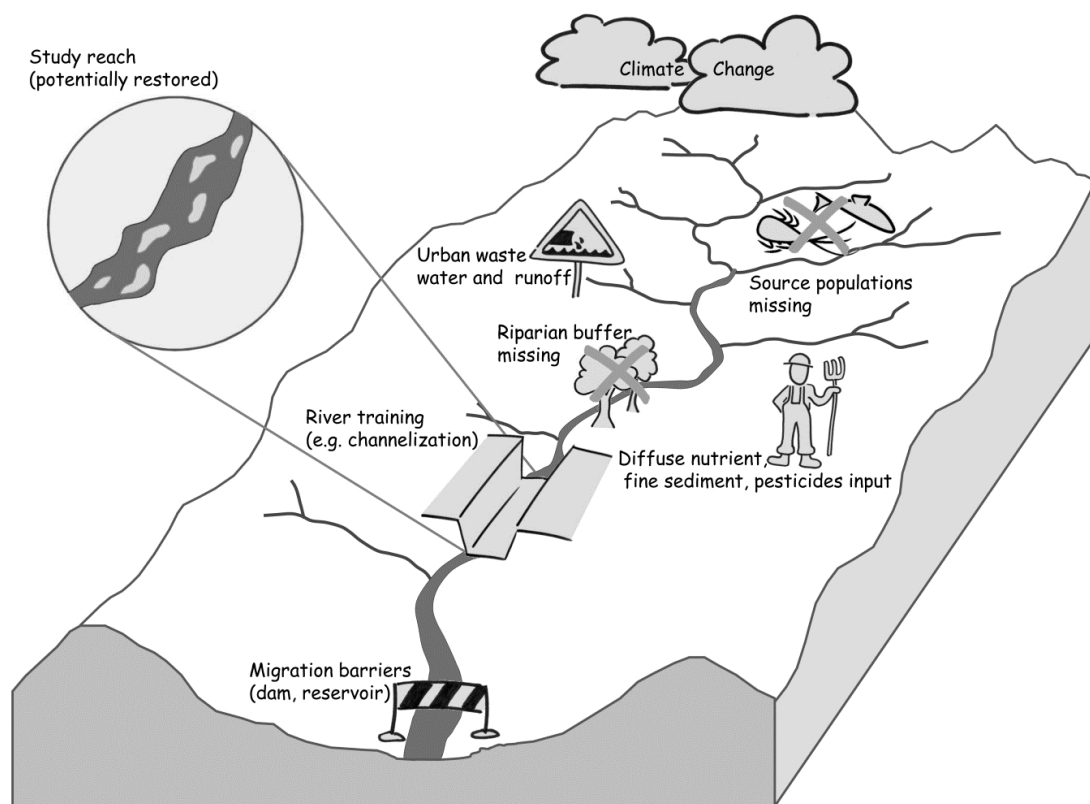


Figure 1: Overview of stressors on different spatial scales influencing the biological community at the reach scale (study reach) according to Kail et al. (2015)

The aquatic environment has been severely altered by i.a. point and diffuse sources of pollution (Cao et al. 1997), habitat degradation (Larsen and Ormerod 2010), and hydrological alterations (Dunbar et al. 2010, Poff and Zimmerman 2010). More specifically, environmental conditions have been impaired by changes in water chemistry due to nutrient enrichment and organic and/or toxic pollution, increased fine

sediment input caused by changes in land use and lack of riparian vegetation (Jones et al. 2012), as well as by changing flow velocities and substratum availability due to channel straightening (Nakano and Nakamura 2008). Beside these changes of the physical habitat also metapopulation dynamics have been strongly subjected to anthropogenic alterations. Recolonization processes have been made more difficult due to an increased construction of instream-barriers such as dams or weirs (Cortes et al. 1998, Lake et al. 2007, Parkyn and B. J. Smith 2011), modified land use within the riverine environment (Allan 2004), and persistent urbanization (Cuffney et al. 2010, Cuffney et al. 2011), all of which promote the fragmentation of local populations. Especially habitats for sensitive species with high ecological demands are often degraded or lacking, limiting the number of source populations in the catchment. In order to reestablish near-natural habitat conditions and associated freshwater communities, the European Water Framework Directive (WFD, Directive 2000/60/EC) came into force in 2000. The directive aims at restoring degraded rivers in order to improve their ecological and chemical status, obligating river management to achieve ‘good’ ecological status until the year 2027 for all surface waters. Within this context, macroinvertebrates have long been used as indicators to assess the ecological status of a river in addition to fish and aquatic flora (Hering et al. 2003, Hering et al. 2004b).

With regard to the above-named factors, the distribution of aquatic invertebrates in freshwaters is considered particularly complex. While there is a general agreement on the nature of the factors presumably influencing the distribution of macroinvertebrates in a catchment, little is known about how interactions between them shape abiotic habitat conditions and ultimately affect the composition of macroinvertebrates on the reach scale. Against this background, the research project IMPACT (Developing an integrated model to predict abiotic habitat conditions and biota of rivers for application in climate change research and water management) was initiated in 2010. The main objective of the project was to develop an integrated modeling framework to disentangle the effect of different pressures and to assess their importance for abiotic habitat conditions and associated river biota at the reach scale.

The consideration of multiple pressures involved the coupling of several consecutive modeling steps in the following order (Kail et al. 2015, Figure 3): a) an ecohydrological model to predict water quantity and quality, b) a 1D hydrodynamic model to predict the water level at the downstream end of the study reach, c) a 2D

hydrodynamic model to predict the hydraulic habitat conditions (e.g. flow velocity, depth, shear stress), and d) habitat models for fish and macroinvertebrates to determine the suitability of predicted abiotic habitat conditions (hydraulic parameters and substrate conditions) according to their autecological habitat preferences. In addition to morphological models focusing on channel geometry, channel planform, and channel bathymetry, dispersal models were added to the modeling framework to assess the effect of a limited species pool for (re-)colonization on the species composition in the study reach (for a more detailed description of the modeling framework see Kail et al. (2015)). Finally, the information provided by the previously mentioned models was synthesized and used to assess their importance for the biological assessment in the study reach. The modeling framework was applied in a near-natural study reach (approximately 300 m in length) for a German sand-dominated lowland river (Treene) and a gravel-dominated mountain stream located in South-West France (Célé) (Figure 2).



Figure 2: Near-natural study reach for the Treene (left) and Célé (right) catchment. (Photo: Björn Guse)

The present thesis was mainly developed within the IMPACT research project and contributed to several tasks within the integrated modeling framework. According to the highlighted components within the general modeling scheme (Figure 3), the main objectives of the thesis were:

- (i) The characterization of species' *habitat preferences* to develop a reach-scale habitat model.
- (ii) The development and application of a reach-scale *habitat model* to assess the effect of predicted abiotic changes on the macroinvertebrate community and ultimately biological assessment.

- (iii) The development and application of a *Species Distribution Model (SDM)* to identify source populations which are used as input for subsequent *dispersal modeling* in order to assess the (re)-colonization potential of selected species within the catchment.

Except for the habitat model (ii), which has been applied to both the Treene and the Célé study reach, remaining model components (iii) have been exclusively applied to the Treene catchment. Motives and background information related to the above-named objectives are provided in the paragraphs below.

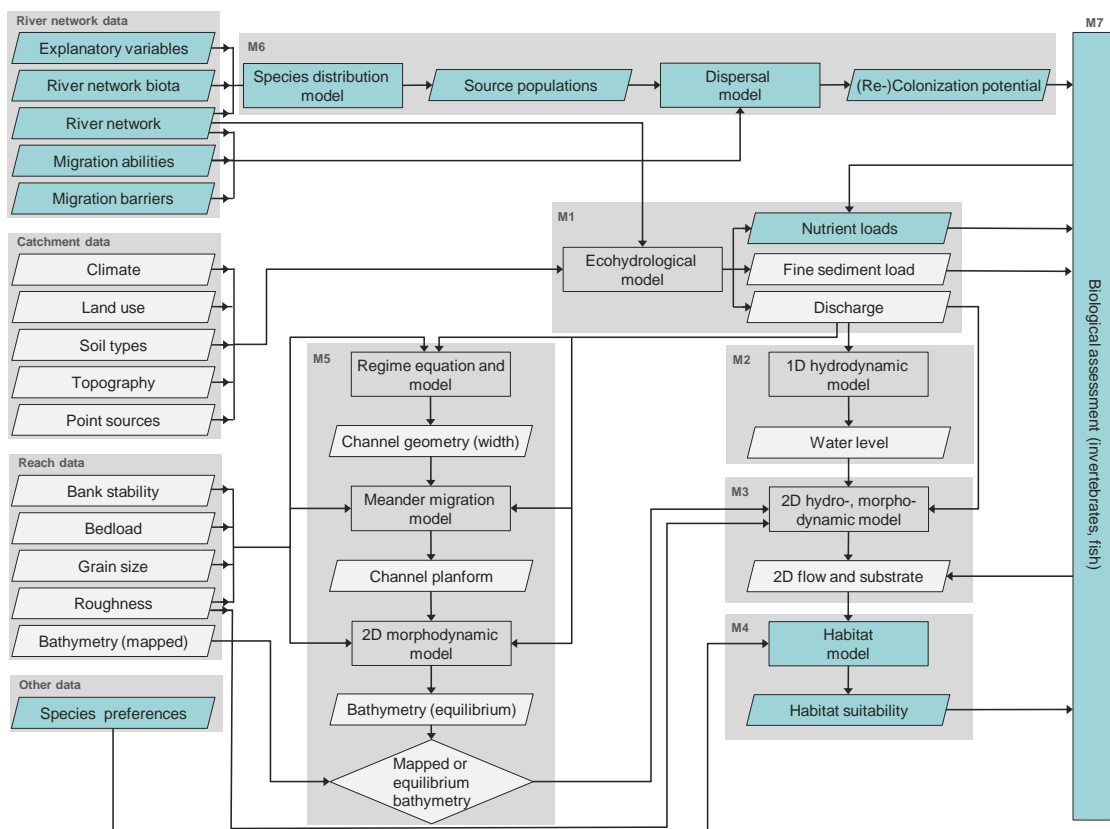


Figure 3: Conceptual overview of the integrated modeling framework according to Kail et al. (2015)

- (i) The characterization of habitat preferences and species traits constitutes one of the central research fields in aquatic ecology. Information on species habitat preferences and species traits have been widely recognized to significantly improve monitoring programs and predictions about how communities respond to disturbance or vary along environmental gradients and between habitats (Poff et al. 2006, Vandewalle et al. 2010, Feld et al. 2014). Although the terms habitat preferences and ecological traits have sometimes been used synonymously in previous publications (Usseglio-Polatera et al. 2000), Verberk et al. (2013)

emphasize the need to clearly distinguish between both terms. According to the authors, species traits refer to attributes which are inherent to the species such as physiological, morphological and life-cycle related features, excluding a species relationship towards its environment. Based on this assumption, the association of a species towards different habitat parameters such as water quality, hydrological preferences or substrate constitutes a habitat preference per se. In general, trait-based approaches often measure the response of species assemblages towards environmental changes based on single or multiple trait-guilds (i.e. the aggregation of several taxa with similar species traits). As the response is not restricted to the species level, trait-based approaches have proven especially useful for comparisons across larger spatial scales, e.g. between different catchments (Dolédec et al. 1999). In contrast, the analysis of habitat preferences follows a taxon-based approach. Taxon-based approaches usually aim at identifying indicator species, whose characteristics (e.g. its presence, absence or abundance) act as a surrogate measure for environmental factors or conditions of interest (e.g. water quality parameters, temperature, urbanization, climate change etc.) (Landres et al. 1988). They are assumed to depict species-environmental relationships more accurately within a limited spatial range (e.g. within a single catchment). Given the envisaged reach-scale application within the IMPACT project, a taxon-based approach was chosen to link relevant habitat descriptors to the occurrence of single species and/or communities in the catchment.

For Europe, species-specific habitat preferences of macroinvertebrates have been compiled in autecological databases such as www.freshwaterecology.info, providing valuable information on e.g. a species temperature preference, stream zonation, and/or substrate preference (Schmidt-Kloiber and Hering 2015). Inferences based on information gathered from autecological databases may however be fraught with uncertainty as many preferences are based on expert judgment as opposed to the analysis of empirical data. Moreover, information on habitat preferences is still incomplete or missing for a substantial amount of macroinvertebrate species.

Against this background, the present thesis aimed to derive habitat preferences from the analysis of primary data. According to the integrated modeling framework, habitat preferences are needed to link species composition or the occurrence of single taxa to predicted abiotic habitat conditions in the

model reach (*habitat model*). For this purpose, species-specific associations to substrate were chosen to establish the connection between abiotic and biotic models. Species-specific associations with particular substratum types have been commonly assumed (Rabeni et al. 2002), and bottom substratum composition has been widely identified as one of the most significant variable for explaining spatial distribution patterns of benthic invertebrates (Pardo and Armitage 1997, Beisel et al. 1998, Beauger et al. 2006, Chakona et al. 2008). Especially specialized species which are dependent on certain substrates are prone to be affected by habitat loss and may be diminished in number or will be completely eradicated from the local species pool if relevant substrates are lacking. Consequently, the degradation and loss of stream bottom habitats has been regarded to adversely affect the macroinvertebrate assemblage and to reduce local biodiversity. In the second chapter of the present thesis, substrate preferences for macroinvertebrates were deduced from empirical data to better understand how benthic invertebrates associate with bottom substrate composition and respond to habitat degradation (Schröder et al. 2013). The results act as significant scientific background information for the reach-scale habitat model.

In addition to habitat preferences, the analysis of tolerances of river biota towards water chemistry parameters is yet another field of research which lacks sound scientific evidence. This seems surprising, since water quality parameters (e.g. nutrients, physio-chemical variables) are known to act as overarching stressors to influence the macroinvertebrate composition on the reach scale and are discussed to mitigate local restoration success (Kail et al. 2012). Water quality issues are especially pronounced in lowland streams such as the Treene catchment, where urbanization, industrialization and agricultural land use are usually most apparent. Here, eutrophication related to increased nutrient loads and human-induced salinization have been considered as severe threats to impact freshwater biota (Millennium Ecosystem Assessment 2005). With respect to the latter aspect, most guidelines (e.g. the Water Framework Directive) addressing the response of river biota towards salinization often give approximate or generalized values from which an impairment is expected. The response towards salinity however is known to vary among species and different groups of biological quality elements (e.g. diatoms, macroinvertebrates and fish) and may further be subjected to regional conditions, consequently

complicating generalized conclusions. Moreover, salinity tolerances of river biota are usually given as broad classifications, e.g. defining ‘high’ or ‘low’ tolerances towards increased salinity loads. As opposed to this descriptive approach, several studies highlight the need to identify precise thresholds of salt stress, beyond which changes in assemblage composition can be expected (King and Baker 2010, Petty et al. 2010). However, respective case studies are rare. Against this background, the third chapter of the present study aimed to describe the effects of salinization on aquatic organisms (macroinvertebrates, diatoms) for a German lowland river (Schröder et al. 2015), with the emphasis on identifying species-specific and community thresholds. The analysis is based on data compiled from the Lippe river, which is similar to the Treene in terms of its hydromorphological characteristics and biological communities (large sand- and loam dominated lowland river, river-type 15, Pottgiesser and Sommerhäuser 2004). As opposed to the Treene, it shows a distinct gradient in salinity within a small spatial scale and thus presents an ideal surrogate study object to investigate salinization effects.

- (ii) Based on substrate preferences of macroinvertebrates analyzed within this thesis, the second main task within the integrated modeling framework focused on the development and application of a habitat model to link abiotic habitat conditions to changes in community composition. Habitat models such as PHABSIM (Milhous et al. 1984) or CASiMiR (Jorde 1996) have long been used in different fields of aquatic ecology and primarily aim at calculating the suitability of a river unit to harbour a certain species. The suitability is given as an index ranging between 0 (unsuitable) and 1 (most suitable) based on univariate relationships of a species towards single habitat parameters. Ultimately, single suitability indices are combined and transferred into a composite habitat suitability, usually given as a measure of Weighted Usable Area (WUA) for a defined river unit. However, model output (WUA) does not provide any information about a species presence and/or abundance. The option to calculate biological indices or metrics based on quantitative species data is consequently lacking, making it difficult to link abiotic habitat alterations to biological assessment results as they are required within the Water Framework Directive. In order to overcome these limitations, the Habitat Evaluation Tool (HET) has been developed by Kiesel et al. (2015), to enable a direct link between com-

munity changes associated to changes in abiotic habitat conditions and metric calculation. HET is a univariate, empirical habitat model that predicts the presence and abundance of invertebrate species for a certain river reach based on previously derived empirical relationships deduced from a large dataset of substrate-specific abundance data (Chapter 2). Hereby, the effects of spatio-temporal substrate changes on the macroinvertebrate community can be assessed. The development, sensitivity analyses and application of the model for selected species has been recently published by Kiesel et al. (2015). As opposed to the application of the model for single species, the HET was used to assess the effect of altered substrate conditions on the entire macroinvertebrate community for the Treene and Célé study reach, which presents the fourth chapter of the present study.

- (iii) In addition to reach-scale habitat conditions, both the regional species pool and species-specific dispersal capacities have been emphasized to determine the distribution of macroinvertebrates within a catchment (Tonkin et al. 2014). Against this background, the fifth chapter of the thesis aimed at coupling Species Distribution Models and dispersal models to estimate the (re-)colonization potential for selected model species. In order to model the dispersal of a species within a catchment, the consideration of the following aspects is essential: a) the location of source populations, and b) information about species-specific dispersal abilities in order to estimate a species dispersal originating from any source population in the catchment, optionally considering terrestrial and aquatic barriers.

Source populations of macroinvertebrates may, on the one hand, be obtained directly from official biological monitoring campaigns. The availability of monitoring data is however limited and information about the occurrence of a species throughout a catchment thus remains incomplete. Here, SDMs present a useful approach to predict a species distribution for an entire catchment. SDMs have been extensively used in fields of aquatic ecology (Guisan and Thuiller 2005, Elith and Leathwick 2009) and are most commonly applied to identify areas of high conservation value for selected species. As a basic principle, SDMs aim at linking species-environmental relationships with statistical learning algorithms in order to predict the distribution of species under current or future environmental conditions (Araújo and P. H. Williams 2000). The prediction

refers to a defined spatial unit (e.g. river reach or grid cell) and is based on presence-absence species data and environmental parameters as proxies (Elith et al. 2006, Elith and Leathwick 2009, Franklin 2010). In the present thesis, both approaches have been used as potential starting points in combination with the subsequent dispersal model to assess the (re-)colonization potential of selected species in the Treene catchment.

While SDMs provide important information about a species presence or absence within the catchment, the consideration of dispersal processes between metapopulations need to be considered in addition to assess if suitable habitats can be colonized by focal species. Assessing a species' dispersal within a catchment seems especially important with regard to restoration measures, since impaired dispersal processes have been highlighted to mitigate biological effects on the reach scale (Sundermann et al. 2011). According to their dispersal abilities, macroinvertebrates can be divided into merolimnic species, which are characterized by a winged adult life stage in addition to their aquatic larval life stages, and hololimnic – strictly aquatic – species, whose movements are confined to the river network. The main dispersal vectors of macroinvertebrates thus refer to aquatic downstream drift (active, passive), active movement of larval stages (upstream, downstream), and the terrestrial, aerial dispersal of imagos (Tronstad et al. 2007, Bogan and Boersma 2012, Bertin et al. 2015). While dispersal distances largely depend on the dispersal mode (aquatic dispersal vs. terrestrial dispersal) (Grönroos et al. 2013), aquatic and terrestrial landscape features have moreover been highlighted to influence species-specific dispersal patterns (I. Petersen et al. 2004).

Against this background, the least-cost modeling approach (Adriaensen et al. 2003, Dedecker et al. 2007) provides a helpful tool to assess the colonization potential of selected species, enabling to consider differences in the permeability of the aquatic and terrestrial landscape. The model approach has been widely applied in ecology, e.g. for terrestrial vertebrates (Adriaensen et al. 2003) and invertebrates (Koch and W. D. Smith 2008), as well as for aquatic organisms (Dedecker et al. 2007, Keller and Holderegger 2013). Recently, the least-cost modeling concept was tested in a mountainous catchment by Sundermann et al. (2015) to investigate the effect of migration barriers on the distribution of three macroinvertebrate species. Within the present study, SDMs and least-cost models were combined to identify the (re-)colonization potential for ten

model species within the Treene catchment. The results were furthermore used to assess the limiting factors for a species' distribution in the Treene catchment and have been recently summarized by Kail et al. (2015).

1.1 Scope of the thesis

According to the previous chapters, the distribution of riverine macroinvertebrates is governed by factors operating on the individual, reach, and catchment scale. Related to these factors, the present thesis divides into four main chapters which are associated to the prior outlined main tasks within the IMPACT project. All chapters represent individual papers which have been partially submitted and published in international peer-reviewed journals. They specifically address the following topics and associated objectives:

- *Substratum associations of benthic invertebrates in lowland and mountain streams*

Within the second chapter, substrate preferences for macroinvertebrates were analyzed and classified. The study aimed to identify those species which prefer specific substratum types (specialists) and those which are distributed among a wide range of different substratum types (generalists). It was examined, how classifications derived from empirical data correspond to existing classifications of species' substratum preferences and whether substrate preferences of the same species differed between lowland populations and mountain streams.

- *Effects of salinity gradients on benthic invertebrate and diatom communities in a German lowland river*

Within the third chapter, the effect of salt pollution on the macroinvertebrate and diatom community was investigated for a German lowland river. More specifically, salinity thresholds for individual species and communities were derived in order to determine ecological change points of salt stress. Indicator species associated to either increasing or decreasing salinity loads were identified and results were compared to existing classifications of salt tolerance.

- *Simulating the effect of substratum composition on macroinvertebrate assessment metrics in two rivers*

Within the fourth chapter, it was investigated whether and to what extent

changes in bottom substratum composition influence WFD assessment metrics and ecological status for a lowland (Treene) and mountainous (Célé) river reach. Moreover, the study aimed to ecologically describe all relevant substrate components and to identify potential key habitats.

- *Coupling Species Distribution Models and dispersal models: the effect of source populations on the colonization potential for 10 macroinvertebrates*

Within the fifth chapter, a methodological approach to couple SDMs and least-cost models was described in order to assess the colonization potential for 10 macroinvertebrate species in the Treene catchment. The study aimed to investigate how source population numbers and different dispersal capacities affect the colonization potential of a species within a catchment.

2 Substratum associations of benthic invertebrates in lowland and mountain streams

2.1 Introduction

It is common knowledge that aquatic invertebrates are patchily distributed on the stream bottom. Many invertebrate species developed various physiological and morphological adaptations that are strongly associated with habitat conditions (Pardo and Armitage 1997). With a flattened body form, some species are able to colonize the surface of larger stones, where they are exposed to strong currents and predominantly feed on biofilms (J. N. Minshall 1967). Others hide in sand and mud, which require adaptations for temporarily low oxygen concentrations, while still others need special food sources such as leaves or wood, restricting them to accumulations of organic matter. Consequently, to a certain extent, many species are supposed to be associated with specific substrates that are composed of either mineral substrates (e.g., sand, gravel, stones) and/or organic matter (e.g., macrophytes, dead leaves and deadwood). All of these habitats provide certain food sources and are characterized by specific current velocities. While some species inhabit a wide range of habitats (Giller and Malmqvist 1998, Kubosova et al. 2010), others are much more specific (Allan 1995, Dallas 2007).

Species-specific associations with particular substratum types have been commonly assumed (Rabeni et al. 2002), and bottom substratum composition has been widely identified as one of the most significant variables for explaining spatial distribution patterns of benthic invertebrates (Rabeni and G. W. Minshall 1977, Pardo and Armitage 1997, Beisel et al. 1998, Beauger et al. 2006, Chakona et al. 2008). The substratum type (Velásquez and Miserendino 2003), substratum composition (Beisel et al. 2000) and substratum size fractions (Culp et al. 1983, Wohl et al. 1995) are among the more specific substratum parameters influencing invertebrate assemblages.

From an applied point of view, the degradation of stream bottom habitats is frequently assumed to negatively influence invertebrate assemblages and reduce bio-

diversity. The impact on benthic invertebrates is most obvious if substrates for specialized species (e.g., wood debris, Hoffmann and Hering (2000)) are lacking. Moreover, the construction of weirs and dams severely alters habitat conditions because fine sediments accumulate directly upstream of the dams, leading to stagnation and complete shifts in community composition. To a lesser degree, residual flow increases the coverage of fine sediments downstream of a barrier and might alter substratum composition as well. In contrast, artificial streambeds may lead to increased current velocities, resulting in the loss of fine grains and associated species.

There have been several attempts to classify substratum preferences of species or higher taxonomic units to describe how benthic invertebrates associate with the bottom substratum composition and respond to habitat degradation. For North America, most genera have been classified by Merritt and Cummins (1995); for parts of Asia, an initial approach was published by Korte (2010); for Europe, Moller-Pillott (1984), Schmedtje and Colling (1996), Moog (1995) and Šporka et al. (2006) compiled substratum preferences mainly at the species level for several thousand taxa. An online database with ecological preferences (including substratum preferences) for 1224 European species is available at <http://www.freshwaterecology.info> (Schmidt-Kloiber et al. 2006, Schmidt-Kloiber and Hering 2012). However, the substratum preferences of many species are still unknown. Furthermore, most of the above-mentioned compilations are based on literature analyses and expert knowledge rather than analyses of primary data.

In recent years, many studies on substratum-specific benthic invertebrate assemblages have been performed (Jähnig et al. 2009, Kiesel et al. 2009, Kramm 2002, Lorenz et al. 2009, Rolauffs 2006, Schattmann 2014, Schmidt-Kloiber et al. 2006, Vlek et al. 2006). Now, for the first time, these studies offer the opportunity to base the classification of species' substratum preferences on original data. Here, we analyzed a dataset of almost 1000 substratum-specific samples from Germany, the Netherlands and Austria to check the validity of existing classifications and to derive new classifications. Specifically, we addressed the following questions:

1. Which species prefer specific substratum types (specialists), and which are distributed among a wide range of different substratum types (generalists)?
2. Are the existing classifications of species' substratum preferences that were derived from expert opinion consistent with the classifications derived from original data?

3. Do lowland populations and mountain populations of the same species have different substratum preferences?

2.2 Methods

2.2.1 Study sites

Our analysis was based on substratum-specific macroinvertebrate samples taken between 2001 and 2009 within the scope of various research projects (Table 1). The samples were taken from 18 streams in Germany, the Netherlands and Austria, comprising a total of 40 sampling sites and equally covering lowland and mountain streams.

The investigated streams, which were classified as lowland streams, were located at an altitude of <200 m.a.s.l., and mountain streams at an altitude of 200–800 m.a.s.l. The catchment size ranged between 10–100 km² for streams classified as ‘small’ (Table 1) and 100–1000 km² for mid-sized streams. The lowland streams were running in ground and terminal moraines as well as sandy deposits and accordingly the channel substrata were dominated by sand and gravel. In addition, there were frequent patches of organic matter composed of fine and coarse detritus, wood or macrophytes. In contrast, prevailing substrates in the mountain streams consisted of small to medium-sized cobbles and large to very large boulders, interspersed with a variable portion of gravel, sand and accumulations of organic materials to a lesser amount.

2.2.2 Sampling and sample processing

The division of streams into visually distinct areas of different substratum types is the basis for the ‘Multi-habitat sampling’, a widely applied monitoring technique for macroinvertebrates (Hering et al. 2003) to implement the EU Water Framework Directive (Directive 2000/60/EC). Based on this technique, a standardized substratum-specific sampling procedure was applied, using a 25 cm × 25 cm frame shovel sampler (500 µm mesh) within all studies considered (compare Table 1). Where the collection of substrate material was impossible (for instance for larger boulders and stones), the substratum was sampled by manually scrubbing an equally sized area of 25 cm × 25 cm of the substratum surface. Each sample was categorized with respect to its dominant substratum type and was stored separately and preserved with 96 % ethanol in the field. There were 422 samples from mountain streams

Table 1: Selected variables and number of substratum-specific samples for lowland and mountain streams; ecoregion names and numbers according to Illies (1978); D = Germany, AT = Austria; for abbreviated substratum types see Table 2.

Country	Year	Ecoregion	Season	Catchment size	Citation	No. of sampling sites	Mineralic substratum types					Organic substratum types				Sum
							AKA	ARG	MAL	MIL	PSA	PEL	POM	MPH	WOO	
DE	2001-2002	Central highlands (9)	Spring summer	Small	Rolauffs (2006)	5	6	12	8	3	3	2	4	3	38	
DE	2004-2005	Central highlands (9)	Summer	Medium	Jähmig et al. (2009)	14	16	18	60	16	18	16	22	18	196	
AT	2005	Central highlands (9)	Summer autumn	Medium	Schmidt-Kloiber et al. (2006)	3	18	42	58	7	17	9	24	13	188	
					Sum	22	40	72	126	26	35	27	50	34	422	
DE	2005	Central lowlands (14)	Summer	Small	Lorenz et al. (2009)	4	3	2	11	19	4	5	12	2	58	
DE	2005-2007	Central lowlands (14)	Summer	Medium	Schattmann (2014)	5	40	22	21	40	32	29	40	11	251	
DE	2002	Central lowlands (14)	Spring summer	Small	Kramm (2002)	4	4	16	16	32	8	8	16	16	64	
DE	2009	Central lowlands (14)	Summer	Small	Kiesel et al. (2009)	1	8	8	16	8	8	8	16	16	80	
NL	2002	Western lowlands (13)	Summer autumn	Small	Vlek et al. (2006)	4	20	32	64	18	36	40	20	20	98	
					Sum	18	71	32	16	64	117	82	88	45	551	

and 551 samples from lowland streams, resulting in a total of 973 samples.

Each sample was subsequently processed in the lab and all organisms were removed from the sample. The samples from Germany were mostly identified to the species level, excluding most Diptera (family level), Chironomidae (genus level, species in exceptional cases) and Oligochaeta (mixed level of family, genus and species). Samples from Austria and the Netherlands were almost entirely identified to the species level. The sampling was predominantly performed during the summer months.

For statistical analyses, nine substratum types were considered (compare Table 2), partly after aggregating substratum types that were defined more specifically for the purpose of the original studies. In particular, we summarized substratum classes that were originally separated as ‘large’ and ‘very large boulders’ to a single substratum class ‘MAL’ (macrolithal, average diameter > 20 cm) and small to mid-sized cobbles to a substratum class ‘MIL’ (microlithal, average diameter 2–20 cm). We also aggregated samples of fine and coarse particular organic material to a single class ‘POM’ (particular organic material) (Table 2).

Table 2: List and description of substratum types (n = 9) included in statistical analyses.

Substratum type abbreviation	Substratum type	Substratum type description
AKA	Akal	Fine to medium sized gravel (2–0.2 cm average diameter)
ARG	Argyllal	Silt and clay (< 6 μ m average diameter)
MAL	Macrolithal	Blocks and large boulders (> 40–20 cm average diameter)
MIL	Microlithal	Cobbles and coarse gravel (20–2 cm average diameter)
MPH	Phytal	Fine roots, floating riparian vegetation and submerged and emergent macrophytes
PEL	Pelal	Mineral mud (< 6 μ m average diameter)
POM	Fine and coarse particulate organic matter	Deposits of fine and coarse particulate organic matter like e.g. dead leaves
PSA	Psammal	Sand (< 2 mm average diameter)
WOO	Wood debris	Dead wood, roots, twigs and branches

2.2.3 Data preparation

As organic pollution might mask substratum-specific assemblages, we calculated the Saprobic Index (German version) for all of the samples to identify and potentially eliminate polluted sites. Nevertheless, all of the samples obtained a ‘good status’ (Saprobic Index < 2.30) concerning saprobic conditions and none of the samples were excluded from further analyses.

Due to the varying taxonomical resolution within and between samples, we evaluated the substratum preferences separately for Diptera and Oligochaeta opposed

to the remaining taxa groups in the dataset. Consequently, the substratum preferences for all of the taxa groups analyzed based on the entire dataset (*dataset I*, 422 samples from mountain streams and 551 samples from lowland streams), while substratum preferences of Diptera and Oligochaeta referred to the samples from Austria (*dataset II*, 188 samples). Lowland samples for Diptera and Oligochaeta were based on four substratum types only and in conclusion an analysis of the substratum preferences would be considered incomplete because most substratum types were lacking. Therefore we limited our analysis of substratum preferences for Diptera and Oligochaeta to mountain samples only.

The reasons for different taxonomic resolution are manifold (Verdonschot 2006) and especially large composite datasets should be checked for taxonomic redundancy in advance of analysis to guarantee unbiased data processing. After a taxonomic adjustment with the elimination of redundant taxa in each dataset (for detailed information on the procedure see (Vlek et al. 2004), taxalists comprised 344 taxa (*dataset I*) and 363 taxa (*dataset II*), respectively.

We omitted rare taxa from the analysis, as the results might be strongly determined by random forces in these cases. We determined substratum type-specific threshold values for the identification of rare taxa for each dataset. The threshold was set as the relative frequency of the substratum type being represented by the lowest number of samples in each dataset. The taxa with a relative frequency falling below this threshold were excluded. The final number of taxa included in the statistical analyses were as follows: *dataset I* (lowland samples $n = 66$, threshold 2.9%; mountain samples $n = 122$, threshold 2.8%) and *dataset II* (mountain samples $n = 102$, threshold 3.7%). The abundances of all of the species were calculated as ind/m² (individuals per square meter) and data were square-root transformed to account for major differences in abundances.

2.2.4 Data analysis

Substratum preferences were identified by applying the package ‘indicpecies’ (version 1.5.2) in the R software (version 2.1.2.2), which provides multiple functions to assess the strength and significance of the relationship between species and combinations of predefined groups (here: substratum groups) (De Cáceres and P. Legendre 2009). Originated from the IndVal method of Dufrêne and P. Legendre (1997), the ‘Multi-level pattern’ analysis offers several indices to analyze substratum preferences (for detailed information see De Cáceres et al. (2010)). The following index (‘Ind-

Val.g') was applied (for a detailed index description, see De Cáceres and P. Legendre (2009)):

$$\sqrt{IndVal_{ind}^g} = \sqrt{A_{ind}^g \times B_{pa}} = \sqrt{\frac{a_p/N_p}{\sum_{k=1}^K a_k/N_k} \times \frac{n_p}{N_p}} \quad (1)$$

where:

- N_p = Number of sites belonging to a specific substratum group
- n_p = Number of occurrences of the species within a specific substratum group
- a_p = Sum of the abundance values within a specific substratum group
- K = Number of substratum groups
- N_k = Number of sites belonging to the k^{th} substratum group
- a_k = Sum of the abundances values of the species in the k^{th} substratum group
- A_{ind}^g = Probability that a site belongs to a specific substratum group (based on the fact that an individual of the target species has been found (group-equalized))
- B_{pa} = Probability of finding a species when the site belongs to a specific substratum group
- $IndVal_{ind}^g$ = Group-equalized indicator value index between a target species and a group of sites (individual-based)

The test statistic ('IndVal.g') indicates the strength of an association between a taxon and its substratum (group) and ranges from 0 (no association) to 1 (maximum association). As with the original IndVal method, two datasets were required as input for the analysis. In addition to a species dataset with abundance values for investigated sites, the analysis requires a data vector of a priori assigned substratum classes for each sample. While the original IndVal method obtains Indicator Values by studying the association between taxa and a single substratum, the 'Multi-level pattern' analysis generates values based on all possible combinations of substratum types.

According to De Cáceres et al. (2010), the identification of a maximum association value for a combination of substrates does not correct for type-I errors, as the selected substratum combinations are not independent of the species pattern. To correct for

type-I errors, the ‘Multi-level pattern’ analysis repeats the selection of a substratum group with the strongest association value after each permutation of the species data by using the maximum association value as the test statistic. Accordingly, the combination of substratum types with the highest Indicator value for a given taxon were obtained and subsequently tested for statistical significance.

However, the associated p -values obtained from the ‘Multi-level pattern’ analysis were not corrected for multiple testing. As we tested substratum preferences for many different species on the same data set, which abundances may not vary independently, p -values were adjusted post hoc. To overcome the problems of multiple testing we used the ‘false discovery rate’ (fdr) approach (for a detailed description see Benjamini and Hochberg (1995)).

Finally, we listed all species (‘fdr’ adjusted p -value ≤ 0.05) and their associated substratum (group) separately for lowland and mountain streams. Species with significant substratum preferences in both lowland and mountain streams are listed separately to compare substratum preferences in both stream types.

In general, substratum preferences were synthesized into three groups:

- I: Species/taxa that show distinct preferences for one or two substratum types (substratum specialists)
- II: Species/taxa that show preferences for three or four substratum types (intermediate substratum preferences)
- III: Species/taxa that show preferences for five or more substratum types (substratum generalists)

Using the package ‘indicspecies’, we were able to calculate a test statistic not only for a combination of substratum groups, but also to obtain the strength of an association between a taxon and each single substratum type. This output is an intermediate step, which later is used in the analysis to test the significance of multiple substratum groups combined. However, we used this intermediate output to derive a 10 point system for the association between a taxon and a given substratum to compare our data based results with the classifications from expert opinion (<http://www.freshwaterecology.info> database). For this purpose, we calculated the relative strength of a taxon to a single substratum component by using the following formula:

$$\begin{aligned}
 & \text{Relative strength of association for a taxon to a substratum type } X \\
 & = \\
 & \left(\frac{\text{Test statistic for substratum type } X}{\text{Sum of test statistics for all substratum types}} \right) \times 10
 \end{aligned} \tag{2}$$

Additionally, we calculated two ratios to assess the consistency between the results from statistical analysis and database records, as well as for the comparison of taxa tested significant in lowland and mountain streams. The first ratio ('ratio.cat') indicates the overall consistency of occupied substratum types for each taxon between two datasets. For each taxon, the number of identically occupied substratum types was counted. The number of matching substratum types was divided by the number of all substratum types afterwards (here: 9). This index takes values between 0 and 1. A value of 0 indicates a completely different allocation of substratum categories between results from statistical analysis and database records. A value of 1 on the contrary indicates that substratum categories were assigned identically.

To assess the deviation in the strength of association between a taxon and a substratum type for two datasets, we calculated a second ratio ('ratio.str'). For each substratum type, a ratio was calculated between the two datasets (for each taxon). All ratios were summarized and divided by the total number of substratum type (here: 9). Similarly, values for this ratio range between 0 and 1, with '1' indicating an even distribution of 10 points among all substratum types for a given taxon in both datasets.

Certainly, the index 'ratio.str' is not independent from the first index 'ratio.cat'. In order to achieve high values for index 'ratio.str', the index 'ratio.cat' needs to take high values in the first place and vice versa. However, values for 'ratio.str' differ for the same 'ratio.cat' values and thus provide the opportunity to discover differences in the strength of association.

2.3 Results

2.3.1 Substratum preferences

Of the 290 taxa analyzed, the 'Multi-level pattern' analyses revealed significant substratum preferences for 188 taxa. In the next paragraphs, we separately deal with substratum preferences for species in lowland and mountain streams and with sub-

stratum preferences for species that were significantly associated with a substratum type (or combination) in both datasets.

2.3.1.1 Substratum preferences for taxa in lowland and mountain streams

In lowland streams, 53 out of 66 taxa significantly preferred (combinations of) substratum types (see Tables 3a, 3b and 3c). Twenty-five taxa were assigned to preference group I (distinct preferences for one or two substratum types), whereas intermediate and widespread substratum preferences were detected for 17 and 11 taxa, respectively. In mountain streams, 135 out of the 224 taxa analyzed were significantly associated with one or several substratum types (Tables 4a, 4b and 4c). Fifty-one taxa were allocated to preference group I, 48 taxa to preference group II and 36 taxa to preference group III. The relative distribution of taxa according to preference groups was similar between lowland and mountain streams (Figure 4).

Table 3a: Summary of the 'Multi-level pattern' analysis and calculated indices ('ratio.cat', 'ratio.str') for taxa in lowland streams (No. of taxa = 53); only significantly tested taxa are listed; significant tested substratum combinations are highlighted; stat = test statistic 'IndVal.g'; for abbreviated substratum types see Table 2. **Preference group I (Taxa significantly associated to 1 or 2 substratum types)**

Taxa group	Taxon name	AKA	ARG	MAL	MIL	MPH	PEL	POM	PSA	WOO	ratio.cat	ratio.str	stat	p.value
Gastropoda	<i>Ancylus fluviatilis</i>	1/-	0/-	5/-	2/-	1/-	0/-	0/-	0/-	1/-	-	-	0.34	0.01
Gastropoda	<i>Bithynia tentaculata</i>	1/-	0/-	5/-	1/-	2/-	0/-	1/-	0/-	0/-	-	-	0.64	0.01
Bivalvia	<i>Pisidium casertanum</i>	2/-	0/-	0/-	0/-	0/-	0/-	2/-	6/-	0/-	-	-	0.35	0.01
Bivalvia	<i>Pisidium nitidum</i>	0/-	0/-	0/-	0/-	0/-	0/-	9/-	1/-	0/-	-	-	0.40	0.01
Bivalvia	<i>Pisidium</i> sp.	0/-	1/-	2/-	1/-	1/-	3/-	1/-	1/-	0/-	-	-	0.62	0.01
Bivalvia	<i>Pisidium subtruncatum</i>	0/-	0/-	0/-	0/-	0/-	0/-	8/-	2/-	0/-	-	-	0.45	0.01
Bivalvia	<i>Sphaerium corneum</i>	1/-	1/-	3/-	1/-	1/-	0/-	1/-	1/-	1/-	-	-	0.59	0.01
Hirudinea	<i>Erpobdella vilnensis</i>	0/-	1/-	3/-	0/-	4/-	0/-	2/-	0/-	0/-	-	-	0.27	0.03
Crustacea	<i>Asellus aquaticus</i>	0/-	0/-	5/-	1/-	2/-	1/-	1/-	0/-	0/-	-	-	0.62	0.01
Ephemeroptera	<i>Ephemera danica</i>	0/2	0/1	0/0	6/1	0/1	2/1	0/0	0/4	2/0	0.44	0.54	0.37	0.01
Ephemeroptera	<i>Serratella ignita</i>	1/1	0/0	0/1	3/2	4/3	0/1	1/0	0/1	1/0	0.44	0.67	0.27	0.04
Plecoptera	<i>Nemurella pictetii</i>	0/1	0/0	0/0	0/0	10/4	0/1	0/3	0/0	0/1	0.55	0.69	0.44	0.01
Heteroptera	<i>Aphelocheirus aestivalis</i>	2/-	0/-	0/-	6/-	0/-	1/-	0/-	1/-	0/-	-	-	0.31	0.01
Megaloptera	<i>Sialis lutaria</i>	0/-	0/-	0/-	0/-	1/-	0/-	9/-	0/-	0/-	-	-	0.49	0.01
Coleoptera	<i>Elmis</i> sp. Lv.	1/-	0/-	0/-	2/-	1/-	0/-	1/-	0/-	5/-	-	-	0.46	0.01
Coleoptera	<i>Limnius</i> sp. Lv.	1/-	0/-	2/-	1/-	0/-	0/-	0/-	1/-	5/-	-	-	0.30	0.03
Coleoptera	<i>Orectochilus villosus</i> Lv.	0/-	0/-	0/-	2/-	2/-	0/-	1/-	0/-	5/-	-	-	0.33	0.01
Coleoptera	<i>Oulimnius</i> sp. Lv.	0/-	0/-	0/-	3/-	1/-	0/-	0/-	1/-	5/-	-	-	0.48	0.01
Coleoptera	<i>Oulimnius tuberculatus</i> Ad.	1/-	0/-	0/-	1/-	0/-	0/-	0/-	0/-	8/-	-	-	0.46	0.01
Trichoptera	<i>Cynurus trimaculatus</i>	0/0	0/0	6/2	1/2	1/6	0/0	0/0	0/0	2/0	0.88	0.75	0.53	0.01
Trichoptera	<i>Limnephilus lunatus</i>	0/0	0/0	0/0	0/0	9/6	1/1	0/2	0/1	0/0	0.77	0.84	0.49	0.01
Trichoptera	<i>Silo nigricornis</i>	9/0	0/0	0/5	1/5	0/0	0/0	0/0	0/0	0/0	0.77	0.73	0.48	0.01
Diptera	<i>Antocha</i> sp.	0/-	0/-	0/-	2/-	0/-	0/-	0/-	1/-	7/-	-	-	0.37	0.01
Diptera	<i>Dicranota</i> sp.	5/-	0/-	0/-	1/-	0/-	0/-	0/-	4/-	0/-	-	-	0.47	0.01
Diptera	<i>Tabanidae</i> Gen. sp.	0/-	0/-	0/-	0/-	1/-	4/-	1/-	3/-	1/-	-	-	0.29	0.02

Table 3b: Summary of the 'Multi-level pattern' analysis and calculated indices ('ratio.cat', 'ratio.str') for taxa in lowland streams (No. of taxa = 53); only significantly tested taxa are listed; significant tested substratum combinations are highlighted; stat = test statistic 'IndVal.g'; for abbreviated substratum types see Table 2. **Preference group II (Taxa significantly associated to 3 or 4 substratum types)**

Taxa group	Taxon name	AKA	ARG	MAL	MIL	MPH	PEL	POM	PSA	WOO	ratio.cat	ratio.str	stat	p.value
Gastropoda	<i>Physa fontinalis</i>	0/-	1/-	2/-	0/-	4/-	0/-	2/-	0/-	1/-	-	-	0.34	0.01
Oligochaeta	<i>Oligochaeta</i> Gen. sp.	1/-	1/-	2/-	1/-	1/-	3/-	1/-	0/-	0/-	-	-	0.74	0.01
Hirudinea	<i>Erpobdella octoculata</i>	0/-	0/-	3/-	1/-	3/-	1/-	1/-	0/-	1/-	-	-	0.41	0.01
Crustacea	<i>Echinogammarus berilloni</i>	3/-	4/-	1/-	1/-	1/-	0/-	0/-	0/-	0/-	-	-	0.32	0.01
Crustacea	<i>Proasellus coxalis</i>	1/-	0/-	3/-	0/-	2/-	1/-	1/-	0/-	2/-	-	-	0.52	0.01
Ephemeroptera	<i>Baetis fuscatus/scambus</i>	2/-	2/-	1/-	3/-	1/-	0/-	0/-	0/-	1/-	-	-	0.56	0.01
Ephemeroptera	<i>Caenis horaria</i>	0/0	0/1	0/1	0/1	3/1	3/3	1/2	1/1	2/0	0.55	0.67	0.27	0.03
Ephemeroptera	<i>Heptagenia sulphurea</i>	2/1	1/0	3/3	2/5	1/1	0/0	0/0	1/0	0/0	0.77	0.80	0.48	0.01
Odonata	<i>Calopteryx splendens</i>	0/-	1/-	3/-	0/-	2/-	1/-	1/-	0/-	2/-	-	-	0.49	0.01
Odonata	<i>Coenagrionidae</i> Gen. sp.	0/-	0/-	0/-	1/-	3/-	2/-	1/-	0/-	2/-	-	-	0.36	0.01
Heteroptera	<i>Corixidae</i> Gen. sp.	0/-	1/-	1/-	1/-	1/-	3/-	1/-	0/-	2/-	-	-	0.37	0.01
Coleoptera	<i>Elmis aenea/maugeti</i> Ad.	1/-	0/-	0/-	2/-	2/-	0/-	1/-	0/-	4/-	-	-	0.39	0.01
Trichoptera	<i>Goera pilosa</i>	3/0	1/0	0/5	5/5	0/0	0/0	0/0	1/0	0/0	0.55	0.71	0.44	0.01
Trichoptera	<i>Hydropsyche angustipennis</i>	1/0	2/0	1/3	3/3	1/2	0/0	1/0	0/0	1/2	0.66	0.69	0.43	0.01
Trichoptera	<i>Psychomyia pusilla</i>	2/0	3/0	1/5	3/5	0/0	1/0	0/0	0/0	0/0	0.66	0.68	0.52	0.01
Diptera	<i>Orthoclaeniinae</i> Gen. sp.	2/-	0/-	0/-	1/-	2/-	0/-	4/-	1/-	0/-	-	-	0.53	0.01
Diptera	<i>Simulium</i> sp.	2/-	0/-	1/-	1/-	4/-	0/-	1/-	0/-	1/-	-	-	0.55	0.01

Table 3c: Summary of the 'Multi-level pattern' analysis and calculated indices ('ratio.cat', 'ratio.str') for taxa in lowland streams (No. of taxa = 53); only significantly tested taxa are listed; significant tested substratum combinations are highlighted; stat = test statistic 'IndVal.g'; for abbreviated substratum types see Table 2. **Preference group III (Taxa significantly associated to 5 and more substratum types)**

Taxa group	Taxon name	AKA	ARG	MAL	MIL	MPH	PEL	POM	PSA	WOO	ratio.cat	ratio.str	stat	p.value
Crustacea	<i>Gammarus fossarum</i>	1/-	2/-	3/-	1/-	1/-	1/-	1/-	0/-	0/-	-	-	0.58	0.01
Crustacea	<i>Gammarus pulex</i>	2/-	0/-	2/-	0/-	3/-	0/-	1/-	1/-	1/-	-	-	0.53	0.01
Crustacea	<i>Gammarus roeselii</i>	1/-	1/-	2/-	1/-	1/-	1/-	1/-	1/-	1/-	-	-	0.69	0.01
Hirudinea	<i>Helobdella stagnalis</i>	1/-	0/-	0/-	1/-	3/-	2/-	2/-	0/-	1/-	-	-	0.40	0.01
Ephemeroptera	<i>Baetis rhodani</i>	1/1	0/0	0/2	2/2	2/1	0/0	1/1	1/1	3/1	0.88	0.83	0.40	0.01
Ephemeroptera	<i>Baetis vernus</i>	2/1	2/0	1/2	1/3	2/2	0/1	1/0	1/0	0/0	0.55	0.63	0.60	0.01
Ephemeroptera	<i>Caenis luctuosa</i>	0/1	1/1	0/1	2/1	1/2	3/1	1/1	1/2	1/0	0.66	0.67	0.29	0.03
Trichoptera	<i>Hydropsyche contubernalis</i> ssp.	2/0	2/0	0/3	3/3	1/2	0/0	1/0	0/0	1/2	0.55	0.64	0.34	0.01
Diptera	<i>Prodiamesinae</i> Gen. sp.	0/-	0/-	1/-	0/-	1/-	2/-	2/-	2/-	2/-	-	-	0.51	0.01
Diptera	<i>Tanypodinae</i> Gen. sp.	1/-	1/-	1/-	1/-	1/-	1/-	2/-	1/-	1/-	-	-	0.74	0.01
Diptera	<i>Ceratopogonidae</i> Gen. sp.	1/-	2/-	1/-	1/-	1/-	2/-	1/-	1/-	0/-	-	-	0.53	0.01

Table 4a: Summary of the 'Multi-level pattern' analysis and calculated indices ('ratio.cat', 'ratio.str') for taxa in mountain streams (no. of taxa = 135); only significantly tested taxa are listed; taxa are listed according to preference groups and significant tested substratum combinations are highlighted; stat = test statistic 'IndVal.g'; for abbreviated substratum types see Table 2. **Preference group I (Taxa significantly associated to 1 or 2 substratum types)**

Taxa group	Taxon name	AKA	ARG	MAL	MIL	MPH	PEL	POM	PSA	WOO	ratio.cat	ratio.str	stat	p.value
Oligochaeta	<i>Aulodrilus japonicus</i>	1/-	-/-	0/-	1/-	1/-	7/-	0/-	0/-	0/-	-	-	0.68	0.01
Oligochaeta	<i>Limnodrilus hoffmeisteri</i>	0/-	-/-	0/-	0/-	1/-	9/-	0/-	0/-	0/-	-	-	0.71	0.01
Oligochaeta	<i>Lumbriculus variegatus</i>	0/-	-/-	0/-	0/-	7/-	1/-	2/-	0/-	0/-	-	-	0.60	0.01
Oligochaeta	<i>Nais variabilis</i>	0/-	-/-	0/-	0/-	7/-	0/-	3/-	0/-	0/-	-	-	0.42	0.03
Oligochaeta	<i>Styodrilus brachystylus</i>	2/-	-/-	1/-	1/-	1/-	0/-	4/-	1/-	0/-	-	-	0.48	0.01
Oligochaeta	<i>Tubifex ignotus</i>	0/-	-/-	0/-	0/-	0/-	7/-	1/-	0/-	2/-	-	-	0.63	0.01
Hirudinea	<i>Helobdella stagnalis</i>	1/-	1/-	0/-	0/-	3/-	1/-	3/-	1/-	0/-	-	-	0.45	0.02
Crustacea	<i>Proasellus coxalis</i>	1/-	2/-	0/-	0/-	1/-	1/-	3/-	1/-	1/-	-	-	0.31	0.04
Ephemeroptera	<i>Baetis alpinus</i>	1/1	0/0	5/5	3/3	0/0	0/1	0/0	0/0	1/0	0.77	0.89	0.43	0.02
Ephemeroptera	<i>Cleon diptera</i>	0/0	0/1	0/0	0/0	1/0	9/6	0/1	0/1	0/0	0.55	0.74	0.56	0.01
Ephemeroptera	<i>Rhithrogena semicolorata-Gr.</i>	1/-	0/-	3/-	5/-	1/-	0/-	0/-	0/-	0/-	-	-	0.47	0.01
Plecoptera	<i>Dinocras cephalotes</i>	0/0	0/0	2/2	1/6	1/0	1/2	0/0	1/0	4/0	0.66	0.68	0.41	0.01
Plecoptera	<i>Perla abdominalis</i>	0/-	0/-	0/-	6/-	0/-	0/-	3/-	0/-	1/-	-	-	0.30	0.03
Plecoptera	<i>Protonemura sp.</i>	0/-	0/-	4/-	2/-	1/-	0/-	1/-	0/-	2/-	-	-	0.47	0.01
Coleoptera	<i>Helophorus sp. Ad.</i>	1/-	3/-	0/-	0/-	0/-	1/-	3/-	1/-	1/-	-	-	0.30	0.03
Coleoptera	<i>Ilybius jaechi Lv.</i>	0/-	0/-	5/-	3/-	1/-	0/-	0/-	0/-	1/-	-	-	0.34	0.03
Coleoptera	<i>Ochthebius sp.</i>	1/-	0/-	6/-	1/-	0/-	1/-	0/-	0/-	1/-	-	-	0.38	0.03
Trichoptera	<i>Anomalopterygella chauviniana</i>	5/0	0/0	0/5	4/5	0/0	0/0	1/0	0/0	0/0	0.66	0.74	0.43	0.01
Trichoptera	<i>Chaetopteryx villosa villosa</i>	1/2	2/0	0/2	0/2	0/0	1/0	5/4	1/0	0/0	0.44	0.61	0.42	0.01
Trichoptera	<i>Lepidostoma hirtum</i>	0/0	0/0	1/2	0/1	1/0	1/0	5/2	0/0	2/5	0.66	0.69	0.59	0.01
Trichoptera	<i>Micrasema minimum</i>	0/0	0/0	7/4	3/2	0/0	0/4	0/0	0/0	0/0	0.88	0.84	0.41	0.03
Trichoptera	<i>Silo pallipes</i>	1/0	0/0	4/5	4/5	0/0	0/0	0/0	1/0	0/0	0.77	0.85	0.34	0.02
Trichoptera	<i>Silo piceus</i>	1/0	0/0	1/5	6/5	1/0	0/0	1/0	0/0	0/0	0.66	0.74	0.33	0.04
Diptera	<i>Aedes sp.</i>	0/-	-/-	0/-	0/-	10/-	0/-	0/-	0/-	0/-	-	-	0.61	0.01
Diptera	<i>Apsectrotanytus trifascipennis</i>	0/-	-/-	0/-	0/-	1/-	5/-	3/-	0/-	1/-	-	-	0.75	0.01
Diptera	<i>Bazarella sp.</i>	0/-	-/-	7/-	1/-	0/-	0/-	2/-	0/-	0/-	-	-	0.46	0.03
Diptera	<i>Brillia bifida</i>	0/-	-/-	0/-	1/-	0/-	1/-	6/-	0/-	2/-	-	-	0.59	0.01
Diptera	<i>Chelifera sp.</i>	0/-	3/-	5/-	1/-	0/-	0/-	0/-	0/-	1/-	-	-	0.41	0.01
Diptera	<i>Chironomus sp.</i>	0/-	-/-	0/-	0/-	9/-	0/-	0/-	0/-	1/-	-	-	0.52	0.01
Diptera	<i>Cricotopus similis</i>	0/-	-/-	6/-	1/-	0/-	0/-	0/-	0/-	3/-	-	-	0.43	0.05
Diptera	<i>Cricotopus tremulus</i>	0/-	-/-	4/-	6/-	0/-	0/-	0/-	0/-	0/-	-	-	0.47	0.03
Diptera	<i>Diamesinae Gen. sp.</i>	1/-	0/-	5/-	1/-	1/-	0/-	0/-	0/-	2/-	-	-	0.46	0.01
Diptera	<i>Dixidae Gen. sp.</i>	0/-	-/-	0/-	0/-	8/-	0/-	0/-	0/-	2/-	-	-	0.50	0.01
Diptera	<i>Eukiefferiella clypeata</i>	0/-	-/-	5/-	4/-	0/-	0/-	1/-	0/-	0/-	-	-	0.64	0.01

Continued on next page

Table 4a: Summary of the 'Multi-level pattern' analysis and calculated indices ('ratio.cat', 'ratio.str') for taxa in mountain streams (no. of taxa = 135); only significantly tested taxa are listed; taxa are listed according to preference groups and significant tested substratum combinations are highlighted; stat = test statistic 'IndVal.g'; for abbreviated substratum types see Table 2. **Preference group I (Taxa significantly associated to 1 or 2 substratum types)** (Continued)

Taxa group	Taxon name	AKA	ARG	MAL	MIL	MPH	PEL	POM	PSA	WOO	ratio.cat	ratio.str	stat	p.value
Diptera	<i>Eukiefferiella devonica/ilkeyensis</i>	0/-	-/-	5/-	3/-	0/-	1/-	0/-	0/-	1/-	-	-	0.57	0.01
Diptera	<i>Eukiefferiella similis</i>	1/-	-/-	6/-	3/-	0/-	0/-	0/-	0/-	0/-	-	-	0.71	0.01
Diptera	<i>Heterotrissocladius marcidus</i>	1/-	-/-	0/-	0/-	1/-	5/-	2/-	0/-	1/-	-	-	0.59	0.01
Diptera	<i>Limnophyes</i> sp.	0/-	-/-	0/-	0/-	7/-	1/-	1/-	0/-	1/-	-	-	0.58	0.01
Diptera	<i>Macropelopia</i> sp.	0/-	-/-	0/-	0/-	1/-	4/-	4/-	0/-	1/-	-	-	0.61	0.01
Diptera	<i>Odontomesa fulva</i>	2/-	-/-	0/-	0/-	0/-	8/-	0/-	0/-	0/-	-	-	0.57	0.01
Diptera	<i>Parametricnemus stylatus</i>	1/-	-/-	1/-	1/-	0/-	0/-	4/-	0/-	3/-	-	-	0.45	0.04
Diptera	<i>Paratrissocladius excerptus</i>	0/-	-/-	0/-	0/-	1/-	7/-	2/-	0/-	0/-	-	-	0.62	0.01
Diptera	<i>Polypedilum aegyptium</i>	1/-	-/-	0/-	0/-	0/-	2/-	2/-	5/-	0/-	-	-	0.55	0.01
Diptera	<i>Polypedilum albicorne</i>	1/-	-/-	0/-	1/-	0/-	2/-	5/-	0/-	1/-	-	-	0.48	0.02
Diptera	<i>Polypedilum laetum</i>	1/-	-/-	0/-	0/-	0/-	4/-	5/-	0/-	1/-	-	-	0.60	0.01
Diptera	<i>Potthastia longimana-Gr.</i>	0/-	-/-	5/-	1/-	0/-	0/-	1/-	0/-	3/-	-	-	0.61	0.01
Diptera	<i>Procladius</i> sp.	1/-	-/-	0/-	0/-	1/-	4/-	4/-	0/-	0/-	-	-	0.69	0.01
Diptera	<i>Prodiamesa olivacea</i>	1/-	-/-	0/-	0/-	0/-	5/-	3/-	0/-	1/-	-	-	0.79	0.01
Diptera	<i>Rheosmittia spinicornis</i>	3/-	-/-	0/-	0/-	0/-	1/-	1/-	5/-	0/-	-	-	0.68	0.01
Diptera	<i>Wiedemannia</i> sp.	0/-	0/-	6/-	1/-	0/-	0/-	1/-	0/-	2/-	-	-	0.39	0.01
Diptera	<i>Zavelimyya</i> sp.	0/-	-/-	0/-	0/-	6/-	4/-	0/-	0/-	0/-	-	-	0.44	0.02

Table 4b. Summary of the 'Multi-level pattern' analysis and calculated indices ('ratio.cat', 'ratio.str') for taxa in mountain streams (no. of taxa = 135); only significantly tested taxa are listed; taxa are listed according to preference groups and significant tested substratum combinations are highlighted; stat = test statistic 'IndVal.g'; for abbreviated substratum types see Table 2. **Preference group II (Taxa significantly associated to 3 or 4 substratum types)**

Taxa group	Taxon name	AKA	ARG	MAL	MIL	MPH	PEL	POM	PSA	WOO	ratio.cat	ratio.str	stat	p.value
Gastropoda	<i>Potamopyrgus antipodarum</i>	1/-	2/-	0/-	1/-	2/-	0/-	3/-	1/-	0/-	-	-	0.33	0.03
Gastropoda	<i>Radix balthica</i>	1/-	2/-	0/-	0/-	1/-	2/-	2/-	1/-	1/-	-	-	0.48	0.01
Bivalvia	<i>Pisidium</i> sp.	1/-	2/-	0/-	1/-	2/-	0/-	2/-	2/-	0/-	-	-	0.59	0.01
Oligochaeta	<i>Eiseniella tetraedra</i>	0/-	-/-	0/-	0/-	3/-	3/-	2/-	0/-	2/-	-	-	0.41	0.04
Oligochaeta	<i>Nais stoli</i>	0/-	-/-	5/-	1/-	0/-	0/-	2/-	0/-	2/-	-	-	0.49	0.05
Ephemeroptera	<i>Baetis melanonyx</i>	1/0	0/0	5/5	3/4	0/0	0/1	0/0	0/0	1/0	0.66	0.81	0.47	0.01
Ephemeroptera	<i>Caenis beskidensis</i>	0/2	0/0	0/0	0/1	5/1	2/3	1/2	0/1	2/0	0.55	0.60	0.38	0.02
Ephemeroptera	<i>Caenis luctuosa</i>	1/1	1/1	0/1	1/1	2/1	1/2	2/1	2/2	0/0	0.88	0.83	0.48	0.01
Ephemeroptera	<i>Epeorus assimilis</i>	1/0	0/0	3/5	3/5	0/0	0/0	0/0	0/0	3/0	0.77	0.79	0.45	0.01
Ephemeroptera	<i>Habrophlebia lauta</i>	0/1	0/0	1/0	1/2	1/2	2/1	3/3	0/1	2/0	0.55	0.65	0.42	0.04
Ephemeroptera	<i>Rhithrogena savoienensis</i>	1/0	0/0	2/0	5/10	0/0	0/0	0/0	2/0	0/0	0.66	0.75	0.37	0.02
Ephemeroptera	<i>Rhithrogena</i> sp.	2/-	0/-	3/-	4/-	0/-	0/-	0/-	1/-	0/-	-	-	0.57	0.01
Plecoptera	<i>Brachyptera</i> sp.	1/-	0/-	3/-	3/-	0/-	1/-	1/-	0/-	1/-	-	-	0.36	0.03
Plecoptera	<i>Capnopsis schilleri schilleri</i>	1/0	0/0	0/0	0/0	3/0	1/3	3/3	0/3	2/1	0.66	0.69	0.32	0.02
Plecoptera	<i>Leuctra geniculata</i>	1/1	2/0	0/4	4/4	0/0	0/0	2/0	1/1	0/0	0.66	0.76	0.53	0.01
Plecoptera	<i>Taeniopteryx auberti</i>	1/0	0/0	4/1	2/1	1/0	0/6	1/1	0/0	1/1	0.66	0.69	0.44	0.02
Megaloptera	<i>Sialis</i> sp.	1/-	2/-	0/-	0/-	3/-	1/-	2/-	1/-	0/-	-	-	0.57	0.01
Coleoptera	<i>Elmis rioloides</i> Ad.	0/-	0/-	4/-	2/-	1/-	1/-	0/-	0/-	2/-	-	-	0.59	0.01
Coleoptera	<i>Esolus parralelepedus</i> Ad.	3/-	2/-	0/-	0/-	0/-	0/-	0/-	1/-	0/-	-	-	0.45	0.01
Coleoptera	<i>Hydraena dentipes</i> Ad.	1/-	1/-	4/-	3/-	0/-	0/-	0/-	0/-	1/-	-	-	0.45	0.01
Coleoptera	<i>Hydrophilinae</i> Gen. sp. Lv.	0/-	1/-	0/-	1/-	1/-	3/-	3/-	0/-	1/-	-	-	0.39	0.01
Coleoptera	<i>Limnius volckmari</i> Ad.	1/-	3/-	0/-	4/-	0/-	0/-	2/-	0/-	0/-	-	-	0.31	0.04
Coleoptera	<i>Platambus maculatus</i> Lv.	0/-	0/-	0/-	0/-	4/-	2/-	3/-	0/-	1/-	-	-	0.33	0.03
Trichoptera	<i>Agapetus ochripes</i>	2/0	0/0	3/5	3/5	0/0	0/0	2/0	0/0	0/0	0.77	0.78	0.38	0.02
Trichoptera	<i>Anabolia nervosa</i>	0/0	0/0	0/0	1/0	2/0	2/6	4/2	0/0	1/2	0.77	0.73	0.29	0.03
Trichoptera	<i>Athripsodes cinereus</i>	0/4	2/0	0/0	1/3	1/0	1/0	3/0	2/3	0/0	0.44	0.56	0.39	0.01
Trichoptera	<i>Cheumatopsyche lepida</i>	0/-	2/-	0/-	5/-	0/-	1/-	1/-	0/-	1/-	-	-	0.38	0.02
Trichoptera	<i>Eclisopteryx dalecarlica</i>	4/0	0/0	2/7	4/3	0/0	0/0	0/0	0/0	0/0	0.88	0.82	0.31	0.03
Trichoptera	<i>Glossosoma</i> sp.	2/0	0/0	3/5	4/5	0/0	0/0	0/0	0/0	1/0	0.77	0.81	0.36	0.04
Trichoptera	<i>Halesus</i> sp.	1/0	0/0	0/-	0/-	1/-	2/-	4/-	0/-	2/-	-	-	0.48	0.01
Trichoptera	<i>Mystacides longicornis/nigra</i>	0/0	4/0	0/0	0/0	2/2	1/4	2/0	1/1	0/3	0.66	0.69	0.30	0.04
Trichoptera	<i>Psychomyia pusilla</i>	1/0	0/0	4/5	3/5	0/0	0/0	0/0	1/0	1/0	0.66	0.78	0.43	0.01
Diptera	<i>Antocha</i> sp.	1/-	3/-	3/-	1/-	0/-	0/-	0/-	0/-	2/-	-	-	0.42	0.01
Diptera	<i>Atherix ibis</i>	0/-	-/-	3/-	3/-	0/-	0/-	1/-	0/-	3/-	-	-	0.70	0.01

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Table 4b. Summary of the 'Multi-level pattern' analysis and calculated indices ('ratio.cat', 'ratio.str') for taxa in mountain streams (no. of taxa = 135); only significantly tested taxa are listed; taxa are listed according to preference groups and significant tested substratum combinations are highlighted; stat = test statistic 'IndVal.g'; for abbreviated substratum types see Table 2. **Preference group II (Taxa significantly associated to 3 or 4 substratum types) (Continued)**

Taxa group	Taxon name	AKA	ARG	MAL	MIL	MPH	PEL	POM	PSA	WOO	ratio.cat	ratio.str	stat	p.value
Diptera	<i>Brillia flavifrons</i>	0/-	-/-	0/-	0/-	2/-	2/-	3/-	0/-	3/-	-	-	0.49	0.01
Diptera	<i>Corynoneura</i> sp.	0/-	-/-	0/-	0/-	4/-	2/-	3/-	0/-	1/-	-	-	0.60	0.01
Diptera	<i>Eloeophila</i> sp.	1/-	-/-	1/-	0/-	0/-	4/-	3/-	1/-	0/-	-	-	0.48	0.03
Diptera	<i>Hemerodromia</i> sp.	0/-	0/-	5/-	1/-	0/-	0/-	1/-	0/-	3/-	-	-	0.40	0.02
Diptera	<i>Microspectra atrofasciata</i> -Agg.	1/-	-/-	2/-	1/-	1/-	1/-	1/-	0/-	3/-	-	-	0.53	0.03
Diptera	<i>Microtendipes chloris</i> -Gr.	1/-	-/-	1/-	0/-	1/-	2/-	1/-	1/-	3/-	-	-	0.47	0.03
Diptera	<i>Natarsia nugax/punctata</i>	1/-	-/-	0/-	0/-	4/-	3/-	2/-	0/-	0/-	-	-	0.50	0.02
Diptera	<i>Prodiamesinae</i> Gen. sp.	1/-	1/-	0/-	0/-	4/-	0/-	2/-	2/-	0/-	-	-	0.68	0.01
Diptera	<i>Rheotanytarsus</i> sp.	0/-	-/-	4/-	1/-	0/-	1/-	1/-	0/-	3/-	-	-	0.70	0.01
Diptera	<i>Simulium reptans</i>	1/-	-/-	3/-	2/-	0/-	0/-	1/-	0/-	3/-	-	-	0.59	0.02
Diptera	<i>Thienemannimyia</i> -Gr.	1/-	-/-	0/-	1/-	1/-	3/-	2/-	0/-	2/-	-	-	0.74	0.01
Diptera	<i>Tipula</i> sp.	2/-	3/-	1/-	0/-	0/-	0/-	2/-	2/-	0/-	-	-	0.36	0.01
Diptera	<i>Tvetenia calvescens</i>	0/-	-/-	4/-	2/-	0/-	1/-	1/-	0/-	2/-	-	-	0.72	0.01
Diptera	<i>Tvetenia verralli</i>	1/-	-/-	4/-	2/-	0/-	0/-	1/-	0/-	2/-	-	-	0.62	0.01

Table 4c: Summary of the 'Multi-level pattern' analysis and calculated indices ('ratio.cat', 'ratio.str') for taxa in mountain streams (no. of taxa = 135); only significantly tested taxa are listed; taxa are listed according to preference groups and significant tested substratum combinations are highlighted; stat = test statistic 'IndVal.g'; for abbreviated substratum types see Table 2. **Preference group III (Taxa significantly associated to 5 and more substratum types)**

Taxa group	Taxon name	AKA	ARG	MAL	MIL	MPH	PEL	POM	PSA	WOO	ratio.cat	ratio.str	stat	p.value
Gastropoda	<i>Ancylus fluviatilis</i>	1/-	1/-	2/-	2/-	1/-	0/-	1/-	1/-	1/-	-	-	0.54	0.02
Oligochaeta	<i>Naididae/Tubificidae</i> Gen. sp.	1/-	1/-	1/-	1/-	2/-	1/-	1/-	1/-	1/-	-	-	0.69	0.05
Oligochaeta	<i>Nais alpina</i>	1/-	-/-	4/-	1/-	0/-	1/-	2/-	0/-	1/-	-	-	0.64	0.02
Oligochaeta	<i>Oligochaeta</i> Gen. sp.	2/-	1/-	1/-	2/-	1/-	1/-	1/-	1/-	0/-	-	-	0.83	0.01
Oligochaeta	<i>Propappus volki</i>	3/-	-/-	1/-	2/-	0/-	1/-	1/-	2/-	0/-	-	-	0.81	0.01
Hirudinea	<i>Erpobdella octoculata</i>	1/-	1/-	0/-	1/-	2/-	1/-	2/-	1/-	1/-	-	-	0.57	0.01
Crustacea	<i>Asellus aquaticus</i>	1/-	1/-	0/-	1/-	1/-	1/-	3/-	1/-	1/-	-	-	0.46	0.02
Crustacea	<i>Gammarus pulex</i>	0/-	1/-	0/-	1/-	1/-	2/-	2/-	2/-	1/-	-	-	0.36	0.03
Ephemeroptera	<i>Baetis fuscatus/scambus</i>	1/-	2/-	1/-	2/-	0/-	1/-	1/-	1/-	1/-	-	-	0.54	0.03
Ephemeroptera	<i>Baetis rhodani</i>	1/1	1/0	2/2	2/2	0/0	1/1	1/1	0/1	2/1	0.77	0.85	0.78	0.01
Ephemeroptera	<i>Centroptilum luteolum</i>	1/1	2/0	1/0	0/0	2/0	1/6	1/1	1/2	1/0	0.55	0.62	0.46	0.01
Ephemeroptera	<i>Ecdyonurus venosus-Gr.</i>	1/-	0/-	1/-	2/-	0/-	1/-	2/-	1/-	2/-	-	-	0.53	0.02
Ephemeroptera	<i>Ephemera danica</i>	1/2	1/1	0/0	1/1	2/1	1/1	2/0	1/4	1/0	0.77	0.73	0.64	0.01
Plecoptera	<i>Chloroperlidae</i> Gen. sp.	2/-	0/-	1/-	2/-	2/-	0/-	2/-	0/-	1/-	-	-	0.45	0.02
Plecoptera	<i>Isoptera</i> sp.	1/-	0/-	3/-	2/-	0/-	1/-	1/-	0/-	2/-	-	-	0.48	0.02
Plecoptera	<i>Leuctra</i> sp.	2/-	1/-	1/-	2/-	1/-	1/-	1/-	0/-	1/-	-	-	0.77	0.01
Coleoptera	<i>Elmisa aenea/mauguetii</i> Ad.	0/-	1/-	1/-	2/-	0/-	2/-	2/-	0/-	2/-	-	-	0.54	0.02
Coleoptera	<i>Elmis</i> sp. Lv.	1/-	1/-	2/-	2/-	0/-	1/-	2/-	0/-	1/-	-	-	0.77	0.01
Coleoptera	<i>Esolus</i> sp. Lv.	2/-	0/-	1/-	3/-	0/-	1/-	1/-	1/-	1/-	-	-	0.65	0.01
Coleoptera	<i>Hydraena gracilis</i> Ad.	1/-	1/-	3/-	2/-	0/-	1/-	1/-	0/-	1/-	-	-	0.57	0.01
Coleoptera	<i>Linnius</i> sp. Lv.	2/-	0/-	1/-	3/-	1/-	0/-	1/-	1/-	1/-	-	-	0.69	0.01
Coleoptera	<i>Oulimnius</i> sp. Lv.	1/-	2/-	0/-	1/-	1/-	1/-	2/-	1/-	1/-	-	-	0.53	0.03
Coleoptera	<i>Oulimnius tuberculatus</i> Ad.	1/-	3/-	0/-	1/-	0/-	2/-	2/-	0/-	1/-	-	-	0.56	0.01
Trichoptera	<i>Hydropsyche sitalai</i>	0/0	1/0	2/3	2/3	1/0	1/2	1/0	0/0	2/2	0.66	0.74	0.51	0.01
Trichoptera	<i>Lepidostoma basale</i>	0/0	0/0	1/1	1/1	1/0	2/0	2/2	0/0	3/6	0.77	0.82	0.47	0.02
Trichoptera	<i>Odontocerum albicorne</i>	2/2	1/0	1/2	1/2	1/0	0/0	3/0	1/2	0/2	0.55	0.62	0.43	0.01
Trichoptera	<i>Polycentropus flavomaculatus</i>	0/0	1/0	1/2	2/2	0/0	3/2	2/2	0/0	1/2	0.88	0.84	0.54	0.01
Trichoptera	<i>Rhyacophila</i> sp.	1/0	1/0	2/5	2/5	0/0	1/0	1/0	0/0	2/0	0.44	0.59	0.72	0.01
Trichoptera	<i>Sericostoma flavicorne/personatum</i>	1/-	0/-	1/-	1/-	2/-	1/-	2/-	1/-	1/-	-	-	0.49	0.04
Diptera	<i>Atherix/lbia</i> sp.	1/-	1/-	2/-	2/-	0/-	1/-	2/-	0/-	1/-	-	-	0.57	0.01
Diptera	<i>Ceratopogonidae</i> Gen. sp.	1/-	2/-	1/-	1/-	1/-	1/-	1/-	2/-	0/-	-	-	0.51	0.01
Diptera	<i>Dicranota</i> sp.	2/-	1/-	1/-	2/-	1/-	1/-	0/-	1/-	1/-	-	-	0.67	0.01
Diptera	<i>Hexatoma</i> sp.	2/-	0/-	1/-	2/-	2/-	0/-	1/-	1/-	1/-	-	-	0.59	0.01
Diptera	<i>Orthocladinae</i> Gen. sp.	1/-	0/-	3/-	1/-	1/-	1/-	1/-	1/-	1/-	-	-	0.70	0.02
Diptera	<i>Simulium</i> sp.	1/-	1/-	2/-	2/-	0/-	2/-	1/-	0/-	1/-	-	-	0.67	0.01
Diptera	<i>Tabanidae</i> Gen. sp.	1/-	2/-	0/-	0/-	3/-	2/-	1/-	1/-	0/-	-	-	0.35	0.01

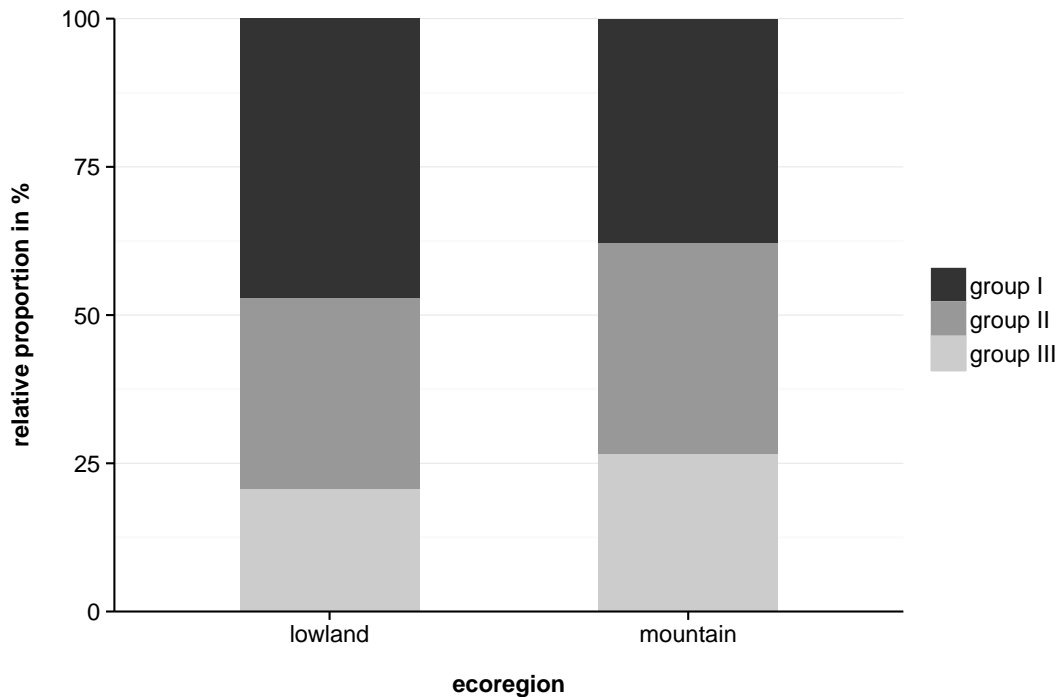


Figure 4: Relative proportion (%) of significant tested species in the ‘Multi-level pattern’ analyses according to preference groups (mountain streams = 135 taxa, lowland streams = 53 taxa).

Taxa identified as specialists or generalists showed no clear association towards a taxonomic group (Figure 5). However, over 50% of all Diptera were assigned to preference group I in mountain streams (Figure 5B) whereas the same taxa group showed no clear preferences in lowland streams (Figure 5A).

The Indicator Values, representing the strength of an association to a specific substratum type (or combination), ranged between 0.27 and 0.74 for taxa in lowland streams and 0.29 and 0.83 for taxa in mountain streams. Mean values for the test statistic (‘IndVal.g’) did not differ significantly between the three preference groups for lowland streams (Kruskal–Wallis test p -value = 0.2516 ($p < 0.05$)) as opposed to mountain streams (Kruskal–Wallis test p -value = 0.0003 ($p < 0.05$)). More specifically, the Tukey HSD test indicated differences for preference group III in comparison to group I and II (p -value = 0.035 for group I and p -value = 0.0001 for group II ($p < 0.05$)).

The number of preferred substrates differed between taxonomic levels (family, genus and species). While taxa analyzed on family level (or higher) showed a mean number of four preferred substrates, taxa on genus and species level preferred an average of three substrates (see Figure 6, Kruskal–Wallis test p -value = 0.0308 ($p < 0.05$)). All test statistics were calculated using STATISTICA 10.

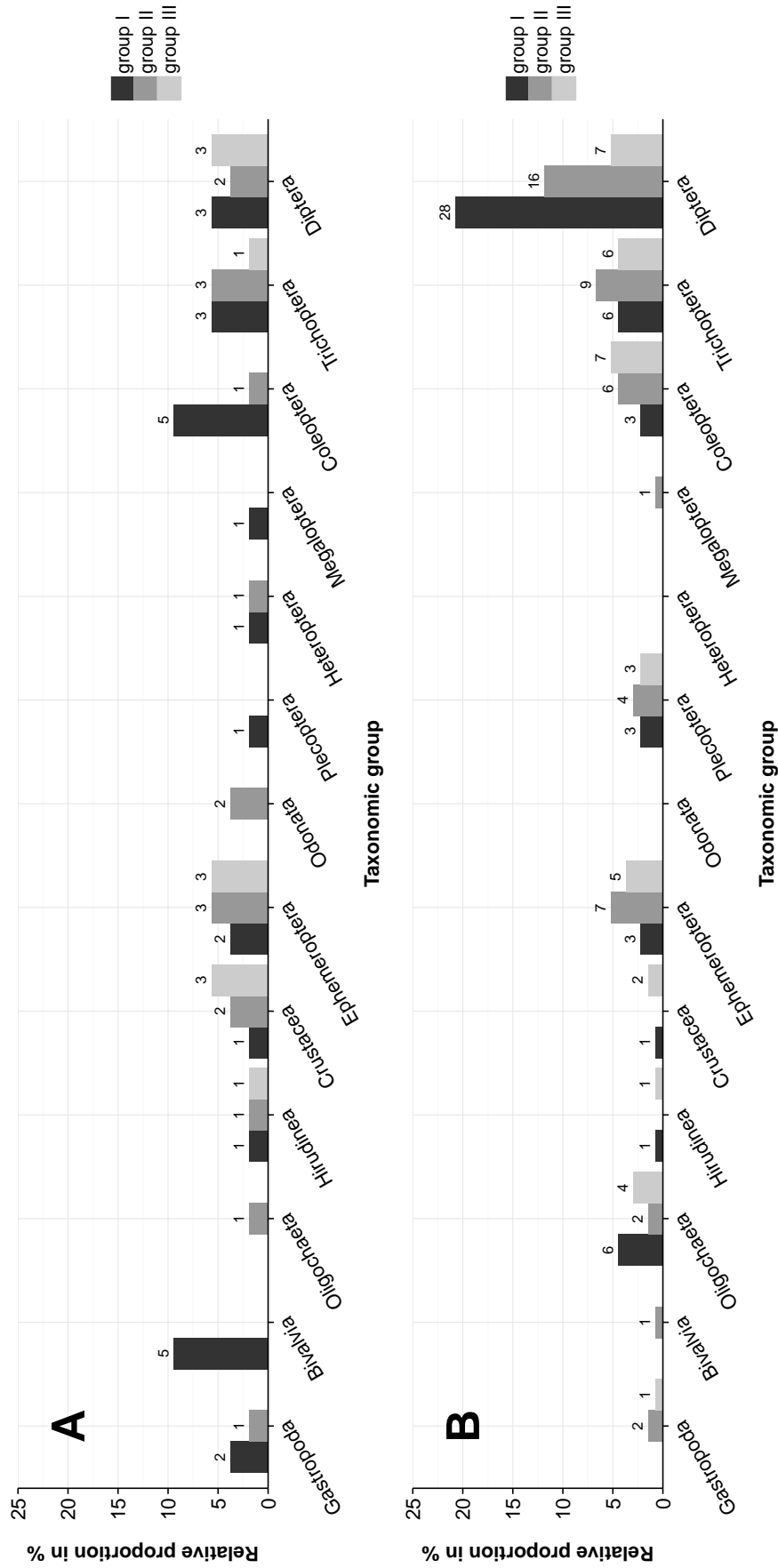


Figure 5: Relative proportion (%) of taxonomic groups in regard to preference groups in lowland (A) and mountain streams (B); the bars represent the relative share of each taxa group in regard to all groups in the analysis; total numbers of taxa are displayed above each bar.

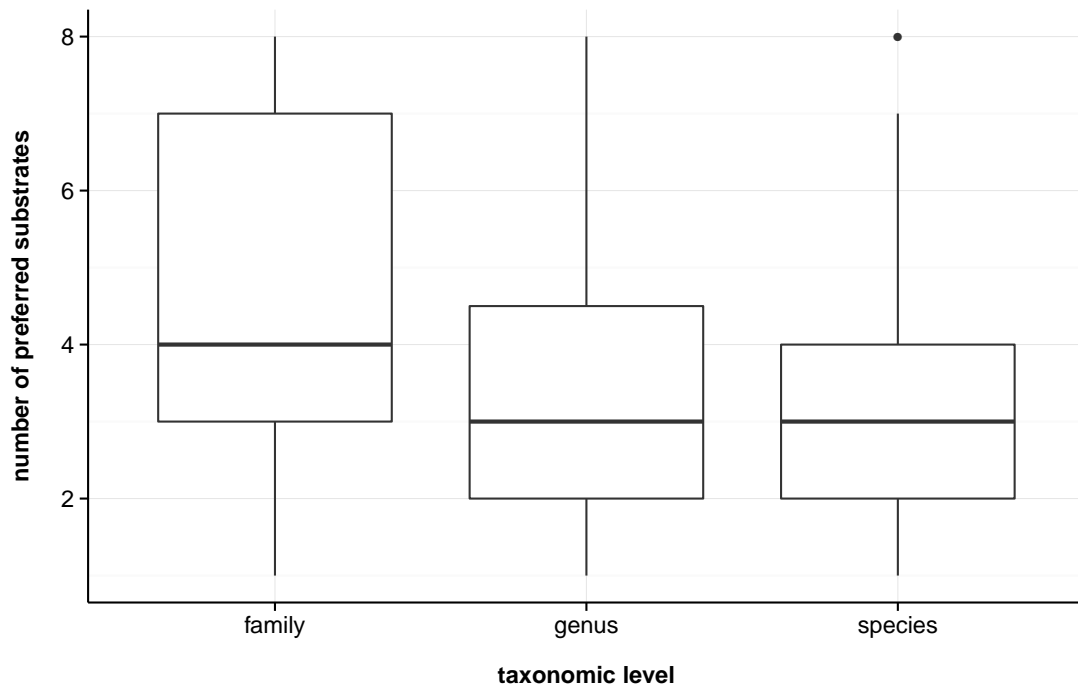


Figure 6: Distribution of the number of preferred substratum types in relation to different taxonomic levels; Kruskal–Wallis test p -value = 0.0308 ($p < 0.05$).

2.3.1.2 Comparison of species' substratum preferences between expert opinion and classifications derived from statistical analysis

In lowland streams, information on substratum preferences from freshwater ecology.info was available for 15 taxa. We considered differences between associations derived from data and expert opinion to be minor, if both ratios ('ratio.cat', 'ratio.str') exceeded a value of 0.7, while values < 0.6 indicated less matching results. For lowland streams, minor differences were observed for five species (*Baetis rhodani*, *Cyrnus trimaculatus*, *Heptagenia sulphurea*, *Limnephilus lunatus*, *Silo nigricornis*) whereas greater differences were detected for seven taxa (*Baetis vernus*, *Caenis horaria*, *Ephemera danica*, *Nemurella pictetii*, *Goera pilosa*, *Hydropsyche contubernalis* ssp., *Serratella ignita*).

In mountain streams, information on substratum preferences was available for 33 out of 135 significantly tested taxa. Minor differences were observed for 13 species (e.g., *Baetis alpinus*, *Caenis luctuosa*, *Micrasema minimum*, *Polycentropus flavomaculatus*, *Silo pallipes*) whereas greater differences were obtained for 7 taxa (e.g., *Caenis beskidensis*, *Athripsodes cinereus*, *Odontocerum albicorne*, *Rhyacophila* sp.).

One could argue that calculated ratios may tend to take higher values, as the

probability to encounter the same substratum type increases with an increasing number of substratum preferences. This, however, was not the case in our study as mean values for both ratios did not differ with preference groups (Kruskal–Wallis test p -value ('ratio.cat') = 0.7803 ($p < 0.05$) and p -value ('ratio.str') = 0.0761 ($p < 0.05$), see Figure 7).

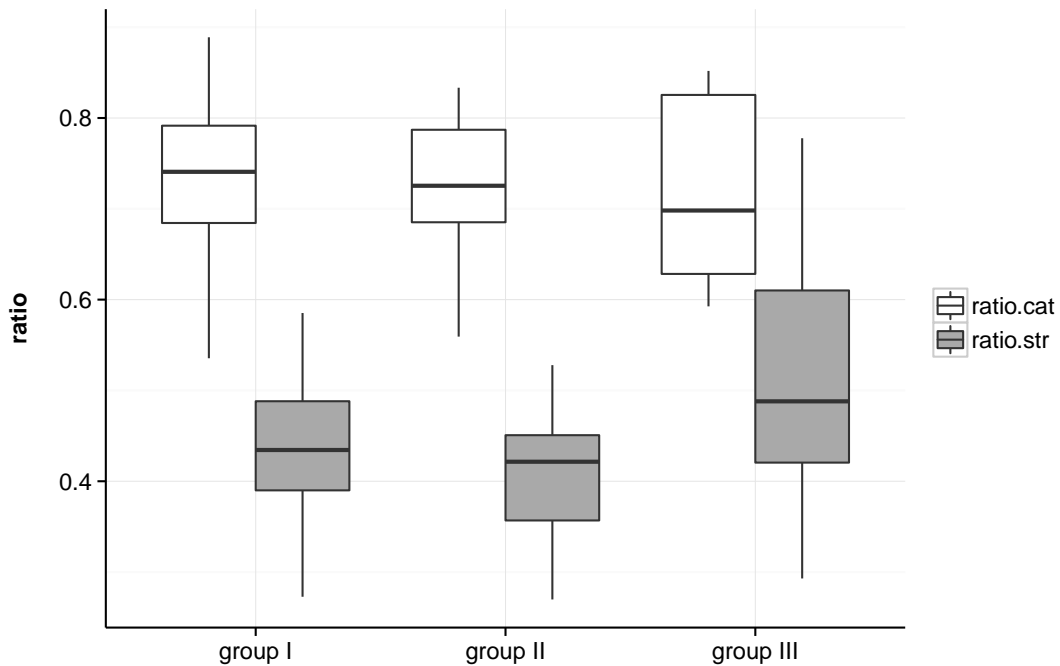


Figure 7: Distribution of values for 'ratio.cat' and 'ratio.str' according to preference groups; Kruskal–Wallis test p -value ('ratio.cat') = 0.7803 ($p < 0.05$) and p -value ('ratio.str') = 0.0761 ($p < 0.05$).

2.3.1.3 Comparison of substratum preferences for taxa in lowland and mountain streams

Overall, 25 species showed significant substratum preferences for both lowland and mountain streams (Table 5). A good agreement was observed for seven species (e.g., *Baetis fuscatus/scambus*, *C. luctuosa*, *Ceratopogonidae* Gen. sp.). Substratum preferences differed considerably between the two stream groups for five species (*Asellus aquaticus*, *Gammarus pulex*, *Erpobdella octoculata*, *E. danica*, *Dicranota* sp.). A qualitative comparison of the allocated substratum preferences though shows, that if not the precise same substratum class was occupied, taxa tend to colonize similar substrates in both stream groups (e.g., *E. octoculata*, *B. rhodani*, *Dicranota* sp.).

Table 5: Comparison of the results of the 'Multi-level pattern' analysis and calculated indices ('ratio.cat', 'ratio.str') for taxa that tested significant in both mountain and lowland streams ($n = 25$); for abbreviated substratum types see Table 2.

Taxa group	Taxon name	Ecoregion	AKA	ARG	MAL	MIL	MPH	PEL	POM	PSA	WOO	ratio.cat	ratio.str
Gastropoda	<i>Ancylus fluviatilis</i>	Low	1	0	5	2	1	0	0	0	1	0.556	0.667
		Mount	1	1	2	2	0	1	1	1	1	1	
Bivalvia	<i>Pisidium</i> sp.	Low	0	1	2	1	1	3	1	1	0	0.66	0.676
		Mount	1	2	0	1	0	2	2	2	0	0	
Oligochaeta	<i>Oligochaeta</i> Gen. sp.	Low	1	1	2	1	1	3	1	1	0	0.888	0.778
		Mount	2	1	1	2	1	1	1	1	0	0	
Hirudinea	<i>Erpobdella octoculata</i>	Low	0	0	3	1	3	1	1	0	1	0.55	0.583
		Mount	1	1	0	1	1	2	2	1	1	1	
Hirudinea	<i>Helobdella stagnalis</i>	Low	1	0	0	1	3	2	2	0	1	0.55	0.667
		Mount	1	1	0	0	1	3	3	1	0	0	
Crustacea	<i>Asellus aquaticus</i>	Low	0	0	5	1	2	1	1	0	0	0.444	0.593
		Mount	1	1	0	1	1	1	3	1	1	1	
Crustacea	<i>Gammarus pulex</i>	Low	2	0	2	0	3	0	1	1	1	0.44	0.583
		Mount	0	1	0	1	2	1	2	2	1	1	
Crustacea	<i>Proasellus coxalis</i>	Low	1	0	3	0	2	1	1	0	2	0.66	0.657
		Mount	1	2	0	0	1	1	3	1	1	1	
Ephemeroptera	<i>Baetis fuscatus/scambus</i>	Low	2	2	1	3	1	0	0	0	1	0.777	0.824
		Mount	1	2	1	2	1	1	1	1	1	1	
Ephemeroptera	<i>Baetis rhodani</i>	Low	1	0	0	2	2	0	1	1	3	0.666	0.75
		Mount	1	1	2	2	1	1	1	1	0	2	
Ephemeroptera	<i>Caenis luctuosa</i>	Low	0	1	0	2	1	3	1	1	1	0.777	0.75
		Mount	1	1	0	1	1	2	2	2	0	0	
Ephemeroptera	<i>Ephemera danica</i>	Low	0	0	0	6	0	2	0	0	2	0.44	0.587
		Mount	1	1	0	1	1	2	2	1	1	1	
Coleoptera	<i>Elmis aenea/maugettii</i> Ad.	Low	1	0	0	2	2	0	1	0	4	0.66	0.752
		Mount	0	1	1	2	2	0	2	0	2	2	
Coleoptera	<i>Elmis</i> sp. Lv.	Low	1	0	0	2	1	0	1	0	5	0.77	0.759
		Mount	1	1	2	2	1	0	2	0	1	1	

Continued on next page

Table 5: Comparison of the results of the 'Multi-level pattern' analysis and calculated indices ('ratio.cat', 'ratio.str') for taxa that tested significant in both mountain and lowland streams ($n = 25$); for abbreviated substratum types see Table 2. (Continued)

Taxa group	Taxon name	Ecoregion	AKA	ARG	MAL	MIL	MPH	PEL	POM	PSA	WOO	ratio.cat	ratio.str
Coleoptera	<i>Limnius</i> sp. Lv.	Low	1	0	2	1	0	0	0	1	5	0.77	0.685
		Mount	2	0	1	3	0	1	1	1	1		
Coleoptera	<i>Oulimnius</i> sp. Lv.	Low	0	0	0	3	1	0	0	1	5	0.55	0.611
		Mount	1	2	0	1	1	1	2	1	1		
Coleoptera	<i>Oulimnius tuberculatus</i> Ad.	Low	1	0	0	1	0	0	0	0	8	0.66	0.682
		Mount	1	3	0	1	2	0	2	0	1		
Trichoptera	<i>Psychoomyia pusilla</i>	Low	2	3	1	3	0	1	0	0	0	0.55	0.646
		Mount	1	0	4	3	0	0	0	1	1		
Diptera	<i>Antocha</i> sp.	Low	0	0	0	2	0	0	0	1	7	0.556	0.616
		Mount	1	3	3	1	0	0	0	0	2		
Diptera	<i>Ceratopogonidae</i> Gen. sp.	Low	1	2	1	1	1	2	1	1	0	1	0.926
		Mount	1	2	1	1	1	1	1	2	0		
Diptera	<i>Dicranota</i> sp.	Low	5	0	0	1	0	0	0	4	0	0.444	0.563
		Mount	2	1	1	2	1	1	0	1	1		
Diptera	<i>Orthocladiinae</i> Gen. sp.	Low	2	0	0	1	2	0	4	1	0	0.66	0.665
		Mount	1	0	3	1	1	1	1	1	1		
Diptera	<i>Prodiamesinae</i> Gen. sp.	Low	0	0	1	0	1	2	2	2	2	0.44	0.659
		Mount	1	1	0	0	0	4	2	2	0		
Diptera	<i>Simulium</i> sp.	Low	2	0	1	1	4	0	1	0	1	0.88	0.789
		Mount	1	1	2	2	2	0	1	0	1		
Diptera	<i>Tabanidae</i> Gen. sp.	Low	0	0	0	0	1	4	1	3	1	0.66	0.7
		Mount	1	2	0	0	2	3	1	1	0		

2.4 Discussion

2.4.1 Substratum preferences for taxa in lowland and mountain streams

Twenty-five taxa in lowland streams and 51 taxa in mountain streams preferred one or two substrates and may be considered as highly specialized. On the other hand, our analyses revealed that the majority of taxa (lowland streams $n = 28$, mountain streams $n = 84$) was associated with a broader range of substrates. This observation is in line with Giller and Malmqvist (1998), who observed widespread substratum preferences and distribution patterns for many species. The association of macroinvertebrates with a broad range of substratum types may best be explained by species' autecological plasticity and the connectivity among habitats (Mérigoux and Dolédec 2004, Kubosova et al. 2010). Although most of the samples we used in our analyses were taken during summer, the overlapping of different life stages may have further facilitated widespread substratum associations due to life cycle-related shifts in substratum preferences.

In general, substratum preferences are important autecological features which in turn are supposed to be closely related to species' particular feeding habits and current preferences (Mérigoux and Dolédec 2004). While some species are dependent on special food sources (e.g., deadwood), other species are able to gather food in a wide range of habitats. This statement is especially true for predacious, mobile aquatic organisms. As nearly all habitats are colonized by potential prey to a certain extent, predators are able to move between habitats to forage. In contrast, grazers and scrapers prefer the surface of larger stones or deadwood (e.g., *Bithynia tentaculata*, *Micrasema longulum*, *Psychomyia pusilla*), where they feed on biofilms (Becker 1994). Collectors and gatherers in lowland streams are most commonly found on fine mineralic substrates and/or substrates with a high content of organic matter (e.g., sand and mineralic or organic mud) (e.g., *C. horaria*, *C. luctuosa*). In mountain streams, patches of macrophytes within the streams and submerged bankside vegetation often cause the sedimentation of fine particles due to reduced flow velocities and may therefore act as equally suitable habitats for gatherers and collectors (e.g., *Eiseniella tetraeda*, *Rheocricotopus fuscipes*). In comparison, passive filter feeders (e.g., *Simulium vernum*-Gr., *Simulium ornatum*-Gr.) preferred stony substrates, macrophytes and deadwood, of all which offer suitable physical characteristics for the species. It can therefore be concluded that species' trophic preferences are often closely related to specific substrates.

Along with substrates, hydraulic conditions are one of the most important in-stream parameters that determine functional macroinvertebrate communities (Beauger et al. 2006, Timm et al. 2011). Regarding species' current preferences, it is well established that substrates commonly found in lentic zones of a stream (e.g., fine/coarse organic material, sand/mud) support a community of burrowers, deposit feeders and shredders (Lamouroux et al. 2004), whereas substrates of lotic stream zones (e.g., stones/rocks and macrophytes) are associated with active and passive filterers. We found that rheophilic and rheobiont species (e.g., *Epeorus assimilis*, *Rhitrogena savoiensis*) predominantly occurred on coarse mineral and organic substrates, which are often exposed to high currents. Many limnophilic species (e.g., *Pisidium casertanum*, *C. beskidensis*, *Anabolia nervosa*) – most of them being prone to high currents – on the other hand, prefer shallow lentic zones where they live between organic deposits or in the sand/mud). These findings support the assumption of a strong interdependence between hydraulic conditions and prevailing substrates with associated species communities. However, as flow velocity itself is a key driver of substratum composition (Wood et al. 1999), it is difficult to disentangle single effects on macroinvertebrate assemblages.

Furthermore, we discovered that over 50 % of all Diptera taxa in mountain streams were assigned to one or two substratum types, whereas no such preference pattern could be observed for Diptera in lowland streams. This might indicate that nutrient loads may act as an additional pressure that indirectly influence and determine substratum preferences for invertebrate species (Vandewalle et al. 2010). In general, mountain streams are known to support a greater variety of taxa which are sensitive to nutrient or organic pollution. Especially upstream reaches are characterized by low nutrient loads and are often characterized by a steep slope and associated coarser sediments. As we found Diptera in mountain streams predominantly associated to medium and large sized mineralic sediments, overarching nutrient pressures might also be indirectly related to species substratum preferences.

Additionally, the association of taxa to a (group of) substratum types seems not to be independent from taxonomic resolution. This stresses the demand for a species-specific investigation of traits, as ecological characteristics might be masked at higher taxonomical units. In summary, beyond the availability of suitable substrata on the river bottom, various other factors like flow conditions and overarching pressures such as nutrient loads influence the occurrence of macroinvertebrates (Feld and Hering 2007) Prevailing substrates may provide suitable conditions for species on

the microhabitat scale, but colonization itself is clearly limited by stressors operating on larger spatial scales.

2.4.2 Comparison with existing classifications of species' substratum preferences

We compared our results with substratum preferences derived from the literature and expert opinion stored in the <http://www.freshwaterecology.info> database. Primarily based on Schmedtje and Colling (1996), this database provided substratum preferences for several of the investigated taxa (mainly focusing on Ephemeroptera, Plecoptera and Trichoptera). Out of the 188 significant taxa in lowland and mountain streams, substratum classifications were available for 48 taxa. We assessed the consistency of substratum preferences between our results and the existing database records by calculating two types of indices ('ratio.cat', 'ratio.str'). It should be noted that the comparison based on the two ratios just provides a numerical assessment of consistency. Additionally, the results need to be analyzed qualitatively, i.e. to check if differences in substratum associations are based on completely different substrate categories (e.g., bedrock instead of macrophytes), or if the colonized substrates resemble each other in terms of their physical characteristics (e.g., macrolithal instead of microlithal).

Differences in the preference of various mineralic fractions were discovered for several lowland species. For instance, [freshwaterecology.info](http://www.freshwaterecology.info) refers to *G. pilosa* as an exclusive species of medium- to large-sized mineral fractions. Our results, however, indicated a preference for gravel and small-sized cobbles in lowland streams. These differences most likely relate to classifications in [freshwaterecology.info](http://www.freshwaterecology.info), which are based on records from mountain streams. Consequently, *G. pilosa* may be a characteristic species of large stones in mountain streams, but it evidently prefers slightly different substrates in the lowlands. Similar statements are valid for *Hydropsyche angustipennis*, *Hydropsyche contubernalis*, *P. pusilla* and *S. nigricornis*, all of which showed a shift towards finer grain sizes compared to the associations given in [freshwaterecology.info](http://www.freshwaterecology.info).

Another frequently observed finding was the colonization of deadwood instead of mineralic components in both lowland and mountains streams (e.g. *C. beskiden-sis*, *C. horaria*, *Habroleptophlebia lauta*, *Rhyacophila* sp.). According to Schmedtje and Colling (1996), most species of the genus *Caenis* are ubiquitous species which equally colonize fine mineral and organic substrates. *C. horaria* has often been

recorded in impounded river sections or residual stretches (Tockner et al. 2009), which are closely related to streams affected by morphological degradation. Associated with the accumulation of fine sediments, the substratum preferences of soft, detritus enriched substrates were well reflected in both our results and database classifications. According to our results, *C. beskidensis* and *C. horaria* both colonized deadwood, which might have acted as surrogate for mineral substrates or attracted the species by high amounts of detritus.

According to our data, *Rhyacophila* sp. showed a similar preference for deadwood, while being primarily associated to mineral substrates in freshwater ecology.info. Although Rhyacophilidae are predacious as opposed to the net-building Hydropsychidae, deadwood may appear as an attractive solid substrate due to life cycle-related substratum preferences. Shortly before pupation starts, Rhyacophilidae spin a cocoon like structure adhered to hard substrates (Waringer and Graf 1997). In conclusion, it is likely, that deadwood might be perceived in a similar way as mineral components. However, it is more likely for species to use deadwood as a surrogate for mineral substrates as it would be the other way around. Species with a clear association to deadwood are often xylophagous and thus restricted to deadwood as main food source (Spänhoff et al. 1999, Hoffmann and Hering 2000)

2.4.3 Comparison of substratum preferences in mountain and lowland streams

To describe substratum preferences more accurately and to account for potential ecoregion-specific differences, we compared substratum-specific colonization patterns between mountain and lowland streams. Most species with significant substratum preferences in both lowland and mountain streams are widely distributed. The comparison of substratum preferences for lowland and mountain streams confirms our assumption that substratum associations in lowland and mountain streams differ. Again, a shift in preferred grain sizes was detected for several species (e.g., *Ancyclus fluviatilis*, *Elmis aenea/mauguetii*, *Limnius* sp. Lv., *P. pusilla*, *Dicranota* sp. *Simulium* sp.). These findings may also explain some of the differences of our results to the database information. To achieve transparency and to account for ecoregion-specific differences, we suggest to specify the data sources from which substratum preferences were derived in autecological databases like freshwater ecology.info.

In general, our observations add to the large body of literature on species substratum preferences and support previously compiled knowledge with statistical evidence. Our results further support the approach to describe substratum preferences

at the species level because substantial variations among species and their ecological characteristics are aggregated at higher taxonomical units and may therefore be masked (Monk et al. 2012). The results of this study contribute to the completion of currently available autecological databases (freshwaterecology.info).

3 Effects of salinity gradients on benthic invertebrate and diatom communities in a German lowland river

3.1 Introduction

Salinity is a principal component of all water bodies and has been regarded as one of the most important factors influencing biological assemblages (W. D. Williams 1987, Piscart et al. 2005b, Kefford et al. 2012a). Salinity tolerance varies profoundly between species. While some species are known to be salt-tolerant, others react sensitively to increasing salinity levels sometimes even ending up in a decline or disappearance of the population (D. D. Williams and N. E. Williams 1998, Piscart et al. 2006a). Accordingly, aquatic biota have been commonly classified by salinity preferences. Beside a general division between freshwater, brackish and marine taxa (Remane and Schlieper 1971), many classification schemes, which evolved over the last decades, more explicitly describe the salinity preferences of macroinvertebrate (e.g. Wolf et al. 2009) and diatom species (e.g. Hustedt 1953, Ziemann 1971, van Dam et al. 1994, Dell'Uomo 2004).

Salinity refers to the total concentration of dissolved inorganic ions in water and is usually measured as the capacity to conduct electrical current (electrical conductivity, EC). The composition and quantity of dissolved ions is highly variable and related to natural sources and anthropogenic pressures within the catchment. Natural sources of salinization refer to climate conditions and the geology within a catchment, as well as its topography, vegetation, and proximity to the sea (Cañedo-Argüelles et al. 2013). As opposed to the gradual natural salinization of rivers, various anthropogenic pressures pose an immediate threat to freshwater communities. Consequently, human-induced salinization has been considered one of the crucial factors to impact freshwater ecosystems (Millennium Ecosystem Assessment 2005). In a recent review, Cañedo-Argüelles et al. (2013) emphasize various sources of secondary salinization, including irrigation measures for agriculture (W. D. Williams 1999, Crosa et al. 2006), mining activities (salt and coal) and the discharge of industrial waste water into the river (Kefford 1998a).

Adverse effects of salinization for aquatic species include the impairment of physiological processes such as the maintenance of their osmotic homeostasis and associated changes in community composition (Waterkeyn et al. 2008). Salinization is a major factor affecting species richness by causing shifts from salinity-sensitive taxa to communities with few tolerant taxa adapted to increased salinity levels (Piscart et al. 2005b). Many freshwater species are osmoregulators; thus, their energy demand increases with salinity to maintain an adequate internal osmotic pressure relative to the surrounding environment. The osmoregulatory mechanisms are likely being affected if salt concentrations in the surrounding medium become too high, requiring an increasing osmoregulatory effort and associated energy demand, and leading to cellular damage and ultimately death of single specimens and entire populations. Beside an increased osmotic stress directly determining the viability of populations, stress induced responses of aquatic organisms include shifts in feeding type composition (Kefford et al. 2012b), the impediment of growth (Roller and Stickle 1985), as well as the impairment of different stages within the insect life cycle such as oviposition, pupation and emergence (Piscart et al. 2006b). Moreover, salinization was found to enhance the establishment of exotic invasive species (Piscart et al. 2005a, Braukmann and Böhme 2011), with brackish water species colonizing freshwater ecosystems.

Recent studies highlight the need to identify threshold values of salt stress, beyond which changes in assemblage composition can be expected (King and Baker 2010, Petty et al. 2010), but respective case studies are rare. This might be due to the lack of rivers showing a distinct salinity gradient within a small geographical scale. Against this background, the lowland river Lippe represents an ideal system to study the effects of salinization on aquatic organisms. During the last century, the Lippe catchment has been significantly influenced by the preceding development of coal mining activities (Brüggemeier 1994). To gain access to the coal seams in deeper ground layers (> 1000 m) it was necessary to continuously pump saline groundwater from the nearby mining shafts to the surface. The drainage of salt-enriched mine water involved subsequent flooding measures of adjacent areas or the direct discharge into the river, which both led to increased NaCl concentrations. Although coal mining activities significantly decreased over the last decades, pumping activities and the salt concentration still remains high and frequently exceeds the threshold concentration for chloride of 200 mg/L (~ 1200 $\mu\text{S}/\text{cm}$) set by German national authorities as a quality target under the Water Framework Directive (Län-

derarbeitsgemeinschaft Wasser 2014).

The main objective of this study was to analyze the effect of salt pollution on the macroinvertebrate and diatom communities of the river Lippe. More specifically, we attempted to derive salinity thresholds for single species and communities in order to determine ecological change points related to increasing salt concentrations more accurately. Furthermore, we aimed at identifying indicator taxa that are influenced by either increasing or decreasing salinity loads and at comparing our results to existing classifications.

3.2 Material and methods

3.2.1 Catchment and data

The Lippe is a large lowland river and a right tributary of the Rhine situated in the Western part of Germany with an overall length of 220 km and a catchment area of approximately 4890 km². Our study focuses on the lower and middle course of the Lippe, where water quality is frequently impaired by coal mining activities causing increased salinity concentrations (Petrucek and Stöffler 2011). Predominant bottom substrates are sand and loam, interspersed with a variable amount of organic material (Pottgiesser and Sommerhäuser 2004).

We compiled macroinvertebrate and diatom samples and corresponding chemical data (electrical conductivity, total phosphorus) from the publicly available database ‘ELWAS-WEB’ (<http://www.elwasweb.nrw.de>, Landesamt für Natur, Umwelt und Verbraucherschutz Land NRW 2015). In case of macroinvertebrates, the data was collected using Multi-Habitat-Sampling (Haase et al. 2004a). A total of 20 sampling units were taken based on the relative proportion of different habitats on the river bottom using a 25 cm × 25 cm frame shovel sampler (500 µm mesh). All samples were pooled and preserved with 96 % Ethanol in the field and subsequently processed in the lab. At least, 350 specimens were identified to species level. Diatoms were collected based on the PHYLIB method (Schaumburg et al. 2004). A total number of 10 stones were removed from the river bottom from zones of intermediate current velocities at low flow conditions. Overall, 400 specimens were determined to species level.

The electrical conductivity measured at times of sampling reflects the NaCl content of the river (linear regression with $R^2 = 0.959$) and was used as a proxy for the overall salinity. Salinity values ranged between 664 µS/cm and 2360 µS/cm. Our

analyses are based on a dataset for macroinvertebrates comprising 16 monitoring stations with 41 samples and a dataset for diatoms covering 19 monitoring stations with 31 samples recorded between 1995 and 2013.

We calculated the saprobic index for all macroinvertebrate samples prior to our analyses to exclude samples from sites strongly affected by organic pollution using the assessment software ASTERICS (ASTERICS 2013, version 4.0.2). The calculations yielded ‘good’ or ‘moderate’ saprobic results, hence no samples were omitted. As high nutrient loads may mask the effect of salinity on the biota, we calculated the Spearman correlation coefficient for total phosphorus and EC using the Software R (R Development Core Team 2013, version 3.1.0). This calculation refers to 31 samples where total phosphorus has been measured in addition to the electrical conductivity.

3.2.2 Composition of communities under different salinities

Conductivity values show a great spatial variability and cover a broad range of salinities (Figure 8). To test if salinity determines community composition we used NMDS on the macroinvertebrate and diatom datasets. The key outcome of a NMDS analysis is a spatial configuration, in which the objects (here: samples) are represented as points. The samples are arranged in a way that their relative distances to each other correspond to the similarities among them: samples characterized by a similar biological community are displayed by points that lie close to each other whereas samples with different communities are located far apart from one another.

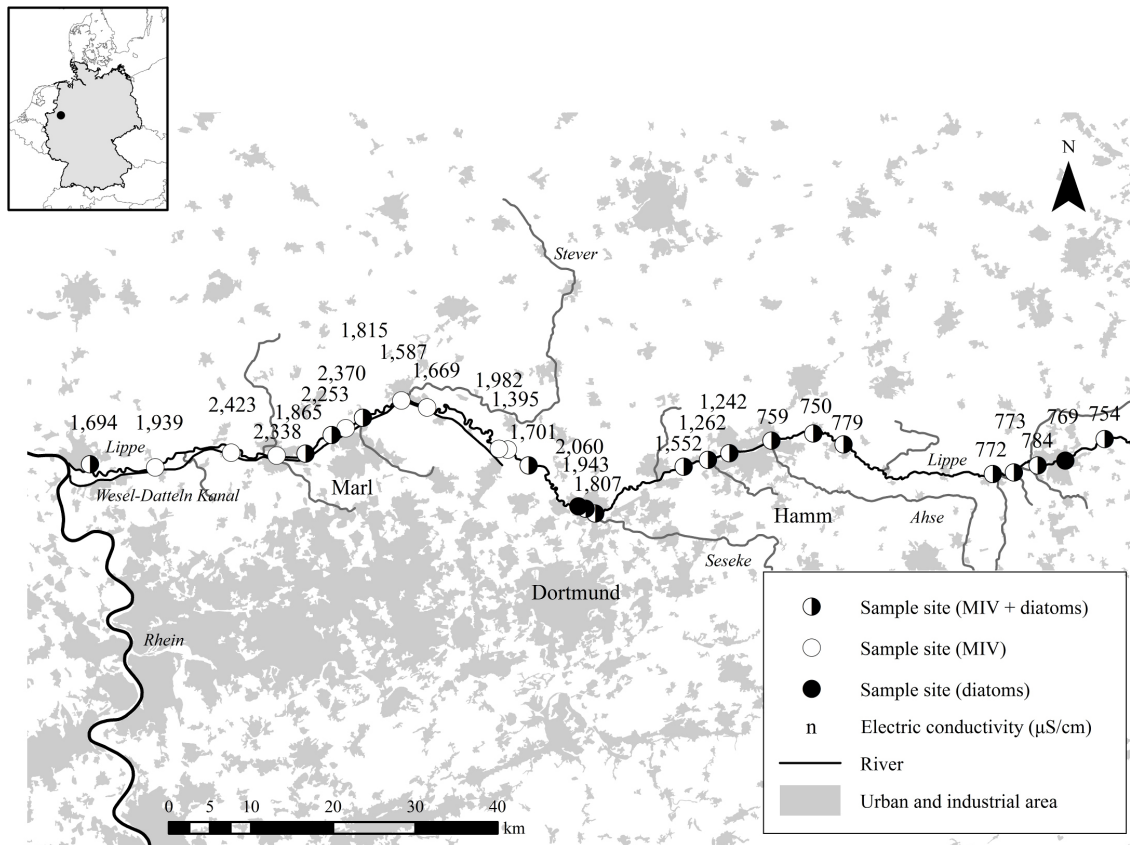


Figure 8: Overview of the monitoring stations along the Lippe. The numbers refer to the average conductivity ($\mu\text{S}/\text{cm}$) measured at the respective station. MIV = macroinvertebrates.

We applied the metaMDS function (available in the *vegan* package within the software R) based on the default settings which included the application of the Bray-Curtis-Index as a distance metric between samples and a previous square-root transformation of the species abundance data. The NMDS was calculated for two dimensions and we used 100 starts from random configurations. The analysis was based on a dataset comprising 249 taxa from 41 samples for macroinvertebrates and 259 taxa from 31 samples for diatoms, respectively. As opposed to other frequently applied ordination techniques such as principal component analysis (PCA) or correspondence analysis (CA), NMDS does not use the amount of variance explained by different axis to assess the model quality. The goodness of fit is the stress value, which reflects how well the ordination summarizes the observed distances among the samples. According to Clarke and Warwick (2001) stress values can be interpreted with the following rule-of-thumb: stress < 0.05: excellent representation; stress < 0.1: good representation; stress < 0.2: acceptable representation, stress > 0.3: unsatisfactory representation, indicating that the ordination of the samples is close to being displayed randomly.

The spatial representation of the samples along the ordination axes was examined after the overlay of the associated conductivity measurements for each sample. To aggregate similar conductivity values, all samples were classified according to the chemical classification scheme for chloride and sulfate concentrations established by the German ‘Länderarbeitsgemeinschaft Wasser’ (Länderarbeitsgemeinschaft Wasser 1997). Overall, samples were assigned to seven conductivity classes ranging from ‘unpolluted’ ($< 645 \mu\text{S}/\text{cm}$) to ‘excessively polluted’ ($> 3134 \mu\text{S}/\text{cm}$, Table 6). For a more condensed graphical representation we aggregated the conductivity classes I-II/III, representing samples of ‘low conductivity’ and the three classes indicating the highest pollution (classes III-IV), representing samples of ‘high conductivity’. To test the statistical significance between groups of ‘high’ and ‘low’ conductivity we applied an analysis of similarity (ANOSIM) using the software PRIMER (Clarke and Gorley 2006, version 6.0). The Global R statistic from ANOSIM usually ranges between 0 and +1 (M. G. Chapman and Underwood 1999), a value of 0 representing no differences between a priori defined groups (Clarke 1993) and a value of 1 indicating no similarities between samples at all.

Table 6: Chloride classification according to Länderarbeitsgemeinschaft Wasser (1997) and aggregation of conductivity classes

Quality class	Status	Conductivity ($\mu\text{S}/\text{cm}$)	Classification
I	Unpolluted	< 645	Low conductivity
I-II	Slightly polluted	< 725	Low conductivity
II	Moderately polluted	< 886	Low conductivity
II-III	Critically salinated	< 1207	Low conductivity
III	Heavily salinated	< 1849	High conductivity
III-IV	Very heavily salinated	< 3134	High conductivity
IV	Excessively salinated	> 3134	High conductivity

3.2.3 Individual taxa and community salinity thresholds

After examining differences in community composition we focused our analyses on the species level to identify those species influenced by either increasing or decreasing salinity, which in turn significantly contribute to changes in the overall community structure. We applied a Threshold Indicator Taxa Analysis (TITAN, Baker and King (2010)) to the macroinvertebrate and diatom datasets using the software R (R Development Core Team 2013, version 3.1.0). This method detects ecological threshold values for individual species and whole communities along an environmental gradient (here: salinity) by combining the methods of change point analysis (nCPA, Qian et al. (2003)) and indicator species analysis (IndVal, Dufrêne and P.

Legendre (1997)). While nCPA aims for deviance reduction to obtain an optimal split point between two groups, TITAN uses the calculated IndVal scores instead to identify species-specific change points. IndVal scores are used to estimate the association of a species for a certain group based on its abundance and frequency and are scaled from 0 to 100. A value of 100, for example, indicates that a species was found in each samples of a certain group and was absent in any other group. In order to find the optimal change point for a species, TITAN continuously partitions the dataset and calculates two IndVal values, one based on all samples above and one based on all samples below a potential split point. The relative strength of the IndVal scores on each side of a potential change point indicates the association of a species with either the left (negative response with respect to increasing salinity loads) or the right (positive response with respect to increasing salinity loads) side. Ultimately, the method identifies the change point across an environmental variable that ideally partitions all samples by maximizing the species-specific scores (Baker and King 2010).

The distribution of all species thresholds across the salinity gradient is furthermore used to obtain a general community threshold. The cumulative responses of all species are considered to reflect fundamental changes in community composition and are given separately for positively and negatively associated taxa. Using a bootstrapping technique, TITAN calculates two key parameters to estimate the quality of a species response and to test its reliability as an indicator organism. The purity parameter, on the one hand, represents the proportion of correct response directions with regard to the observed response pattern by randomly resampling the original data. A pure indicator is characterized by purity values of ≥ 0.95 , indicating a consistent species response for the majority of bootstrapping repetitions. The reliability parameter reflects the proportion of IndVal scores yielding p -values below a predefined probability level (here: $p < 0.05$). Reliable indicators (≥ 0.95) do not show a large variation in calculated IndVal values and are characterized by stable IndVal maxima (Baker and King 2010). The uncertainty around individual and community change points was estimated by the calculation of empirical quartiles (5%, 95%).

As input for the analysis we used a crosstable with columns representing log (+1) transformed abundance data and rows displaying sample units (41 for macroinvertebrates, 31 for diatoms). As the method is reported suitable for taxa with low occurrences (Baker and King 2010), we included all taxa with ≥ 4 occurrences. Overall, we

addressed 87 macroinvertebrate and 98 diatom taxa. In addition to the species input table, an environmental text file is required with column data representing surface water conductivity measurements ($\mu\text{S}/\text{cm}$). 500 permutations were used to determine species specific z-scores as our calculations are based on a small dataset and we aimed for high precision in the individual taxa z-scores. Default settings were used for all other arguments. To compare our results to the literature, we used the salinity classifications based on Wolf (2004) for macroinvertebrates and Besse-Lototskaya et al. (2007) and van Dam et al. (1994) for diatoms provided by the autecological database <http://www.freshwaterecology.info> (Schmidt-Kloiber and Hering 2012, version 5.0).

3.3 Results

3.3.1 Composition of assemblages under different salinities

For both datasets, NMDS showed a clear split between samples of high and low salinities. Macroinvertebrate samples from sites with high salinity are arranged on the right side of the ordination diagram (Figure 9A), while most samples yielding lower salinity loads are located on the left side. Similarly, diatom samples with high salinity loads are placed within the upper part as opposed to samples with low salinity loads displayed in the lower part of the diagram (Figure 9B). The calculated stress was 0.20 for macroinvertebrates and 0.16 for diatoms, indicating acceptable representations. The ANOSIM results revealed statistically significant ($p < 0.01$) large differences (Global R = 0.61) for macroinvertebrates and moderate differences (Global R = 0.39) for diatoms between samples of 'low' and 'high' salinity. The correlation between total phosphorus and EC showed a moderate relationship ($R^2 = 0.429$).

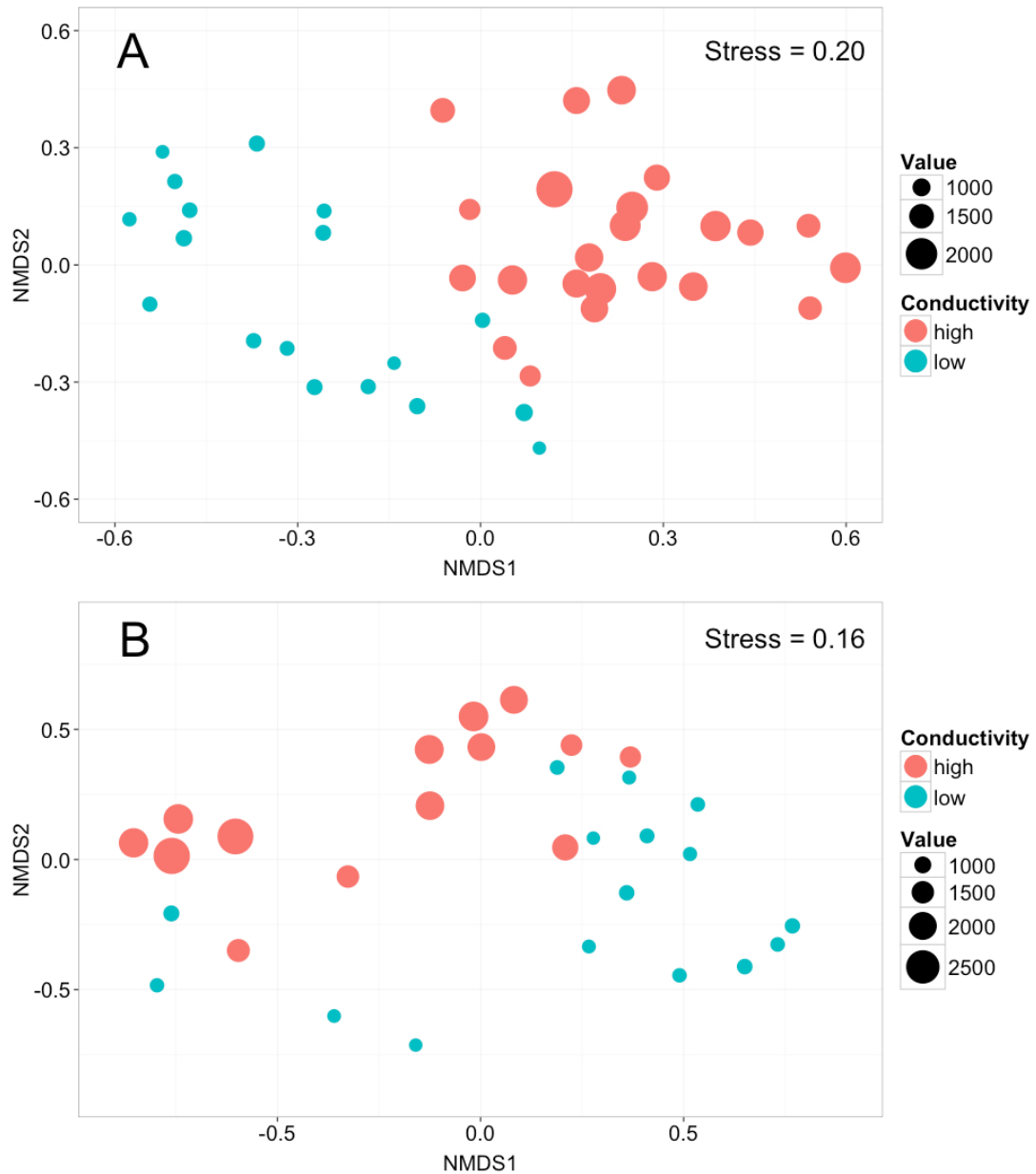


Figure 9: Graphical NMDS representation of macroinvertebrate (A) and diatom samples (B) with associated stress values. Conductivity values are classified according to Table 6. Values are given in $\mu\text{S}/\text{cm}$.

3.3.2 Individual taxa and community salinity thresholds

Significant salinity threshold values were obtained for 50 macroinvertebrate species ($p < 0.05$, Figure 10). The majority of taxa showed a negative association with increasing salinity ($n = 34$) with Crustacea (4x), Ephemeroptera (7x), Coleoptera (5x) and Trichoptera (3x) representing the dominant taxa groups (Table 7). On the other hand, 16 taxa were positively associated with salinity, of which most species can be attributed to Crustacea (3x), Diptera (2x) and Oligochaeta (5x).

IndVal scores range between 20 and 76.5 for taxa that indicated a negative association, whereas taxa preferring high salinities displayed IndVal values between 17 and 90.3. According to criteria listed by Baker and King (2010), 23 taxa (46 %) can be reported as reliable indicator organisms with seven taxa exhibiting a positive association towards increasing salinities (Table 7). Most of these taxa are nonindigenous species such as *Corbicula fluminea*, *Potamopyrgus antipodarum*, *Dikerogammarus villosus*, *Gammarus tigrinus* and *Hypania invalida*. The threshold concentration on community-level for negatively associated taxa (z-) peaked at 926 $\mu\text{S}/\text{cm}$ and steeply declined afterwards (Figure 12A). No distinct peak was observed for taxa preferring high salinities. The accumulative species scores (z+) increased around 900 $\mu\text{S}/\text{cm}$ and remained stable just above a value of 1500 $\mu\text{S}/\text{cm}$, hereafter showing a slight decrease which determined the community threshold level at 1464 $\mu\text{S}/\text{cm}$.

Table 7: TITAN environmental change points (env.cp.) and bootstrap confidence intervals (5% and 95%) for macroinvertebrate species (n = 50). Species' association (Assoc.) is either positive (+) or negative (-). Indicator values (IndVal) and associated significance values (pval) refer to the $p \leq 0.05$ significance level. Purity is the mean proportion of correct response direction (-) or (+) assignments, reliability is the mean proportion of p-values < 0.05 , freq. is the number of observations. salfr = freshwater, salol = oligohalobous, salme = mesohalobous, salpo = polyhalobous, saleu = euryhalobous. Reliable indicators (purity and reliability ≥ 0.95) are in bold letters.

Taxonomic group	Taxon	Shortcode	Assoc.	freq	IndVal	pval	Change point			Reliability			Salinity preference (Wolf 2004)		
							env.cp	5%	95%	purity	≤ 0.05	salfr	salol	salme	salpo
Turbellaria	Dugesia goniocephala	DUGEONO	-	6	35.3	0.006	926	790	1429	1	0.95
Gastropoda	Theodoxus fluviatilis	THEOFLUV	-	7	41.2	0.002	926	808	1429	1	0.98	6	2	2	0
Bivalvia	<i>Musculium lacustre</i>	MUSCLACU	-	4	22.2	0.04	1098	760	1429	0.99	0.62	10	0	0	0
Bivalvia	<i>Pisidium</i> sp.	CASESP.	-	15	46.5	0.04	1098	824	1981	0.68	0.55
Oligochaeta	<i>Eiseniella tetraedra</i>	EISETETR	-	4	47.1	0.012	760	760	1551	0.91	0.6	7	3	0	0
Hirudinea	<i>Erpobdella octoculata</i>	ERPOOCTO	-	7	32.8	0.014	1098	815	1634	0.96	0.81	7	3	0	0
Hirudinea	Glossiphonia complanata	GLOSCOMP	-	6	40	0.002	875	790	1239	1	0.97	7	3	0	0
Crustacea	Asellus aquaticus	ASELAQUA	-	16	61.8	0.002	1429	790	1634	1	1	7	3	0	0
Crustacea	Echinogammarus berilloni	ECHIBERI	-	13	76.5	0.002	926	811	1429	1	1
Crustacea	Gammarus pulex	GAMMPULE	-	11	54.8	0.002	840	779	1327	0.98	0.96	10	0	0	0
Crustacea	Gammarus roeselii	GAMMROES	-	16	74.8	0.002	1327	855	1551	1	1	10	0	0	0
Ephemeroptera	<i>Baetis fuscatus</i>	BAETFUSC	-	4	23.5	0.046	926	760	1419	0.96	0.76	10	0	0	0
Ephemeroptera	<i>Baetis vernus</i>	BAETVERN	-	9	39.8	0.006	926	780	1551	0.99	0.91
Ephemeroptera	Brachycercus harrisella	BRACHARI	-	6	35.3	0.008	926	780	1327	1	0.96
Ephemeroptera	Centroptilium luteolum	CENTLUTE	-	7	72.6	0.008	760	760	1327	1	0.96	10	0	0	0
Ephemeroptera	Ephemera danica	EPHEDANI	-	10	58.8	0.002	926	811	1429	1	1
Ephemeroptera	<i>Ephemera glaucops</i>	EPHEGLAU	-	4	49.5	0.012	760	760	1431	0.94	0.65
Ephemeroptera	Serratella ignita	EPHEIGNI	-	10	58.8	0.002	926	808	1429	1	1
Odonata	<i>Calopteryx splendens</i>	CALOSPLE	-	14	45.2	0.036	1781	811	1818	0.99	0.88	10	0	0	0
Odonata	<i>Platycnemis pennipes</i>	PLATPENN	-	9	31.2	0.034	1429	760	1689	0.95	0.79	10	0	0	0
Heteroptera	<i>Corixa</i> sp.	CORISP.	-	4	25.8	0.032	815	760	1781	0.86	0.6
Heteroptera	<i>Corixidae</i> Gen. sp.	CORDAEGE	-	7	37.4	0.002	885	803	1429	0.99	0.86
Heteroptera	<i>Micronecta</i> sp.	MICRONSP	-	7	48	0.004	803	780	1419	0.98	0.92
Megaloptera	<i>Sialis lutaria</i>	SIALLUTA	-	6	30	0.036	885	803	1732	0.9	0.74	7	3	0	0
Coleoptera	Elmidae sp.	ELMISP.1	-	6	35.3	0.004	926	760	1419	1	0.95
Coleoptera	Elmis aenea	ELMIAEN1	-	6	35.3	0.004	926	760	1327	1	0.96	10	0	0	0
Coleoptera	Laccophilus hyalinus	LACCCHYA1	-	6	37.5	0.006	885	760	1419	1	0.95	10	0	0	0
Coleoptera	<i>Oulimnius</i> sp.	OULISP.1	-	6	32.9	0.016	875	803	1471	0.96	0.85
Coleoptera	Oulinnius tuberculatus	OULITUB1	-	11	58.8	0.002	926	780	1419	1	1	10	0	0	0
Trichoptera	<i>Brachycentrus subnubilus</i>	BRACSUBN	-	4	23.5	0.022	926	760	1429	0.98	0.71	10	0	0	0
Trichoptera	<i>Lepidostoma hirtum</i>	LEPIHIRT	-	5	33.3	0.006	760	926	1551	1	0.92	7	3	0	0
Trichoptera	<i>Mystacides nigra</i>	MYSTNIGR	-	4	20	0.04	1327	824	1551	0.96	0.54	10	0	0	0

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Table 7: TITAN environmental change points (env.cp.) and bootstrap confidence intervals (5% and 95%) for macroinvertebrate species (n = 50). Species' association (Assoc.) is either positive (+) or negative (-). Indicator values (IndVal) and associated significance values (pval) refer to the $p \leq 0.05$ significance level. Purity is the mean proportion of correct response direction (-) or (+) assignments, reliability is the mean proportion of p-values < 0.05 , freq. is the number of observations. salfr = freshwater, salol = oligohalobous, salme = mesohalobous, salpo = polyhalobous, saleu = euryhalobous. Reliable indicators (purity and reliability ≥ 0.95) are in bold letters. (Continued)

Taxonomic group	Taxon	Shortcode	Assoc.	freq	IndVal	pval	Change point			Reliability			Salinity preference (Wolf 2004)		
							env.cp	5%	95%	purity	≤ 0.05	salfr	salol	salme	salpo
Diptera	Atherix ibis	ATHEIBIS	-	6	35.3	0.002	926	760	1419	1	0.95
Diptera	<i>Tanypodinae</i> Gen. sp.	TANNAEGE	-	18	56	0.012	885	803	1657	0.89	0.85
Gastropoda	Ancylus fluviatilis	ANCYFLUV	+	19	66.8	0.002	1098	855	1634	1	1	10	0	0	0
Gastropoda	Potamopygus antipodarum	POTAANTI	+	37	83.1	0.014	811	790	1551	0.99	0.96	6	2	2	0
Bivalvia	Corbicula fluminea	CORBFLUA	+	19	67.5	0.002	1551	924	1842	1	0.99	7	3	0	0
Polychaeta	Hypania invalida	HYPAINVA	+	15	75.7	0.002	1689	1239	1946	1	1
Oligochaeta	<i>Limnodrilus claparedeanus</i>	LIMNCLAP	+	4	61.8	0.018	1981	1327	1981	0.97	0.76	7	3	0	0
Oligochaeta	<i>Oligochaeta</i> Gen. sp.	OLICHGEN	+	9	43.6	0.006	1634	926	1793	0.98	0.9
Oligochaeta	<i>Potamothrix moldaviensis</i>	POTAMOLD	+	6	27.3	0.032	1239	875	1981	0.99	0.85	7	3	0	0
Oligochaeta	<i>Tubifex tubifex</i>	TUBITUBI	+	4	17	0.02	1551	811	1793	0.82	0.39
Oligochaeta	<i>Tubificidae</i> Gen. sp.	TUBIGEN.	+	18	51.4	0.02	1730	811	1948	0.91	0.78
Crustacea	Dikerogammarus villosus	DIKEVILL	+	25	90.3	0.002	926	855	1551	1	1
Crustacea	Gammarus tigrinus	GAMMTIGR	+	15	59	0.002	1429	855	1981	0.99	0.97	2	2	2	2
Crustacea	<i>Limnomysis benedeni</i>	LIMNBENE	+	11	35.7	0.048	926	760	1781	0.78	0.57
Ephemeroptera	<i>Caenis</i> sp.	CAENSP	+	4	23	0.036	1689	810	1818	0.9	0.58
Trichoptera	Psychomyia pusilla	PSYCPUSI	+	8	50	0.002	1612	1327	1793	1	1	10	0	0	0
Diptera	<i>Chironomini</i> Gen. sp.	CHIINIGE	+	29	78.8	0.012	1946	803	1981	0.61	0.55
Diptera	<i>Prodiamesa olivacea</i>	PRODOLIV	+	18	70.5	0.018	1981	780	1981	0.72	0.67	10	0	0	0

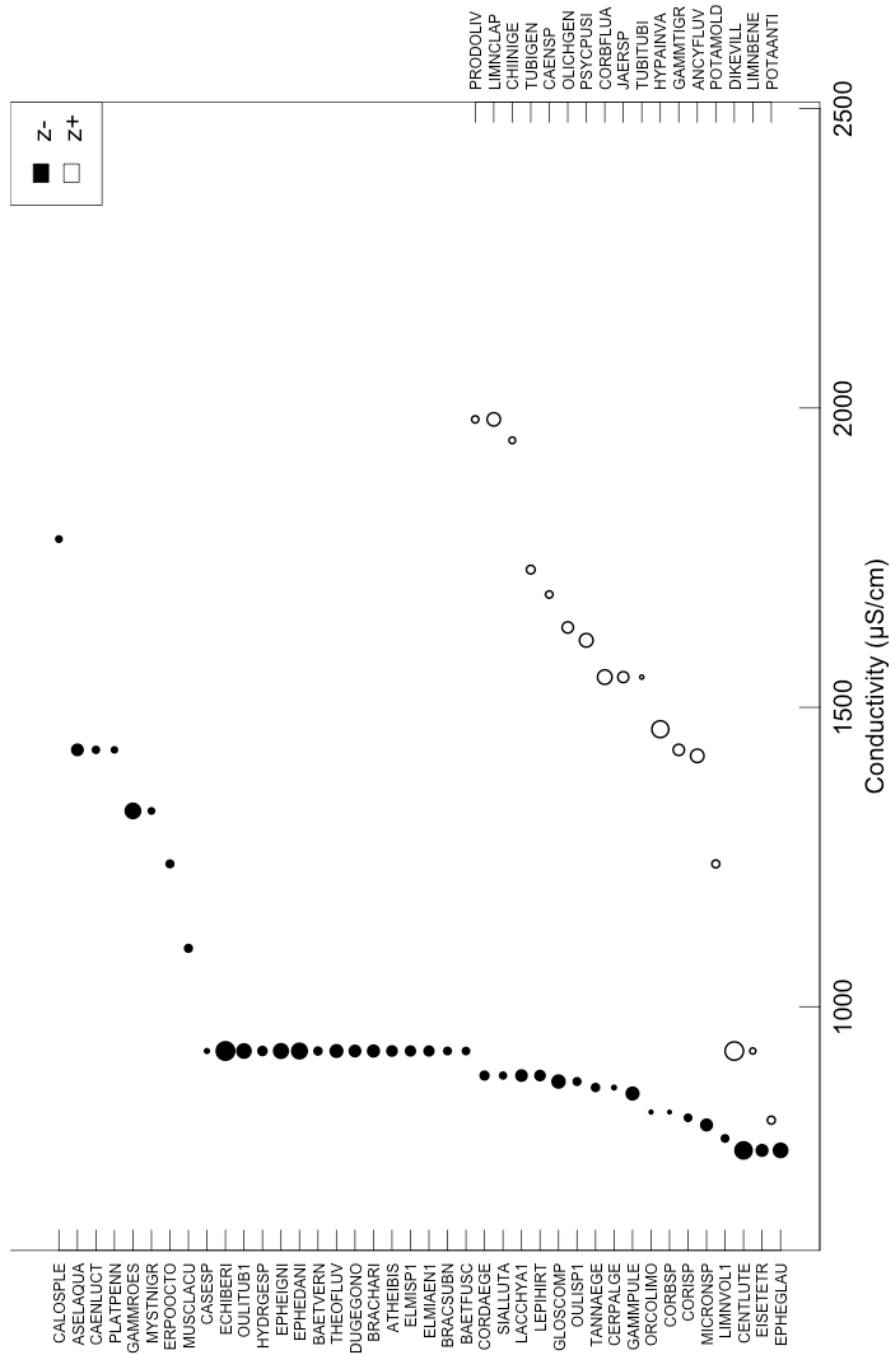


Figure 10: Graphical representation of significant threshold levels along a salinity gradient for macroinvertebrate species according to the Threshold Indicator Analysis (TITAN). Negatively associated taxa (z-) are arranged on the left side of the diagram, positively associated taxa (z+) on the right side. Taxa abbreviations are given in Table 7.

For diatoms, 58 taxa displayed significant thresholds values ($p < 0.05$) with most species establishing a negative relationship towards increasing salinity ($n = 43$, Figure 11). The calculated IndVal scores lie between 26.7 and 93.7 for negatively associated taxa, whereas taxa showing a positive relationship revealed IndVal values between 44.2 and 85.5 (Table 8). Among all species, 18 (31%) were characterized as reliable indicator organisms, of which five species exhibit a positive association with increasing salinities (*Amphora libyca*, *Bacillaria paxillifer*, *Navicula subhamulata*, *Nitzschia inconspicua*, *Rhoicosphenia abbreviata*). As for macroinvertebrates, the community threshold value for taxa, which are impacted by high salinity, was located within a similar range (910 $\mu\text{S}/\text{cm}$) while the upper threshold value ($z+$) was considerably higher by comparison (2140 $\mu\text{S}/\text{cm}$, Figure 12B, Table 9). Several species, which were assigned a negative response to increasing salinity, showed individual threshold levels exceeding the value of 910 $\mu\text{S}/\text{cm}$ by far and thus do not correspond with the estimated community threshold.

Table 8: TITAN environmental change points (env.cp.) and bootstrap confidence intervals (5% and 95%) for diatom species (n = 58). Species' association (Assoc.) is either positive (+) or negative (-). Indicator values (IndVal) and associated significance values (pval) refer to the $p \leq 0.05$ significance level. Purity is the mean proportion of correct response direction (-) or (+) assignments, reliability is the mean proportion of p-values < 0.05, freq. is the number of observations. Results are compared to salinity classification of Besse-Lototskaya et al. (2007) (B-L 2007) & van Dam et al. (1994) (vD 1994). lx = halophobous, oh = indifferent-oligohalobous, hp = oligohalobous-halophilic. Reliable indicators (purity and reliability ≥ 0.95) are in bold letters.

Taxon	Shortcode	Assoc.	freq	IndVal	pval	Change point			Reliability		Salinity preference				
						env.cp	5%	95%	purity	≤ 0.05	B-L 2007			Salinity after	
											hx	oh	hp	hx	hp
<i>Achnanthes lanceolata</i> ssp. <i>rostrata</i>	ACHNLARO	-	4	40.2	0.002	785	745	876	0.94	0.78				2	
<i>Achnantheidium minutissimum</i> var. <i>minutissimum</i>	ACHIMIMI	-	19	68.8	0.006	1471	820	1988	0.99	0.97	x			.	
<i>Amphora pediculus</i>	AMPHPEDI	-	31	85.9	0.006	2155	785	2155	0.96	0.88	x			.	
<i>Cocconeis placentula</i> var. <i>placentula</i>	COCCPLPL	-	25	79.2	0.002	795	760	885	0.99	0.99	x			2	
<i>Cocconeis pseudothumensis</i>	COCCPSTH	-	8	50	0.004	910	774	1471	1	0.96				2	
<i>Craticula buderi</i>	CRATBUDE	-	8	45.5	0.004	845	775	1530	0.98	0.81				.	
<i>Cymatopleura solea</i> var. <i>solea</i>	CYMASOSO	-	9	54.6	0.002	875	775	1419	1	0.96	x			2	
<i>Diatoma vulgare</i>	DIATVULG	-	14	71.4	0.002	875	802	1695	1	1	x			2	
<i>Diploneis oculata</i>	DIPLOCUL	-	7	61.9	0.006	775	745	885	0.98	0.92				2	
<i>Eolimna minima</i>	EOLIMINI	-	17	64.2	0.016	1988	845	2075	0.97	0.91	x			2	
<i>Fragilaria acus</i>	FRAGACUS	-	4	31.4	0.05	802	745	1165	0.99	0.65	x			2	
<i>Fragilaria brevistriata</i> var. <i>brevistriata</i>	FRAGBRBR	-	12	78.7	0.006	775	745	1165	0.99	0.97				.	
<i>Fragilaria leptostauron</i> var. <i>dubia</i>	FRAGLEDU	-	4	26.7	0.05	885	806	1471	0.93	0.45				.	
<i>Fragilaria martyi</i>	FRAGMART	-	6	37.5	0.012	910	820	1530	0.94	0.73				2	
<i>Fragilaria pinnata</i> var. <i>pinnata</i>	FRAGPIPI	-	16	78.7	0.002	910	775	1530	1	1				.	
<i>Fragilaria ulna</i> var. <i>ulna</i>	FRAGULUL	-	12	59.6	0.002	875	802	1471	0.98	0.9				.	
<i>Gomphonema olivaceum</i> var. <i>olivaceum</i>	GOMPOLOL	-	25	69.6	0.008	1530	875	2140	0.93	0.83	x			2	
<i>Gomphonema pumilum</i> var. <i>pumilum</i>	GOMPPUPU	-	7	42.2	0.022	785	745	1911	0.97	0.74				.	
<i>Gyrosigma acuminatum</i> var. <i>acuminatum</i>	GYROACAC	-	5	46.8	0.042	775	745	2155	0.87	0.66	x			.	
<i>Hippodonta capitata</i>	HIPPACAP	-	9	50	0.004	1416	785	1695	1	0.96	x			2	
<i>Hippodonta costulata</i>	HIPPACOST	-	5	31.3	0.042	910	802	1530	0.96	0.63				2	
<i>Karayevia clevei</i> var. <i>clevei</i>	KARACLCL	-	16	69.6	0.002	1988	875	2110	0.99	0.98				.	
<i>Karayevia ploenensis</i>	KARAPLOE	-	16	60.7	0.026	2027	785	2140	0.88	0.71				.	
<i>Mayamaea atomus</i> var. <i>permitis</i>	MAYAATPE	-	7	39.9	0.01	845	774	1471	0.97	0.8				2	
<i>Melobira vartans</i>	MELOVARI	-	19	76.3	0.002	1695	845	2075	0.98	0.95	x			2	
<i>Navicula antonii</i>	NAVANTO	-	22	63.9	0.034	2027	745	2155	0.7	0.61				.	
<i>Navicula capitata</i> var. <i>capitata</i>	NAVICACA	-	4	45.9	0.03	745	745	2110	0.68	0.51				.	
<i>Navicula capitatoradiata</i>	NAVICAPI	-	4	40	0.006	806	745	875	1	0.83		x		2	
<i>Navicula gregaria</i>	NAVIGREG	-	28	93.7	0.002	1695	885	1988	1	1	x			3	
<i>Navicula lanceolata</i>	NAVILANC	-	24	78.6	0.002	910	820	1988	1	0.98	x			3	
<i>Navicula reichardiana</i> var. <i>reichardiana</i>	NAVIRERE	-	16	63	0.016	1530	774	2027	0.99	0.94				2	

Continued on next page

Table 8: TITAN environmental change points (env.cp.) and bootstrap confidence intervals (5% and 95%) for diatom species (n = 58). Species' association (Assoc.) is either positive (+) or negative (-). Indicator values (IndVal) and associated significance values (pval) refer to the $p \leq 0.05$ significance level. Purity is the mean proportion of correct response direction (-) or (+) assignments, reliability is the mean proportion of p-values < 0.05 , freq. is the number of observations. Results are compared to salinity classification of Besse-Lototskaya et al. (2007) (B-L 2007) & van Dam et al. (1994) (vD 1994). lx = halophobous, oh = indifferent-oligohalobous, hp = oligohalobous-halophilic. Reliable indicators (purity and reliability ≥ 0.95) are in bold letters. (Continued)

Taxon	Shortcode	Assoc.	freq	IndVal	pval	Change point			Reliability		Salinity preference			
						env.cp	5%	95%	purity	≤ 0.05	B-L 2007		Salinity after	
											hx	oh	hp	vD 1994
<i>Navicula upsaliensis</i>	NAVIUPSA	-	5	31.3	0.05	910	775	1471	0.97	0.65				2
<i>Navicula veneta</i>	NAVIVENE	-	13	50	0.034	1165	802	2110	0.85	0.66	x			3
<i>Nitzschia microcephala</i>	NITZMICR	-	9	38.4	0.04	820	745	1911	0.91	0.65				2
<i>Nitzschia paleacea</i>	NITZPALE	-	14	54.4	0.024	845	775	2077	0.98	0.89				2
<i>Nitzschia recta</i> var. <i>recta</i>	NITZRERE	-	11	46.9	0.024	910	745	2027	0.94	0.84				.
<i>Nitzschia sigmoidea</i>	NITZSIGM	-	5	35.7	0.002	875	760	1165	1	0.82				2
<i>Planothidium dubium</i>	PLANDUBI	-	6	37.5	0.012	910	802	1530	0.98	0.77				.
<i>Planothidium frequentissimum</i> var. <i>frequentissimum</i>	PLANFRFR	-	17	65.4	0.012	2110	795	2140	0.93	0.82				.
<i>Planothidium lanceolatum</i>	PLANLANC	-	7	39.7	0.01	875	785	1471	0.98	0.81	x			2
<i>Planothidium rostratum</i>	PLANROST	-	13	56.9	0.008	910	844	2075	0.99	0.97	x			2
<i>Platessa conspicua</i>	PLATCONS	-	6	33.3	0.05	1416	759	1695	0.95	0.59				1
<i>Sellaphora pupula</i> var. <i>pupula</i>	SELLPUPU	-	5	33.3	0.02	885	795	1471	0.99	0.67	x			.
<i>Amphora libyca</i>	AMPHLIBY	+	10	55.7	0.002	1471	885	2155	0.98	0.95				2
<i>Amphora ovalis</i>	AMPHOVAL	+	10	67.4	0.018	2140	819	2155	0.99	0.93	x			2
<i>Bacillaria paxillifer</i>	BACIPAXI	+	7	53.9	0.002	1416	875	2155	1	0.99		x		4
<i>Caloneis bacillum</i>	CALOBACI	+	17	85.4	0.004	2155	775	2155	0.83	0.69				2
<i>Fragilaria ulna</i>	FRAGULNA	+	7	67.5	0.014	2140	745	2155	0.67	0.64				.
<i>Gyrosigma nodiferum</i>	GYRONODI	+	8	44.2	0.02	2027	760	2155	0.84	0.69				3
<i>Navicula menisculus</i> var. <i>menisculus</i>	NAVIMEME	+	8	57.7	0.008	2110	760	2155	0.87	0.74				2
<i>Navicula subhamulata</i>	NAVISUBH	+	8	62.7	0.002	2027	885	2155	0.96	0.95				2
<i>Nitzschia amphibia</i>	NITZSAMPH	+	14	58.7	0.01	875	806	2155	0.99	0.91				.
<i>Nitzschia constricta</i>	NITZCONS	+	19	77.9	0.006	2110	775	2155	0.96	0.9				.
<i>Nitzschia frustulum</i> var. <i>frustulum</i>	NITZFRFR	+	13	50	0.03	1165	820	2110	0.81	0.61		x		3
<i>Nitzschia heufferiana</i>	NITZHEUF	+	5	48.5	0.01	2075	885	2155	0.94	0.79				2
<i>Nitzschia inconspicua</i>	NITZINCO	+	8	64.1	0.004	2027	910	2155	1	0.98				3
<i>Nitzschia sociabilis</i>	NITZSOCI	+	8	58.9	0.012	2155	774	2155	0.63	0.52				2
<i>Rhicosphenia abbreviata</i>	RHOIABBR	+	30	85.2	0.002	865	802	1530	1	1	x			2

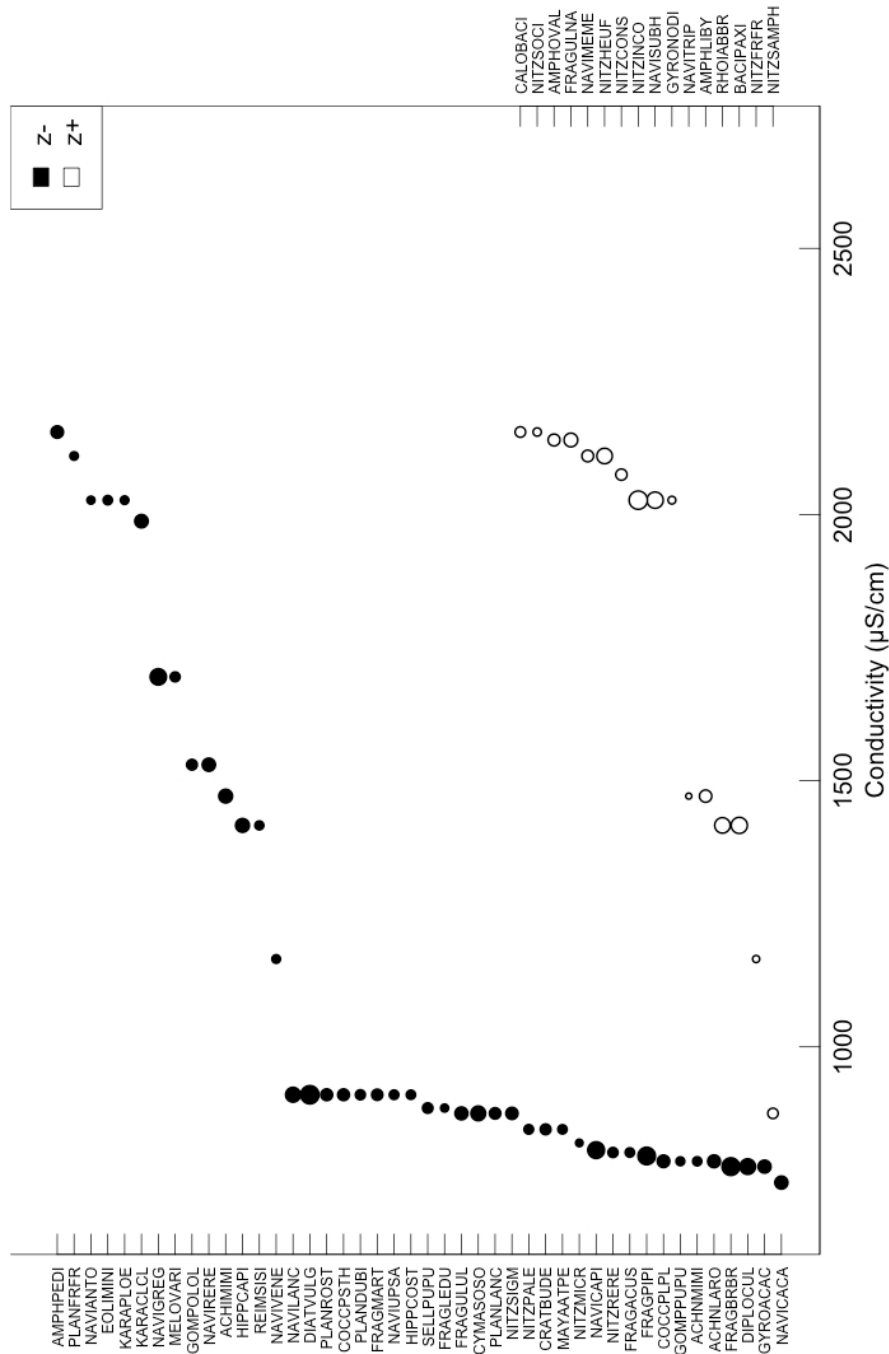
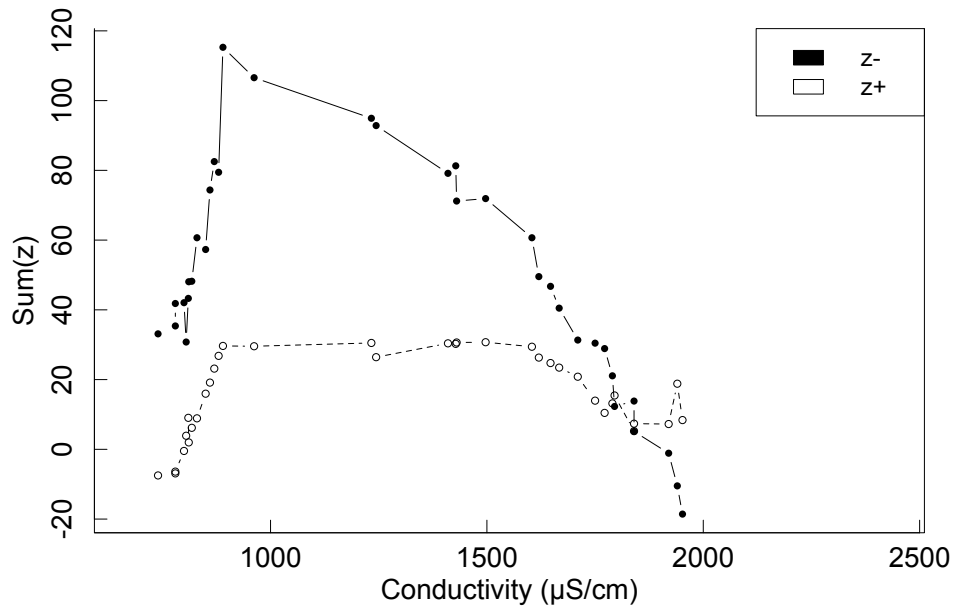
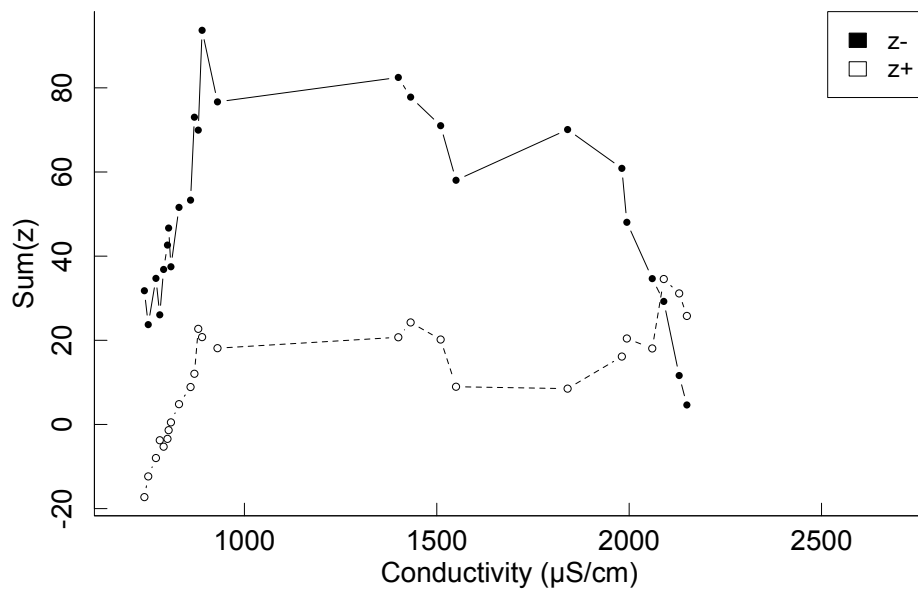


Figure 11: Graphical representation of significant thresholds levels along a salinity gradient for diatom species according to the Threshold Indicator Analysis (TITAN). Negatively associated taxa (z-) are arranged on the left side of the diagram, positively associated taxa (z+) on the right side, respectively. Taxa abbreviations are given in Table 8.



(a) Results for macroinvertebrates



(b) Results for diatoms

Figure 12: Graphical representation of the Threshold Indicator Analysis (TITAN) community response results for macroinvertebrates (a) and diatoms (b). Sum(z) are the accumulated species z-scores. The response is given for negatively (z-) and positively (z+) associated taxa.

Table 9: Threshold Indicator Analysis (TITAN) community response results for observed change points (Obs.) and bootstrap confidence intervals (5 % and 95 %). Community thresholds are given for negatively (sumz-) and positively (sumz+) associated taxa.

	Community change points ($\mu\text{S}/\text{cm}$)		
	Obs.	5 %	95 %
Macroinvertebrates			
sumz-	926	840	1429
sumz+	1464	885	1981
Diatoms			
sumz-	910	806	1530
sumz+	2140	1165	2155

3.4 Discussion

3.4.1 Indicator taxa and salinity thresholds for macroinvertebrates

Salinity largely influences the distribution of macroinvertebrates in the river Lippe and presumably acts as an overarching stressor to limit the distribution of macroinvertebrates (Bäthe and Coring 2011, Braukmann and Böhme 2011).

Based on the present analyses, Coleoptera, Crustacea, Ephemeroptera and Trichoptera represented the dominant taxa groups among all salt-sensitive species identified. Especially crustacean species (*Asellus aquaticus*, *Echinogammarus berilloni*, *Gammarus pulex*, *Gammarus roeseli*) and Ephemeroptera (*Brachycerus harrisella*, *Centroptilum luteolum*, *Ephemerella danica*, *Serratella ignita*) were reliable indicators. This observation corresponds with previous studies which revealed groups such as Ephemeroptera and Trichoptera as salt-sensitive indicators (Hart et al. 1991, Kefford 1998b, Halse et al. 2003). As opposed to our results, Crustaceans, Coleoptera and several Diptera were described to exhibit a broader salinity tolerance (Berezina 2002, Kefford et al. 2004, Kefford et al. 2006). However, Dunlop et al. (2008) showed that salinity preferences varied profoundly between Coleoptera families. Among them, species of the family Elmidae appeared to be particularly vulnerable towards high salinity. A general assessment of salinity preferences thus seems to be challenging, as studies often do not yield consistent results. Different autecological properties among species and the individual plasticity of organisms make it difficult to describe a uniform response on a broad taxonomic level which in turn emphasizes the need to determine species-specific change points.

Few species showed a positive association with salinity, of which most species are known to occur in brackish waters as well as under freshwater conditions (Table 7, Wolf 2004). Among them, the caddis larvae *Psychomyia pusilla* (salinity threshold

value of 1612 $\mu\text{S}/\text{cm}$) and the gastropod *Ancylus fluviatilis* (salinity threshold value of 1098 $\mu\text{S}/\text{cm}$) have previously been characterized to prefer water with low salinity (Wolf et al. 2009). Also Piscart et al. (2005b) found *Psychomyia pusilla* to predominantly colonize river sections of low salinity in the Meurthe river (France), while Bätke and Coring (2011) recorded *Psychomyia pusilla* in salinized sections of the river Werra as well. These differences might be related to the permanent exposure to high saline concentrations that may lead to physiological adaptations and hence may increase the salt tolerance of single species (Kay et al. 2001). Beisel et al. (2011) for example showed that populations of *Corophium curvispinum* exhibit a wider salinity tolerance under high salinity conditions as opposed to populations under low salinity conditions. There is strong evidence that such adaptations manifest on the evolutionary level and are passed on to the next generation (Lee and C. H. Petersen 2003).

While salinity threshold levels vary considerably between species, a general response is also reflected at the community level (Dunlop et al. 2005, Horrigan et al. 2005). The authors described shifts in community composition for macroinvertebrates between 800 and 1000 $\mu\text{S}/\text{cm}$. This observation corresponds to the community threshold levels we obtained for salt-sensitive species (926 $\mu\text{S}/\text{cm}$). We furthermore determined a community threshold for salt-tolerant taxa at 1416 $\mu\text{S}/\text{cm}$, which is closely related to the finding of Kefford et al. (2011), who described a significant reduction of species richness above 1500 $\mu\text{S}/\text{cm}$.

3.4.2 Nonindigenous species as indicators of high salinity

The salinization of rivers has been proposed to promote the establishment of invasive species while similarly impacting its native community (Braukmann and Böhme 2011). In our study, the majority of salt-tolerant indicator species are invasive (*Corbicula fluminea*, *Gammarus tigrinus*, *Dikerogammarus villosus*, *Potomopyrgus antipodarum*, *Hypania invalida*), all of which have colonized the river Lippe since several years (Sommerhäuser et al. 2009). Among them, the euryhaline and euryoecious amphipod *Gammarus tigrinus* is reported as one of the most abundant species in salt polluted river sections (Wolf 2004, Piscart et al. 2005a, Piscart et al. 2007, Piscart et al. 2010, Braukmann and Böhme 2011). Wijnhoven et al. (2003) indicate the competitive advantage of *G. tigrinus* at higher temperature and salinity levels as opposed to its native relative *G. pulex* and highlight the conductivity as crucial factor to determine their spatial distribution. While an increasing salinity seems to

negatively affect indigenous crustaceans such as *G. pulex* and *G. roeseli*, *G. tigrinus* benefits from the weakened populations and replaces them in their ecological niche. In the present study a similar pattern was observed, with *G. tigrinus* preferring conductivity levels above 1500 $\mu\text{S}/\text{cm}$ (salinity threshold value of 1419 $\mu\text{S}/\text{cm}$) as opposed to *G. pulex* and *G. roeseli*, both of which occurred at considerably lower salinity. Another indicator species is the large amphipod *Dikerogammarus villosus* (salinity threshold value of 926 $\mu\text{S}/\text{cm}$). *D. villosus* is known to thrive in high conductivity conditions (Brujjs et al. 2001) and frequently preys upon populations of smaller, salt-tolerant gammarid species such as *G. tigrinus* (Krisp and Maier 2005). Several authors emphasize the large predatory impact of *D. villosus* and predict the species to potentially replace *G. tigrinus* in the future (e.g. Dick and Platvoet 2000). We observed a high frequency ($n = 25$) and average densities per sample (505 specimens) for *D. villosus* as opposed to *G. tigrinus* ($n = 13$, 194 specimens) throughout all samples. This finding may indicate the proceeding replacement of the latter species by its stronger competitor *D. villosus*.

While ecological tolerance and increased transport opportunities are stated to enhance the success of invaders over indigenous species (Wolff 2000, Brujjs et al. 2001, Grabowski et al. 2007), physiological and evolutionary properties of species are referred to further contribute to their invasive success (Lee and Bell 1999, Kay et al. 2001). High nutrient loads along with increased salinity evidently induce physiological stress on the native community, leaving them vulnerable and prone to invaders. The greater osmoregulatory efforts and associated energetic costs of exotic species to cope with freshwater conditions are energy demanding, which in turn make them especially successful in polluted river sections. In consequence, sufficient food supply both in terms of quality and quantity may significantly limit the invasion of foreign species (Lee et al. 2013). In the present study, a moderate relationship ($R^2 = 0.43$) between conductivity ($\mu\text{S}/\text{cm}$) and total phosphorus concentrations (mg/L) was observed which may point to the interdependence of both nutrients and salinity to facilitate invasion events.

3.4.3 Indicator taxa and salinity thresholds for diatoms

The majority of reliable indicator species for low salinity conditions in the river Lippe are typical residents of lowland rivers. Most of them are known to exhibit a broad ecological range considering their salinity (e.g. *Fragilaria brevistriata* var. *brevistriata*, *Melosira varians*), trophic preferences (e.g. *Diatoma vulgare*, *Navicula*

lanceolata) and/or saprobic tolerances (e.g. *Hippodonta capitata*, *Karayevia clevei* var. *clevei*) (Hofmann et al. 2013). Their broad ecological amplitude is reflected by their individual salinity threshold values, which often exceeded the community threshold level of 910 $\mu\text{S}/\text{cm}$ by far. The dominance of these euryoecious and ubiquitous taxa might be related to the vast extent of anthropogenic degradation in the Lippe catchment, as suitable habitats for more sensitive species are largely missing. Accordingly, the described species-threshold values should be considered with caution, as the associated species do not present indicators of low salinity per se, but may rather show their distribution in competition with even more tolerant species. The predominant occurrence of euryoecious taxa may as well be reflected on the community level. While diatom communities of low and high salinity separate according to our results (Global R = 0.39), the obtained differences are not as distinct as for macroinvertebrates (Global R = 0.61). This is due to the fact that many species similarly occur in both samples of low and high salinity within our dataset.

According to the literature, most salt-tolerant indicator species identified in our analyses are widely distributed throughout Germany and colonize rivers of different salinity. Among them, *Bacillaria paxillifera* (salinity threshold value of 1416 $\mu\text{S}/\text{cm}$) is known as the most salt tolerant species and mainly occurs in marine habitats along coastlines as well as in brackish inland water bodies (van Dam et al. 1994, Jahn and Schmid 2007, Hofmann et al. 2013). *Nitzschia inconspicua* (salinity threshold value of 2027 $\mu\text{S}/\text{cm}$) seems to prefer weakly brackish waters (Horton et al. 2006). However, ecological preferences of *N. inconspicua* have yet to be described more precisely, as the species has not been differentiated from the morphologically similar species *N. abbreviata* during regular monitoring (Hofmann et al. 2013). Both *Navicula subhamulata* (salinity threshold value of 2027 $\mu\text{S}/\text{cm}$) and *Rhoicosphenia abbreviata* (salinity threshold value of 865 $\mu\text{S}/\text{cm}$) are euryoecious species in terms of their salinity preferences and trophic state and are found in various ecoregions throughout Germany (Hofmann et al. 2013).

Similar to macroinvertebrates, we determined a community threshold value at 910 $\mu\text{S}/\text{cm}$ for taxa which are impacted by high salinity. A different threshold was observed by Ziemann et al. (2001) who revealed that a chloride concentration of 400 mg/L (600 $\mu\text{S}/\text{cm}$) should not be exceeded in order to maintain the dominance of freshwater diatom species. These differences partly appear to be data-dependent as salinity values never fall below 600 $\mu\text{S}/\text{cm}$ in our dataset. On the other hand, high nutrient conditions are another factor to potentially elevate individual (and thus

community) salinity thresholds. To cope with an increased osmotic stress at high salinities, diatoms need to produce osmolytes which usually contain high amounts of nitrogen (Fritz 2007). Consequently, nutrient-rich waters comply with the species' higher nutrient requirements and may facilitate their adaptation under high salinity conditions (Saros and Fritz 2000).

3.5 Conclusion

Both macroinvertebrates and diatoms show a distinct shift in community composition between 900 and 1000 $\mu\text{S}/\text{cm}$. A reduction of the average salinity below this threshold may have positive effects on the overall species richness and the persistence of sensitive taxa in the river Lippe. The generated thresholds may provide valuable information to prevent both changes to single species and aquatic communities. The threshold values are, however, subject to certain limitations. Some studies, for instance, emphasize the different effects of ion composition on aquatic species (Potapova and Charles 2003, Braukmann and Böhme 2011). For the Lippe catchment, NaCl represents the dominant ions and species responses should thus be interpreted accordingly. Interactions of salinity with e.g. water temperature (Kennedy et al. 2004), lime content (Soucek and Kennedy 2005) and pH-value (Dunlop et al. 2005) may mitigate or enhance species' salinity tolerances. Given these circumstances, species thresholds should not be regarded as fixed values as they are subject to certain fluctuations and might change throughout time and with environmental conditions.

4 Simulating the effect of substratum composition on macroinvertebrate assessment metrics in two rivers

4.1 Introduction

Bottom substratum composition has been widely identified as one of the most significant variables for explaining spatial distribution patterns of benthic invertebrates on a micro scale (Beisel et al. 1998, Bournaud et al. 1998, Hering et al. 2006, Duan et al. 2009, Barnes and H. M. Chapman 2014). Distinct affinities of species for certain habitats have been commonly linked to morphologic adaptations (Pardo and Armitage 1997), locomotion types, and feeding preferences (G. W. Minshall 1967, Lemly and Hilderbrand 2000) and shifts in species traits are assumed to be related to the variation in availability and/or quality of these resources. In particular, the association of benthic invertebrates towards substratum type (Buss et al. 2004, Schröder et al. 2013), substratum composition (Beisel et al. 2000), substratum texture (Boyero 2003) and substratum particle size (Cummins and Lauff 1969, Wohl et al. 1995) has been described, and certain substrates are assumed to act as hot spots of local biodiversity (Drury and Kelso 2000, Johnson 2002).

Natural channel dynamics, however, have been severely impaired by human interventions during the last century e.g. the channelization of streams, the drainage of wetlands, and the loss of riparian buffer zones (Malmqvist and Rundle 2002, Statzner and Bêche 2010, Tockner et al. 2010). These alterations led to the degradation of habitats and to respective shifts in macroinvertebrate community composition (Feld 2013). Especially species directly depending on the availability of certain substrates (e.g. deadwood) are prone to be diminished in numbers or to disappear completely from the local species pool if certain substrates are missing (Hoffmann 2000, Hoffmann and Hering 2000, Spänhoff et al. 2000, Sarriquet et al. 2007).

Against this background, many restoration projects have been initiated in recent years to improve the ecological situation of freshwaters (Palmer et al. 1997, Palmer et al. 2007). In Europe, the primary goal is often to achieve 'good' ecological status as it has been stipulated within the Water Framework directive (WFD, EG/2000/60).

Within this context, the alteration of physical habitat still constitutes one of the major objectives to enhance structural heterogeneity and finally invertebrate diversity (Palmer et al. 2010). Commonly applied restoration techniques include the reconfiguration of channel morphology to initiate or reinforce natural channel dynamics (Kail 2003, Gillilan et al. 2005) as well as the direct introduction of artificial or natural habitat components to the stream (Nakano and Nakamura 2006). The latter influence on the macroinvertebrate community has been intensively analyzed and tested for large woody debris (Hilderbrand et al. 1997, Gerhard and Reich 2000, Lemly and Hilderbrand 2000, Larson et al. 2001, Spänhoff et al. 2006a, Entrekin et al. 2009, Gabriel et al. 2010, Testa III et al. 2011), coarse particular organic matter (Haapala et al. 2003, Pretty and Dobson 2004, Lepori et al. 2005), large boulders (Tikkanen et al. 1994, Negishi and Richardson 2003), and gravel (Shaw and G. W. Minshall 1980, Harrison et al. 2004, Albertson et al. 2011, Pedersen et al. 2014).

Several of these studies noticed an increase in habitat availability and heterogeneity following the restoration measures (Jähnig et al. 2008, Jähnig et al. 2010, Pedersen et al. 2014). However, the beneficial effects of habitat enhancement measures for the macroinvertebrate community on the reach scale have yet been assessed minor (Jähnig et al. 2008, Lorenz and Feld 2013, Feld et al. 2014) and often remain unclear (Dewson et al. 2007, Miller et al. 2010).

Potential reasons for these observations relate to large scale pressures and factors (Kail et al. 2012) as well as to processes that are inherent to the restoration measure itself. For instance, restoration measures may fail to create habitats that match with the species' ecological demands (Jähnig et al. 2009, Albertson et al. 2011). Haase et al. (2013) furthermore point out that invertebrates may be more strongly influenced by sediment composition or the presence of key habitats, stressing the importance to meet the specific ecological requirements of focal species. Moreover, several authors argue that changes in bottom habitats induced by restoration are often marginal and might not be strong enough to significantly change the macroinvertebrate assemblage (Lepori et al. 2005, Hering et al. 2015). The success of restoration measures may furthermore be inhibited by disregarding hydromorphological processes which are relevant to maintain newly created habitats (Lorenz et al. 2009). Finally, persistent pollution (Langford et al. 2009), the lack of source populations (Haase et al. (2013)), and insufficient dispersal capabilities (Sundermann et al. 2011) may mask biological effects from a catchment scale perspective.

While there is a general agreement on the nature of the factors which presumably

impair biological results, there is yet no sound understanding about their complex interactions that determine the structure of local populations (Downes 2010). Metapopulation dynamics, including the dispersal of macroinvertebrates for example are assumed to play an important role in recolonizing newly created habitats (Feld et al. 2011, Sundermann et al. 2011). The reliability of predictions obtained from associated species distribution or dispersal models, however, is often low (Pearson et al. 2006). High uncertainties associated with these processes consequently make it difficult to accurately estimate biological restoration success (Lawton 2000).

Even on the reach scale it largely remains unclear how habitat composition needs to be changed in order to yield biological effects. The identification of optimal substrate composition may however prove useful in order to either maximize the effect of restoration measures or to just enhance local biological quality. Against this background, we aim to single out the direct effect of altered substrate composition on the macroinvertebrate community. We investigated whether and to what extent changes in aquatic substrate conditions influence WFD assessment metrics and ecological status for a respective river reach and how different substratum components relate to these effects. In particular, we aim i) to ecologically describe all relevant substrate components and identify potential key habitats, and ii) to analyze the response of assessment metrics to simulated changes in substratum composition and furthermore relate results to (measured) baseline substrate conditions.

For this purpose, substrate-specific macroinvertebrate samples were collected within a study reach for a German lowland river (Treene, North-Germany) and a mountain stream located in South-West France (Célé). In a first step, cluster techniques were applied to test for resembling macroinvertebrate assemblages between substrates and to potentially identify key habitats. Subsequently, macroinvertebrate assemblages were simulated for predefined substrate compositions using the recently developed Habitat Evaluation Tool (HET, Kiesel et al. 2015). The model generates composite taxalists which can be considered as virtual samples reflecting real-world samples taken under different substrate compositions. All lists were finally analyzed afterwards using the WFD compliance assessment software ASTERICS (ASTERICS 2013, version 4.0.3).

Overall, our analyses provide the opportunity to more accurately assess the potential effect of substratum composition for aquatic invertebrates and WFD compliant assessment results, and contribute to improvements in restoration designs.

4.2 Material and methods

4.2.1 Study area

The study was carried out in two catchments: i) the Treene catchment, located in Northern-Germany and ii) the Célé catchment, located in the South-Western part of France. Within both streams, a representative, near-natural study reach was selected.

The Treene is a mid-sized lowland river with a catchment size of approximately 481 km². The catchment land use is dominated by intensive agriculture (80 %) with an increasing cultivation of energy crops while forested (8 %) and urban areas (10 %) cover the catchment to a lesser extent (Guse et al. 2014). The dominant bed material is sand and loam, interspersed with a variable amount of gravel and organic material. Elevations range from 2–80 m above sea level (Guse et al. 2014). The study reach is 260 m in length and is located in the lower part of the catchment (227 km²) surrounded by grassland (54°35'2.65"N, 9°20'22.10"E). The channel was moderately incised (mean bankfull depth = 1.4 m). The predominant invertebrate assemblage for sand-dominated lowland rivers is diverse, although specialized species are usually lacking from the species pool (Pottgiesser and Sommerhäuser 2004). Most species are known to prefer deposited organic habitats characterized by low flow velocities. Rheophilic species are rather rare and limited to naturally occurring hard substrates such as wood, gravel or macrophytes.

The Célé River is a mid-sized mountain river with a catchment size of approximately 1346 km². The upper and middle courses are naturally braiding and meandering and substratum composition is dominated by small to large stones (2–40 cm) as well as sparsely distributed organic material (e.g. deadwood, fallen leaves). In the middle course, river banks are frequently fixed due to a predominant agricultural land use. The meandering study reach is 260 m long and located in the middle course of the river (44°35'21"N, 1°57'29"E, 761.3 km²). According to reference stream type conditions, flow velocity patterns are diverse and create a mosaic of lotic and lentic habitats. The macroinvertebrate assemblage is usually species-rich with a high number of specialized species. We considered the Célé river in France in our analysis as near-natural river reaches and associated characteristic macroinvertebrate communities for large mountain streams are virtually absent in Germany.

4.2.2 Macroinvertebrate sampling

The general macroinvertebrate sampling procedure refers to German monitoring guidelines summarized by Meier et al. (2006a). Macroinvertebrates were collected in the model reach in March 2011 (Treene, N-Germany) and June 2011 (Célé, SW-France). The date of sampling was set within the recommended rivertype-specific sampling period for macroinvertebrates in large lowland and mountain streams (Meier et al. 2006a). In addition, the proportion of substrates on the river bottom was assessed for each model reach during macroinvertebrate sampling (Meier et al. 2006a).

We applied substrate-specific macroinvertebrate sampling, using a 25 cm × 25 cm frame shovel sampler (500 µm mesh). Each sample consisted of one type of substrate only and was stored separately and preserved with 96 % ethanol in the field. Eight replicates were taken for each substrate type, resulting in a total number of 160 substrate-specific samples for both streams (Table 10). Samples of each substrate type were distributed randomly within the model reach. Naturally rare substrates (e.g. deadwood) were also sampled within short distance upstream or downstream if there were not sufficiently frequent in the study reach.

Table 10: Number of macroinvertebrate samples and corresponding substrate clusters for the Treene and Célé model reach. Abbreviations: GR = gravel, SA = sand and other fine substrates, LO= silt/loam, OR = organic material, ST_L= large stones, ST_S = small stones, LP = living parts of terrestrial plants, WO = deadwood and woody debris.

Substrate type	Abbreviation	No. of replicates (25 × 25 cm)		Substrate cluster	
		Treene	Célé	Treene	Célé
Large rocks (> 40 cm)	MEGA		8		ST_L
Large stones (40-20 cm)	MAKRO		8		ST_L
Medium stones (20-6 cm)	MESO		8		ST_L
Stones and large gravel (6-2 cm)	MICRO		8		ST_S
Fine-medium gravel (2 cm-0.2 cm)	AKAL	8		GR	
Sand (< 2 mm)	PSAM	8	8	SA	SA
Moving sand (< 2 mm)	PSAM_M	8		SA	
Mineralic mud (< 6 cm)	PELAL	8	8	SA	OR
Silt/Loam (< 6 cm)	ARGY	8		LO	
Deposits of fine particular organic matter	FPOM	8	8	SA	OR
Deposits of coarse particular organic matter	CPOM	8	8	OR	OR
Fine roots, floating riparian vegetation	LPTP	8	8	OR	LP
Emerse and submerse macrophytes	PHYT	8		OR	
Fallen trees, larges pieces of deadwood	XYLAL	8	8	OR	WO

Each sample was subsequently sorted in the lab; samples from the Treene were mostly identified to species level, excluding most Diptera (family level), Chironomidae (genus level, species in exceptional cases) and Oligochaeta (mixed level of family, genus and species). Samples from the Célé were equally processed, though the determination of most Ephemeroptera was to genus level only. In total, 93 taxa (4956

specimens) from 14 taxonomic groups were identified in the Treene. For the Célé, 99 taxa (2839 specimens) from 13 taxonomic groups were recorded, respectively.

4.3 Data analysis

4.3.1 Substrate cluster analysis

To test for resembling macroinvertebrate assemblages between substrates, different cluster techniques were applied in order to aggregate substrates with similar invertebrate communities into clusters. Prior to the similarity analyses, total abundances of species were summarized for each substrate type and log+1 transformed. Cluster analyses were based on the Bray-Curtis dissimilarity matrix of macroinvertebrate assemblages and were performed separately for both streams.

Out of the many different types of clustering methods (P. Legendre and L. Legendre 2012), we applied the following clustering techniques according to Borcard et al. (2011): i) Single Linkage Agglomerative Clustering (single), ii) Complete Linkage Agglomerative Clustering (complete), iii) Average Agglomerative Clustering (average) and iv) Wards Minimum Variance Clustering (ward). Clustering does not present a typical statistical method per se as the results (i.e. partitions) cannot be tested for statistical significance. Nevertheless, there are few measures available that may be used to better interpret and compare cluster results among each other. In order to determine the most reliable cluster technique for our dataset, we used the cophonetic correlation and the Gower (1983) distance (Borcard et al. 2011). The cophonetic correlation ranges between 0 and 1 and highest values may indicate the optimal clustering method. The Gower (1983) distance, in comparison, takes smallest values to reflect the most reliable clustering method. The optimal number of clusters based on the best clustering method was subsequently estimated using the Mantel correlation coefficient (Pearson's R) (Borcard et al. 2011). The coefficient is calculated for $n-1$ clusters, where n is the total number of objects (here: substrates). The optimal number of clusters is identified where the correlation coefficient takes the highest value.

We used taxa number to indicate alpha diversity in each substrate cluster. Shannon diversity, Shannon evenness and the number of ecological valuable/poor taxa according to the German Fauna-Index were calculated in addition. Differences among substrate clusters were tested using one-way ANOVA (Chambers and Hastie 1992). All analyses were performed with R version 3.1.2 (R Development Core Team 2013)

using the HCLUST and STATS package.

4.3.2 Simulation of macroinvertebrate assemblages

Macroinvertebrate assemblages under different assumed substrate combinations were simulated using the Habitat Evaluation Tool (HET, Kiesel et al. 2015). HET is a statistical habitat model that predicts the presence and abundance of invertebrate species for a river reach based on empirically derived relationships between Habitat sensitivity classes (HSCs) and species presence and abundance (for detailed information see Kiesel et al. (2015)). HSCs may be represented by habitat parameters such as flow velocity, depth, substrate or combinations of these. In this study, we chose a univariate application, using substrate clusters only as HSCs. To account for the variation in species' abundances, the average number of individuals, as well as their minimum and maximum occurrence was determined for one sample unit (25 cm × 25 cm). Average, minimum and maximum individual numbers were set for each HSC and species present in the model reach. Overall, three species lists were compiled for each HSC representing the average, minimum and maximum species distribution. These lists were used as basis for the subsequent simulations.

Based on the spatial information about the distribution of substrates in a river reach, the HET offers the opportunity to perform an 'electronic Multi-Habitat Sampling' (MHS). Field MHS is based on the concept of substrate-associated colonization patterns of macroinvertebrates and is implemented as standard sampling method within the WFD (Hering et al. 2004b). For this method, the relative proportion of all prevailing substratum types in a river reach needs to be assessed first. Afterwards, a total of 20 substrate-specific sampling units are distributed over the river bed according to the prior defined percentages using a 25 cm × 25 cm frame shovel sampler (500 µm mesh). Only habitats with a share of > 5% habitat coverage are taken into account. All 20 samples are finally pooled and compiled in a composite taxalist. This list ultimately reflects the representative macroinvertebrate assemblage at a sampling site for a defined substrate composition (Haase et al. 2004b).

In order to simulate the colonization of macroinvertebrates for a model reach under different substrate compositions, percentages for all present substrate components needed to be defined first. Substrate percentages were defined as absent, low, moderate, or high (Table 11). States were defined using expert knowledge, considering the hydromorphologic river type-specific reference conditions proposed by Pottgiesser and Sommerhäuser (2004). Simulations were based on the prior delin-

eated substrate clusters. Substrate clusters were combined randomly and all possible combinations yielding 100 % coverage were taken into account for simulation runs.

Table 11: Percentage of substrate coverage on the river bottom for each substrate type based on different states (low, moderate, high, and absent). For abbreviations see Table 10.

Substrate cluster	Substrate	% substrate coverage on the river bottom			
		Low	Moderate	High	Absent
Treene					
GR	AKAL	5	10	20	0
LO	ARGY	5	10	20	0
OR	CPOM	5	10	20	0
OR	XYLAL	5	10	20	0
OR	LPTP	5	10	20	0
OR	PHYT	10	40	80	0
SA	PSAM	30	60	90	-
SA	PELAL	5	10	20	0
SA	FPOM	5	10	20	0
Célé					
SA	PSAM	5	10	20	0
OR	CPOM	5	10	20	0
OR	FPOM	5	10	15	0
OR	PELAL	5	10	15	0
LPTP	LPTP	5	10	15	0
WO	XYLAL	5	10	15	0
ST_L	MAKRO	5	10	20	0
ST_L	MEGA	5	10	15	0
ST_L	MESO	25	45	65	-
ST_S	MIKRO	25	45	65	-

Within the HET, information about the substrate composition was provided in tabular form i.e. as an excel spreadsheet. The 20 samples were then distributed according to specific substrate proportions. For each 5 % threshold, one random sample was taken from the corresponding HSC-specific species list and all individuals were automatically transferred into a composite taxa list. In total, composite taxa lists were generated for 552 model runs for the Treene and 1710 model runs for the Célé, which can be considered as virtual samples reflecting real-world MHS samples taken under different substrate compositions.

All lists were subsequently analyzed with ASTERICS (ASTERICS 2013, version 4.0.3), a software used for assessing macroinvertebrate assemblages for the WFD. For each composite taxalist, the ecological quality class and a selection of metrics were calculated. The metrics used include five groups: i) general metrics (abundance, number of taxa), ii) diversity metrics (Shannon diversity, Shannon evenness), iii) feeding types (% active filter feeders, % gatherers/collectors, % grazers/scrapers, % passive filter feeders, % predators, % shredders), iv) taxonomical groups (% Bivalvia, % Coleoptera, % Crustacea, % Diptera, % Ephemeroptera, % Gastropoda, % Odonata, % Oligochaeta, % Plecoptera), and v) streamtype-specific assessment metrics (core-metrics, Table 12).

The association between metrics and substrate clusters was tested using the squared Pearson R coefficient. P-values were adjusted for multiple comparisons using the Holms correction (Holm 1979). Only significant associations with an $R^2 \geq 0.2$ were shown (significance level $p \leq 0.1$). Dispersion statistics (standard deviation, variation coefficient) and the median were calculated in addition.

Table 12: List and ecological description of relevant assessment metrics (core-metrics) for the Treene and Célé model reach. Tr = Treene, Ce = Célé

Core metric	Stream	Description	Ecological relevance	References
% EPT	Tr, Ce	Relative abundance of Ephemeroptera, Plecoptera and Trichoptera taxa	Many Ephemeroptera, Plecoptera, and Trichoptera taxa are sensitive towards hydromorphologic degradation and poor water quality. High metric values may indicate an intact macroinvertebrate assemblage within an undisturbed aquatic/terrestrial environment.	Barbour et al. 1998 Hering et al. 2004a Meier et al. 2006a
Fauna-Index	Tr, Ce	Index, based on species-specific indicator values	Indicator values range between -2 and +2. Species that occur in near-natural river sections are characterized by positive values (+1, +2) while negatively associated species (-2, -1) primarily occur in morphologically degraded river sections.	Lorenz et al. 2004 Hering et al. 2004a Meier et al. 2006a
% litoral taxa	Tr	Percentage of specimens predominantly occurring in litoral zones	Litoral taxa prefer shallow zones of freshwaters, characterized by low flow velocities and the dominance of fine substrates. A high share of litoral taxa may indicate reduced flow conditions and a low diversity in habitats.	Moog 1995 Hering et al. 2004a Meier et al. 2006a
No. Trichoptera	Tr	Number of Trichoptera taxa	Many Trichoptera taxa react sensitively towards degradation and some are highly depended on organic substrates such as fallen leaves or woody debris etc. for foraging and caddis building. High values indicate near-natural stream conditions with a high diversity in species richness and habitats.	Lorenz et al. 2004 Hering et al. 2004a Meier et al. 2006a
% metarhithral taxa	Ce	Percentage of specimens predominantly occurring in metarhithral regions	Metarhithral taxa are adapted to higher flow velocities, coarser bottom substrates, higher amounts of oxygen, and lower water temperatures. They primarily feed on allochthonous organic material. Changes in water quality and habitats may lead to a low share of metarhithral taxa.	Vannote et al. 1980 Moog 1995 Hering et al. 2004a
No. EPTCBO	Ce	Number of Ephemeroptera, Plecoptera, Trichoptera, Coleoptera, Bivalvia and Odonata taxa	Many EPTCBO taxa show high ecological demands and react sensitive towards hydromorphological and chemical degradation. A high number of EPTCBO taxa indicate a diverse macroinvertebrate assemblage under near-natural habitat conditions.	Böhmer et al. 2004 Hering et al. 2004a Meier et al. 2006a

4.4 Results

4.4.1 Substrate cluster analysis

Among all cluster methods considered, average agglomerative clustering performed best for both datasets (Table 13). Cophonetic distance was 0.83 for the Treene and 0.95 for the Célé dataset, while Gower distance was 0.19 and 0.16, respectively. Mantel statistic indicated highest values for four partitions for the Treene (0.72) and six partitions for the Célé (0.75). For the Treene, the following substrate clusters were identified: i) GR (AKAL), ii) LO (ARGY), iii) OR (CPOM, LPTP, PHYT, XYLAL), and iv) SA (PSAM, PSAM_M, FPOM, PELAL) (Table 10). Differences between substrate clusters were tested significant for species richness, Shannon diversity and Shannon evenness and the number of ecologically valuable taxa (one-way ANOVA with significance level $p \leq 0.01$, Table 14). GR clearly differed from the remaining clusters and showed the highest values for species richness (18 ± 1), Shannon diversity (8.49 ± 0.28) and the number of valuable taxa (8 ± 0). Substrate clusters for the Célé divide into i) SA (PSAM), ii) OR (CPOM, FPOM, PELAL), iii) LP (LPTP), iv) WO (XYLAL), v) ST_L (MEGA, MAKRO, MESO), and vi) ST_S (MICRO) (Table 10). With the exception of Shannon evenness ($p = 0.103$, significance level $p \leq 0.01$), statistics significantly differed between clusters. Best values for species richness (13 ± 1), Shannon diversity (8.69 ± 0.76) and Evenness (0.07 ± 0.05) were determined for cluster ST_S, while metrics for the species assemblage on sand patches (SA) performed poorly.

Table 13: Statistics for different cluster methods based on the substrate-specific macroinvertebrate dataset for the Treene and Célé model reach. The best cluster method is indicated in bold letters. The optimal number of clusters is given for the best cluster method.

	Cluster method			
	Single	Complete	Average	Ward
Treene				
Cophonetic correlation	0.71	0.65	0.83	0.66
Gower distance	0.64	1.04	0.19	5.7
Mantel statistic	.	.	0.72	.
Number of clusters	.	.	4	.
Célé				
Cophonetic correlation	0.94	0.87	0.95	0.83
Gower distance	0.56	1.28	0.16	6.9
Mantel statistic			0.75	
Number of clusters			6	

Table 14: Diversity metrics for substrate clusters. Alpha diversity is expressed as the number of species, Shannon diversity, and Shannon evenness (mean \pm SEM). The number of ecologically valuable (FI+) and poor (FI-) taxa is given in addition. Differences among substrate clusters were tested using one-way ANOVA (significance levels: *** $p < 0.001$, ** $p < 0.01$, n.s. = not significant). For abbreviations of substrate clusters see Table 10.

Substrate cluster	No of species	Shannon diversity	Shannon evenness	No of species (FI+)	No of species (FI-)
Treene					
GR	18 \pm 1	8.49 \pm 0.28	0.48 \pm 0.02	8 \pm 0	1 \pm 0
LO	7 \pm 1	3.65 \pm 0.58	0.58 \pm 0.08	3 \pm 0	0 \pm 0
OR	14 \pm 1	5.58 \pm 0.62	0.41 \pm 0.03	6 \pm 1	1 \pm 0
SA	8 \pm 1	5.27 \pm 0.55	0.72 \pm 0.03	3 \pm 0	1 \pm 0
p	0.000 ***	0.042 *	0.000 ***	0.000 ***	n.s.
F	6.1	2.6	15.1	5.9	1.7
Célé					
SA	2 \pm 0	1.41 \pm 0.22	0.88 \pm 0.07	1 \pm 0	1 \pm 0
OR	6 \pm 1	4.42 \pm 0.54	0.72 \pm 0.03	2 \pm 0	1 \pm 0
LP	11 \pm 1	7.56 \pm 0.69	0.69 \pm 0.05	5 \pm 1	2 \pm 0
WO	11 \pm 2	7.54 \pm 1.00	0.74 \pm 0.05	4 \pm 1	1 \pm 0
ST_L	11 \pm 1	6.89 \pm 0.48	0.67 \pm 0.03	3 \pm 0	1 \pm 0
ST_S	13 \pm 1	8.69 \pm 0.76	0.07 \pm 0.05	5 \pm 1	2 \pm 0
p	0.000 ***	0.000 ***	n.s.	0.000 ***	0.001 ***
F	11	11.7	1.9	5.1	5

4.4.2 Substrate simulations

Simulations yielded ‘good’ and ‘moderate’ results for the ecological assessment within the Treene model reach. Results significantly improved with an increased amount of gravel (5–10%), organic matter (25–45%) and a fine substrate cover ranging between 55–70%. ‘Moderate’ results on the other hand were attributed to the dominance of fine substrates (95–100%) with the lack of remaining substrate components. Greatest variation was found for the number of Trichoptera taxa and the percentage of litoral taxa, covering ‘very good’, ‘good’ and ‘moderate’ assessment classes. For the latter, substrate cover significantly different between assessment classes for fine substrates (55–70%, 60–75%, 95–100%) and organic matter (30–40%, 25–40%, 0–5%) (Table 15, Treene). The same trend was observed for the number of Trichoptera taxa with percentages of organic matter (30–40%, 7.5–40%, 0%), gravel (5–10%, 0–5%, 0%) and loam (5–10%, 0–5%, 0%) decreasing and fine substrates increasing (55–65%, 75–90%, 100%) along with low assessment results. Significant correlations (confidence interval = 0.95) between metrics were identified for gravel patches (GR), organic material (OR), and fine substrates (SA), whereas no association was detected for cohesive bed material (LO, Table 16). High amounts of fine substrates adversely affected core-metric performance, while an increase in organic material and gravel patches was found to exhibit a positive influence. The

abundance of species significantly increased with the amount of organic material, such as fallen leaves, deadwood or woody debris as opposed to rather low individual numbers found on fine substrates. Species richness, however, slightly increased with the amount of gravel. Among all metric groups considered, substrate alterations most strongly affected the taxonomic structure of the invertebrate assemblage in relation to the present substrate conditions (Figure 13a). Substrate simulations led to a significant increase in abundances for Odonata, Crustacea, Oligochaeta and Plecoptera. Despite significant results (two-sided one sample t-test), generally weak responses were observed for remaining metrics.

Table 15: Results for assessment metrics (core-metrics) based on substrate simulations for the Treene (n = 552) and associated percentages of substrate clusters. Results indicate the median and 75% quantile value (median/75%). Substrate proportions between assessment classes were tested using one-way ANOVA (significance levels: *** $p < 0.001$, ** $p < 0.01$, n.s. = not significant, n.a. = not applicable). For abbreviations of substrate clusters see Table 10.

Core metric	Substrate cluster (%)	Assessment quality class					F	p
		Very good	Good	Moderate	Poor	Bad		
Ecological assessment	GR	.	5/10	0/0	.	.	9.87	0.002
	LO	.	5/10	2,5/7,5	.	.	n.s.	n.s.
	OR	.	25/40	0/0	.	.	18.15	0
	SA	.	55/70	95/100	.	.	36.66	0
Fauna-Index	GR	.	5/10	.	.	.	n.a.	n.a.
	LO	.	5/10	.	.	.	n.a.	n.a.
	OR	.	25/40	.	.	.	n.a.	n.a.
	SA	.	55/70	.	.	.	n.a.	n.a.
% EPT taxa	GR	.	.	.	5/10	.	n.a.	n.a.
	LO	.	.	.	5/10	.	n.a.	n.a.
	OR	.	.	.	25/40	.	n.a.	n.a.
	SA	.	.	.	55/70	.	n.a.	n.a.
No. Trichoptera	GR	5/10	0/5	0/0	.	.	15.52	0
	LO	5/10	0/5	0/0	.	.	15.52	0
	OR	30/40	7,5/40	0/0	.	.	10.96	0
	SA	55/65	75/90	100/100	.	.	45.12	0
% litoral taxa	GR	5/10	5/10	0/5	.	.	n.s.	n.s.
	LO	5/10	5/10	0/5	.	.	n.s.	n.s.
	OR	30/40	25/40	0/5	.	.	7.1	0.001
	SA	55/70	60/75	95/100	.	.	12.92	0

Table 16: Association between metrics and substrate clusters based on model simulation runs for the Treene ($n = 552$). Only associations with $R^2 > 0.2$ are listed. Positive correlations are indicated with (+), negative correlations with (-). The strength of the correlation (R^2) corresponds to the used symbols as follows: -/+ = 0.4-0.6 R^2 , --/++ = 0.6-0.8 R^2 , ---/+++ = $> 0.8 R^2$. sd = standard deviation, Var_coeff = Variation coefficient, for abbreviations of substrate clusters see Table 10.

Metric	Median \pm sd	Var_coeff	Substrate cluster			
			GR	LO	OR	SA
Core-metrics						
% EPT	30.3 \pm 1.5	0.05			++	---
Fauna-Index	0.74 \pm 0.03	0.04	+			--
% littoral taxa	6.7 \pm 2.8	0.37			+++	---
No. Trichoptera taxa	10 \pm 1	0.08
General metrics						
Abundance (ind/m ²)	1239 \pm 1486	0.73			+++	---
No. taxa	82 \pm 8	0.1	+			
Diversity						
Evenness	0.72 \pm 0.11	0.15			---	+++
Shannon diversity	3.12 \pm 0.48	0.15	+		---	+
Feeding type						
% active filterers	16.6 \pm 5.6	0.31			---	+++
% gatherers/collectors	20.3 \pm 1.5	0.07	-		--	+++
% grazers/scrapers	9.6 \pm 2.7	0.26	+++			--
% passive filterers	11.4 \pm 4	0.35			+++	--
% predators	12.4 \pm 2.1	0.17			+++	---
% shredders	19.2 \pm 6.1	0.31			+++	---
Taxonomic group						
% Bivalvia	11.2 \pm 4.2	0.35			---	+++
% Coleoptera	3 \pm 3.2	0.71	+++			-
% Crustacea	22.9 \pm 12.1	0.55			+++	---
% Diptera	25.2 \pm 4	0.17	---			
% Ephemeroptera	11.5 \pm 2.2	0.19	-		-	+++
% Gastropoda	1.6 \pm 1	0.57	+++		-	
% Odonata	2.5 \pm 0.9	0.39			+++	---
% Oligochaeta	4.8 \pm 1.7	0.34			---	+++
% Plecoptera	2.1 \pm 1.3	0.48			++	---

Simulation runs for the Cél  model reach yielded ‘very good’ and ‘good’ results for the overall ecological assessment. Here, the substrate coverage between assessment classes differed significantly for organic matter (10–20 %, 20–30 %), living parts of terrestrial plants (5–10 %, 10–15 %), deadwood (5–10 %, 0 %), large boulders and stones (35–45 %, 30–35 %) and small stones and pebbles (25–45 %, 25 %) (Table 17, C l ). The results for the percentage of EPT and metarhithral taxa were allocated to three assessment classes, yielding ‘very good’ to ‘moderate’ and ‘good’ to ‘poor’ results, respectively. The amount of organic matter significantly increased along with low assessment results for the percentage of EPT taxa, while the cover of deadwood, large boulders and small stones simultaneously decreased. Best results for the percentage of metarhithral taxa were associated with a high coverage of large stones and boulders (ST_L) and low amounts of organic substrate components (OR, LP). Significant associations were identified for all substrate clusters, with sandy patches (SA) and deadwood (WO) exhibiting the lowest number of correlations between

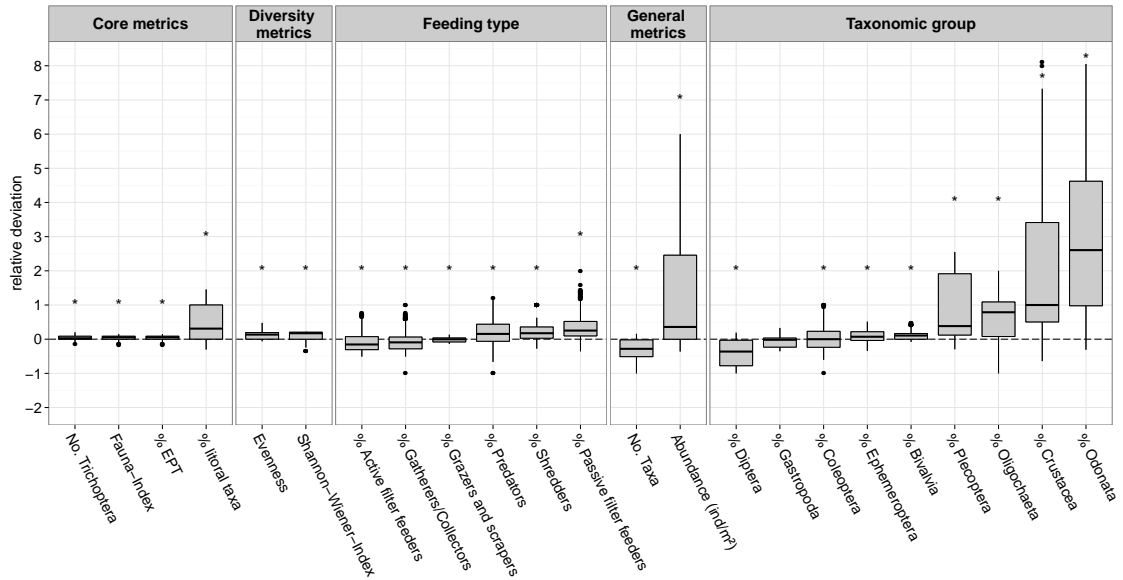
metrics (Table 18). Positive effects on assessment metrics were associated with an increase in deadwood (WO) and larger stones < 6 cm (ST_L) while deposited organic material (OR) such as fallen leaves and woody debris impaired metric results for % EPT and metarhithral taxa. No consistent effect on assessment metrics was found for living parts of terrestrial plants (LP) and small stones (ST_S). As in the case of the Treene, the strongest deviation from the present substrate distribution among all simulations was observed for taxonomic groups, especially for Coleoptera, Crustacea, Odonata and Oligochaeta, while remaining metrics mainly exhibited a weak response (Figure 13b).

Table 17: Results for assessment metrics (core-metrics) based on substrate simulations for the Célé ($n = 1710$) and associated percentage of substrate clusters. Results indicate the median and 75% quantile value (median/75%). Substrate proportions between assessment classes were tested using one-way ANOVA (significance levels: *** $p < 0.001$, ** $p < 0.01$, n.s. = not significant, n.a. = not applicable). For abbreviations of substrate clusters see Table 10.

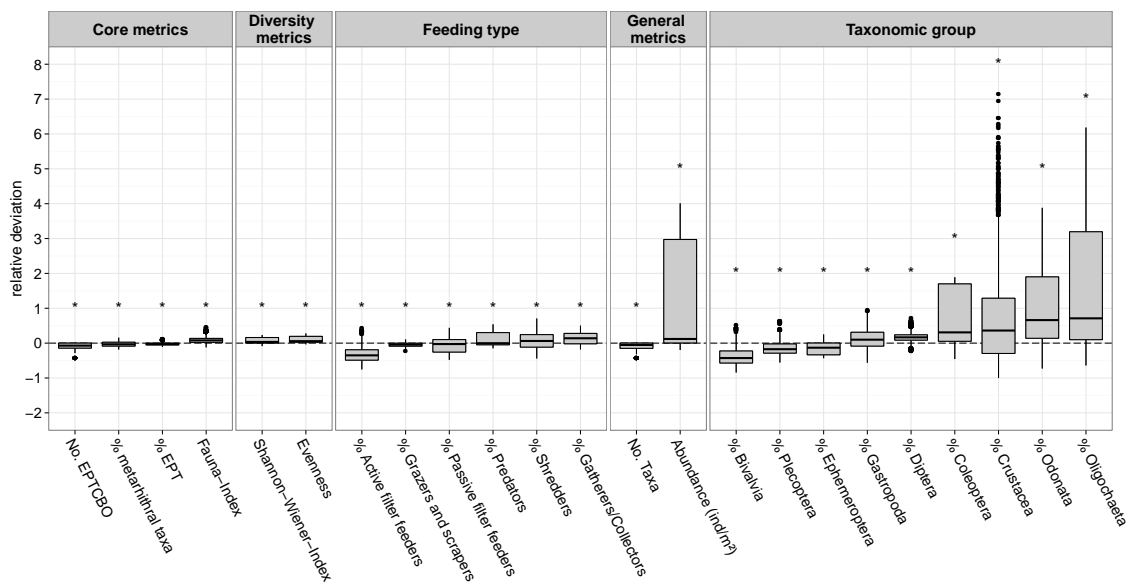
Core metric	Substrate cluster (%)	Assessment quality class					F	p
		Very good	Good	Moderate	Poor	Bad		
Ecological assessment	SA	5/10	5/10	.	.	.	n.s.	n.s.
	OR	10/20	20/30	.	.	.	141.82	0
	LP	5/10	10/15	.	.	.	117.26	0
	WO	5/10	0/0	.	.	.	144.83	0
	ST_L	35/45	30/35	.	.	.	61.92	0
	ST_S	25/45	25/25	.	.	.	14.04	0
Fauna-Index	SA	5/10	n.a.	n.a.
	OR	10/20	n.a.	n.a.
	LP	5/10	n.a.	n.a.
	WO	5/10	n.a.	n.a.
	ST_L	35/45	n.a.	n.a.
	ST_S	25/45	n.a.	n.a.
% EPT taxa	SA	5/10	5/10	5/10	.	.	n.s.	n.s.
	OR	0/0	10/20	45/50	.	.	213.09	0
	LP	5/10	5/10	0/0	.	.	11.66	0
	WO	5/10	5/10	0/0	.	.	n.s.	n.s.
	ST_L	45/55	35/45	25/25	.	.	65.15	0
	ST_S	45/45	25/25	25/25	.	.	52.06	0
No. EPTCBO	SA	5/10	n.a.	n.a.
	OR	10/20	n.a.	n.a.
	LP	5/10	n.a.	n.a.
	WO	5/10	n.a.	n.a.
	ST_L	35/45	n.a.	n.a.
	ST_S	25/45	n.a.	n.a.
% metarhithral taxa	SA	.	0/5	5/10	5/10	.	n.s.	n.s.
	OR	.	0/5	10/20	30/35	.	105.86	0
	LP	.	0/5	5/10	10/15	.	16.2	0
	WO	.	0/5	5/10	0/5	.	23.3	0
	ST_L	.	65/70	35/40	30/35	.	87.48	0
	ST_S	.	25/25	25/45	25/25	.	21.05	0

Table 18: Association between metrics and substrate clusters based on model simulation runs for the Célé (n = 1710). Only associations with $R^2 > 0.2$ are listed. Positive correlations are indicated with (+), negative correlations with (-). The strength of the correlation (R^2) corresponds to the used symbols as follows: -/+ = 0.4-0.6 R^2 , --/++ = 0.6-0.8 R^2 , ---/+++ = > 0.8 R^2 . sd = standard deviation, Var_coeff = Variation coefficient, for abbreviations of substrate clusters see Table 10.

Metric	Median \pm sd	Var_coeff	Substrate cluster					
			SA	OR	LP	WO	ST_L	ST_S
Core-metrics								
% EPT	46.8 \pm 1.8	0.04		---				+
Fauna-Index	0.8 \pm 0.08	0.09			-	+		
% metarhithral taxa	14.5 \pm 1.1	0.07		-			+++	-
No. EPTCBO	65 \pm 7	0.11			+			
General metrics								
Abundance (ind/m ²)	950 \pm 1286	0.72	--	-			++	
No. taxa	89 \pm 9	0.11			+			
Diversity								
Evenness	3.62 \pm 0.06	0.08						
Shannon diversity	3.39 \pm 0.28	0.08		+	+		--	
Feeding type								
% active filterers	4.7 \pm 1.5	0.31	++				--	+
% gatherers/collectors	26 \pm 3.7	0.14		+++			-	
% grazers/scrapers	24.9 \pm 1.5	0.06		---			+	+
% passive filterers	22 \pm 4.7	0.22		--			+++	
% predators	14.4 \pm 2.7	0.17			++		--	
% shredders	2.7 \pm 0.6	0.23					--	+++
Taxonomic group								
% Bivalvia	3.6 \pm 1.5	0.39	++				--	+
% Coleoptera	4.7 \pm 2.8	0.47				+++	-	
% Crustacea	0.1 \pm 0.2	0.84		+	++		-	
% Diptera	26.3 \pm 3.3	0.12		+++				-
% Ephemeroptera	25.6 \pm 5.4	0.21		---			+++	
% Gastropoda	2.4 \pm 0.6	0.26					+++	-
% Odonata	2.5 \pm 1.6	0.55		++	+		-	-
% Oligochaeta	0.8 \pm 0.8	0.7		+++			-	
% Plecoptera	6.1 \pm 1.5	0.24					-	+++



(a) Treene



(b) Célé

Figure 13: Relative deviation of metric groups from present substrate conditions for Treene (a) and Célé (b) model simulations. A two-sided one sample t-test (confidence interval = 0.95) was performed to test if mean values significantly differed from zero (species composition based on the substrate distribution at the time of sampling). Significant tested metrics are labeled with *.

4.5 Discussion

4.5.1 Substrate characteristics and key habitats

Sand-dominated lowland streams are characterized by low bed stability (Spänhoff et al. 2006b) and a paucity of stable substrates (Nakano and Nakamura 2008). Stable substrates such as deadwood and gravel are used as food source either directly (xylophagous species) or indirectly (feeding on associated biofilms) as well as for refuge against predators and during high flows, attachment for filter feeding, and life cycle related requirements (e.g. ovoposition, pupation, emergence) (Testa III et al. 2011). These features are closely linked to the common assumption that these habitats support a diverse macroinvertebrate community and thus act as biodiversity hot spots within a stream bed largely dominated by fine substrates (Hoffmann and Hering 2000, Benke and Wallace 2003, Muotka and Syrjänen 2007). Against this background, gravel and deadwood augmentation present commonly applied restoration techniques to improve habitat heterogeneity (Hering and Reich 1997, Sarriquet et al. 2007).

The role of such key habitats was partially confirmed for the Treene model reach. Here, the invertebrate assemblage on gravel patches varied substantially from assemblages associated to other substrate components and showed highest values by far for species richness, Shannon diversity and the number of valuable taxa. Gravel patches may thus be considered important features for sand-dominated river sections of the Treene. No distinct community, on the other hand, was identified for large woody debris. Together with other organic substrates, deadwood formed an additional cluster, likewise showing high values for diversity metrics. Despite the fact that similar colonization patterns have been observed in previous studies for different kinds of organic material (Schröder et al. 2013), we expected the macroinvertebrate assemblage on deadwood to be clearly distinguishable from other substrate components.

Lacking differences may be attributable to the design and method of sampling as well as to the woods' state of decay (Collier 2014) which is closely associated to the wood type and its duration of submergence (Lyon et al. 2009). The hardness of wood and its surface complexity greatly influences wood-associated colonization patterns, with moldy, soft surfaces usually favoring the establishment of typical xylophagous species, mostly absent in our samples. The applied sampling technique may furthermore not be adequate for deadwood, since the scraping of the surface alone does not capture wood-burrowing invertebrates which ultimately may mask

potential differences (Coe et al. 2009). Lastly, differences might be mitigated by moving sand particles sediments covering the woods surface.

Fine substrates on the other hand expectedly indicated lowest values for species diversity. This is not surprising, since they have been frequently considered unsuitable for the majority of invertebrate species providing little food resources and no refugia against drift or predators (D. C. Erman and N. A. Erman 1984, Wood and Armitage 1997, Rinella and Feminella 2005). Habitat conditions are known to become even more severe if particles are subjected to constant movement (Amstler et al. 2009, Wang et al. 2009). However, no difference in species composition was found between stable and moving sand patches in the Treene. This may be due to the constant erosion of sand particles, leading to the homogenization of the stream bed and consequently preventing the establishment of stable zones of sand for colonization of specialized species.

The low number of obtained substrate cluster in the Treene furthermore points to the dominance of ubiquitous taxa. This is in contrast to the Célé model reach, where community variation at the habitat level was much more apparent. Here, only few substrates were characterized by similar communities. Many substrates consequently formed single partitions within cluster analyses which may be attributable to an increased number of habitat specialists. Consequently, no explicit key habitat was identified, as many substrate components supported equally valuable communities. The macroinvertebrate assemblage in the Célé is largely affected by the grain size of the bed substrate. Above a certain size (< 6 cm), stones and large boulders showed similar colonization patterns (Doeg et al. 1989, Barnes and H. M. Chapman 2014) as opposed to smaller pebbles and stones (2–6 cm) (Rempel et al. 2000). The latter habitat scored highest values for species richness, Shannon diversity and Evenness. These results may be related to an increased surface area associated with optimal interstitial dimensions and porosity of the stream bed (Culp et al. 1983, Parker 1989, Gayraud and Philippe 2003). In concordance with other studies (Harrison et al. 2004, Duan et al. 2009), our results showed that large boulders and stones as well supported high species richness and densities as they are not very susceptible towards hydraulic alterations and consequently tend to be relatively stable over time.

4.5.2 Response of assessment metrics to simulated changes in substratum composition

Our results and previous studies have indicated that some habitats are demonstrably associated with a distinct fauna (J. V. Ward 1975, Jähnig and Lorenz 2008). The simple restoration of these functional habitats however has often proven to fail restoration expectations as no major local effects on the macroinvertebrates community were observed (Bernhardt et al. 2005).

In order to investigate the direct effect of reach scale microhabitat variation, we performed a simulation to approximate the single effect of substratum composition on the macroinvertebrate assemblage and ultimately on WFD assessment metrics. Overall, core-metrics and ecological status showed minor to moderate variations in assessment classes related to different substrate scenarios. Thus we conclude that substrate alterations alone do exert only minimal influence on the overall ecological assessment and core-metric performance. On the one hand, this may be considered as an indication to highlight the importance of reach scale and catchment scale pressures for the distribution of aquatic invertebrates (Feld and Hering 2007, Ormerod et al. 2010). On the other hand, our results may suggest that once community composition complies with reference stream conditions, resilience of assessment results to habitat alterations is elevated. The results for the Treene show that only drastic changes in substrate composition lead to a decline in assessment classes once community composition complies with ecological standards.

This may especially be true for lowland streams which are characterized by the dominance of ubiquitous species that tend to colonize a variety of different substrates (Schröder et al. 2013). As habitat requirements of those species are low, limited habitat availability may therefore be compensated by broad species habitat preferences whilst maintaining good results for WFD assessment metrics. In our study, the effect of key habitats becomes apparent for the Treene, since even small amounts of gravel (5–10 %) contributed to an overall improved assessment. The use of gravel for restoring lowland rivers is well documented (e.g. Albertson et al. 2011, Pedersen et al. 2014). Feld et al. (2011) however found that water managers tend to add too much gravel to the channel which poses the risk to severely alter the overall nature of a lowland stream. Similar observations have been made by Pedersen et al. (2014) who stated that the introduction of large quantities of coarser substrates may bias natural substrate composition for lowland rivers in Denmark.

Based on these findings and on our own results we suggest keeping gravel additions

minimal as positive effects might arise even under low gravel enhancement. For organic matter, the optimal amount ranged between 25 and 40%. In our study, organic material accounted for the vast number of specimens. This observation is in line with Collier and Halliday (2000) who found densities of invertebrates being much higher on woody debris compared to mineral substrates. Similar findings have been made by Benke et al. (1984) who observed species richness to be double on woody debris as opposed to assemblages living on sand and mud. However, hydromorphological processes and riparian land use need to be taken into account in order to maintain habitats and associated positive biological effects (Harrison et al. 2004).

While the consideration of few key habitats may improve results for the Treene, the maintenance of substrate diversity seems to be crucial for the Célé model reach in order to achieve high assessment results. The low coverage of different lentic habitats such as fine roots, coarse organic material and deadwood indicated a positive influence on the overall assessment. Especially the absence of deadwood adversely affected the overall assessment. This finding points to the importance of deadwood and lentic stream zones (e.g. fine roots on the river margins) in mountain streams as they provide important habitats for obligate xylophagous (e.g. *Macronynchus quadrituberculatus*) and detritus-dependent species (Benke and Wallace 2003). This finding is in line with Hering et al. (2001) who also highlighted the importance of an increased proportion in lentic stream zones under potentially natural conditions in mountain streams.

Despite strong correlations between metrics and substrate components, changes in substrate conditions were only apparent on the taxonomic level and did not translate to higher assessment levels when compared to baseline substratum composition. Here, abundances for Odonata, Crustacea, Oligochaeta and Plecoptera (Treene) and Coleoptera, Crustacea, Odonata and Oligochaeta (Célé) significantly increased, indicating that suitable habitats for these groups might be lacking in the respective study reach in its present state.

4.5.3 Methodological considerations

Our results are subjected to several methodological constraints. Despite the fact that we accounted for variation in species abundances by considering minimum and maximum abundances within model simulations, species abundances may have been reflected only insufficiently due to small replicate numbers. Replicate numbers

may as well be too low to detect differences in species composition between similar substrates (e.g. moving sand, stable sand, different organic substrates). However, we expect sampling effort to be sufficient overall, as the ecological status for measured baseline substratum composition yielded ‘good’ results for the Treene and ‘very good’ results for the Célé, respectively.

Despite meeting WFD ecological standards, the invertebrate assemblage has not been captured in its entirety and characteristic species which may have impacted assessment metrics and cluster analysis results may have been missed during sampling. Moreover, model simulations are only based on invertebrate species which already occur in the study reach and the results obtained in our analysis refer to variations in species abundances only. Our results may therefore be interpreted as the minimal expected changes in community composition and species abundances without considering colonization processes originating from outside the study reach. In other words, while the simulated loss of habitats consequently leads to the omission of species from the species pool, the model does not account for potential immigration of species from adjacent river reaches.

Of course, this assumption does not hold true in reality as freshwaters are highly dynamic systems (Moss 2010) with emi- and immigration events governing the local invertebrate structure (Brederveld et al. 2011, Baguette et al. 2013). Especially with regard to local restoration measures, the consideration of dispersal processes seems crucial. Sundermann et al. (2011) for example found that the success of restoration measures was linked to the availability of source population within a 5 km radius from the restoration site. A species dispersal originating from source populations within a catchment may thus be seen as an important process to enhance local restoration success, enabling species to (re-)colonize formerly degraded river sections. The simulation of a species dispersal has been targeted in several approaches, including various metapopulation models (Hawkes 2009) or least-cost models (Dedecker et al. 2007, Sundermann et al. 2015). The modeling of metapopulation dynamics considering dispersal events and individual behavior however remains highly complex and predictions are often fraught with uncertainties as most models are usually based on rather generalized assumptions about a species dispersal (Lek et al. 2005).

We nevertheless agree that the integration of such models would contribute to more realistically depict macroinvertebrate patterns as they have been described in our study. Within this context it is important to note that, according to our

main objectives, simulations are based on species-specific habitat preferences only. Given this simplistic simulation approach, the model does not account for inter- and intraspecific competition and neglects potential changes in the aquatic environment induced by shifts in substrate composition (Cornell and Lawton 1992).

Results for assessment metrics for the Célé model reach may furthermore be biased as we applied an assessment scheme designed for the application in German rivers and streams. The consideration of the Célé river in our opinion is nevertheless meaningful, as the fauna of large mountain rivers in Germany is usually heavily degraded and biological reference conditions are virtually nonexistent (Hering et al. 2001). Here, many sensitive species are eradicated or at best restricted to local populations. The Célé, on the contrary, harbors several formerly widespread sensitive species also present in German mountain streams, which makes it an especially valuable study object. Invertebrate composition and ultimately habitat-specific colonization patterns are subjected to seasonal variations (Leunda et al. 2009). Nevertheless we consider our results to be representative as macroinvertebrates were collected within the recommended sampling period according to WFD guidelines (Meier et al. 2006a).

In this context it is important to note that correlations need to be interpreted with regard to the underlying habitat-specific species lists used for the HET substrate simulations. The strong association of mayflies (Ephemeroptera) towards fine substrates in the Treene for example can be attributed to the dominance of *Ephemera danica*, a characteristic species for sand-dominated lowland streams which lives within fine sediments related to its burrowing habits. Thus, results cannot be transferred to other catchments or even other parts of the same catchment, as substrate-specific colonization patterns may even differ for substrates between reaches of the same stream (Heino et al. 2004).

4.6 Conclusion

In accordance with previous studies, our results showed that community composition was highly substrate-specific for both river reaches. The increase, decrease or loss of (key) substrates however influenced the overall assessment only to a limited extent. While habitat alterations lead to a minor change in assessment metrics and ecological assessment, dispersal processes may instead be regarded as the limiting factor to improve biological quality (Brederveld et al. 2011, Sundermann et al. 2011). The

identification of optimal substrate composition may however prove useful to adjust restoration designs and provides a link between potential measures and improvement in ecological status. Despite the fact that substrate proportions are significantly different between assessment classes for metrics and the overall ecological assessment, there may be no such thing as ‘the best’ substrate composition in reality. Macroinvertebrate colonization patterns are subjected to seasonal variations and substrate preferences may vary within different live stages of the same species, which makes general conclusions increasingly difficult. Against this background we strongly suggest to evaluate the importance of substrate composition separately within seasons. In general we believe that the continuous implementation of substrate-specific sampling campaigns are crucial in order to assess the effect of local habitat structure on the macroinvertebrate community more accurately.

5 Coupling Species Distribution Models and Dispersal models: the effect of source populations on the colonization potential for 10 riverine macroinvertebrates

5.1 Introduction

Aquatic invertebrates are patchily distributed within a river network (I. Petersen et al. 2004). A prerequisite for the occurrence of a species is the matching of prevailing environmental conditions and the species' ecological requirements (Wiens et al. 2010). These requirements can be described for eggs, larvae, pupae and adults and include its preferences in terms of water quality (Slooff 1983, Heino 2000, Buffagni et al. 2004), habitats (Beisel et al. 2000) and food sources (Peeters et al. 2004), the combination of which constitute a species' niche (McGill et al. 2006). Biotic interactions may further complicate distribution patterns as a species might be out-competed or eradicated by a predator even if environmental conditions are suitable (Holomuzki et al. 2010). Finally, local populations might vanish following catastrophic events (Mackay 1992, Tonkin and Death 2012, Tonkin et al. 2012) and environmental or demographic stochasticity (Wallace 1990). In many cases a species' occurrence is therefore the result of a recolonization event from other populations of the metapopulation within a catchment (Gray and Fisher 1981, Resh 1982, Hanski 1998).

In recent times, local population extinctions have got more common, as niches have strongly been altered by humans, e.g. by pollution (Cao et al. 1997), habitat degradation (Feld and Hering 2007, Larsen and Ormerod 2010) and hydrological alterations (Dunbar et al. 2010, Poff and Zimmerman 2010). At the same time, recolonization processes have been made more difficult due to an increased construction of instream-barriers (Lake et al. 2007, Parkyn and B. J. Smith 2011), modified land use within the riverine environment (Allan 2004), and persistent urbanization (Cuffney et al. 2010, Cuffney et al. 2011), all of which promote the fragmentation of local

populations. As a result, in addition to environmental conditions also metapopulation dynamics have been strongly subjected to anthropogenic alterations. Modeling a species' distribution within a catchment has therefore to consider both aspects: the matching of environmental conditions with the species' niche (Cassini 2011) and dispersal processes within the catchment (Thompson and Townsend 2006, Allouche et al. 2008).

The association between environmental parameters and a species' occurrence form the basis of recent species distribution modeling. Species Distribution Models (SDMs) have been frequently applied in fields of aquatic and terrestrial ecology (Guisan and Thuiller 2005, Elith and Leathwick 2009) and aim at linking these relationships with statistical learning algorithms in order to predict the distribution of species under current or future environmental conditions (Araújo and P. H. Williams 2000). The set of predictors varies greatly between studies but is generally restricted by the data availability for the spatial area of interest and may furthermore be driven by ecological relevance and transferability to other catchments (Gies et al. 2015). Predictor variables may reflect environmental conditions on different spatial scales including variables from fields such as hydrology, topography, bioclimate, land use and hydromorphology. Some studies incorporate single variable categories only (Jähnig et al. 2012) while others consider variable combinations of these (Domisch et al. 2011, Kuemmerlen et al. 2014) and aim to account for interactions between species (Godsoe and Harmon 2012). Beside the choice of predictors, the (predictive) performance of SDMs may be influenced by the number and spatial distribution of species presences within a catchment used as input data (Wisz et al. 2008) and the choice of model algorithm applied (Leathwick et al. 2006, Lobo et al. 2010, Kuemmerlen et al. 2014).

While SDMs provide valuable information about the availability of suitable habitats and thus potential source populations for species within a catchment, the colonization of these habitats is primarily determined by their ability to reach these habitats (Allouche et al. 2008, Cañedo-Argüelles et al. 2015). Given the dynamic nature of rivers and streams local population extinctions are common events, in particular in sections supporting only small populations. In addition, many populations have been eradicated by water pollution or habitat degradation and a recolonization is required once the conditions have improved (Sundermann et al. 2011). Against this background, dispersal is regarded one of the main processes for the (re-)colonization of habitats (Brederveld et al. 2011, Feld et al. 2011). While lateral

dispersal between watersheds has been observed for some species (I. Petersen et al. 1999, Macneale et al. 2004), most species prefer to disperse along the stream corridor or in its close proximity (I. Petersen et al. 2004, R. F. Smith et al. 2009). In general, macroinvertebrates are able to move within the aquatic and terrestrial domain by a number of different ways, including aquatic downstream drift (active, passive), active movement of larval stages (upstream, downstream), the terrestrial, aerial dispersal of imagos (Mackay 1992, Coulson et al. 2003, Tronstad et al. 2007, Bogan and Boersma 2012, Bertin et al. 2015), and the dispersal via waterbirds (Figuerola and Green 2002, van Leeuwen et al. 2012, Viana et al. 2013). Not only considering the most likely considerable intraspecific variability, the dispersal distances largely depend on the dispersal mode (aquatic dispersal vs. terrestrial dispersal) (van De Meutter et al. 2007, Grönroos et al. 2013), with aquatic and terrestrial landscape features both influencing the species-specific dispersal patterns (I. Petersen et al. 2004, Larsen and Ormerod 2010, Nihwatiwa et al. 2011, Heino 2013). Here, raster-based modeling techniques, such as the least-cost-modeling approach (Adriaensen et al. 2003, Dedecker et al. 2007, Sundermann et al. 2015) provide a helpful tool to assess the colonization potential of selected species while taking into account differences in the permeability of the aquatic and terrestrial landscape, such as in-stream barriers (Blakely et al. 2006) or different types of land use (Briers et al. 2002, I. Petersen et al. 2004).

Both the regional species pools (source populations) and species specific dispersal capacities have previously been described as important factors to influence the species composition at a sampling site and to determine restoration success (Jähnig et al. 2009, Feld et al. 2011, Sundermann et al. 2011, Tonkin et al. 2014). However, the interactions between these factors are yet poorly understood and models targeting the species' niche and its dispersal patterns have not yet been combined for benthic invertebrates. In our study we propose a methodological approach to use SDMs and dispersal models in order to determine the colonization potential for 10 macroinvertebrate species within a lowland catchment. In particular, our study aims to test how number and distribution of source populations in combination with different dispersal capacities affect the distribution of invertebrates. We examined how the estimated dispersal distances interact with the number of source populations and ultimately influence a species' colonization potential within a catchment. We furthermore discuss potential bottlenecks and methodological limitations for the applied methods and suggest improvement. For this purpose, we set up SDMs based

on predictor sets including hydromorphological and land use variables. SDMs were applied to identify potential source populations within the catchment which were used as starting points for the least-cost dispersal modeling in a subsequent step.

5.2 Material and methods

5.2.1 Catchment

The study was carried out in the catchment of the Treene, a lowland river located in the northern part of Germany (Federal state of Schleswig-Holstein) with a catchment size of 481 km². The downstream parts of the catchment are influenced by the tide and have not been considered. The catchment land use is dominated by intensive agriculture (80 %) with an increasing cultivation of energy crops (maize) while forested (8 %) and urban areas (10 %) cover the catchment to a lesser extent (Guse et al. 2014). River morphology is assessed moderate to poor for large parts of the river network according to the national standard assessment method. Predominant bottom substrates are sand and gravel, interspersed with a variable amount of organic material (Pottgiesser and Sommerhäuser 2004). Mean elevations range from 2–80 m above sea level (Guse et al. 2014).

5.2.2 Biological and environmental data

Biological data for benthic invertebrates was compiled from the state monitoring campaigns provided by the State Agency for Agriculture, Environment and Rural Areas (LLUR, Schleswig-Holstein). We considered sampling sites at which monitoring were performed in three seasons (spring, summer and autumn) to account for seasonal variation in benthic invertebrate occurrences. Overall, we compiled biological data from 77 sampling sites. Benthic invertebrates were collected using ‘Multi-Habitat-Sampling’ (Hering et al. 2004b). According to this method, a total of 20 sampling units were taken based on the relative proportion of different habitats on the river bottom using a 25 cm × 25 cm frame shovel sampler (500 µm mesh). Only habitats with a share of > 5 % habitat coverage were taken into account. All samples were pooled and preserved with 96 % ethanol in the field and subsequently processed in the lab. Benthic invertebrate data was given in abundance classes (classes 1-7) according to the national sampling protocol for benthic invertebrates (Meier et al. 2006b). The abundance data was transformed into presence/absence data for the purpose of the analysis. A taxon was described present when it was

assigned an abundance class of ≥ 2 (≥ 3 individuals).

Environmental variables (land use, hydromorphology) were calculated or extracted from existing data sources. Land use parameters were taken from the fine scale land cover survey (Landesamt für Vermessung und Geoinformation 2004) and hydro-morphological variables were recorded by the hydro-morphological assessment method for rivers and streams (Gellert et al. 2014) with the modification for Schleswig-Holstein. Several studies have shown that benthic invertebrate communities are not only impacted by local structures in the immediate surroundings of a sampling site but rather by the combined effect of upstream land cover (Sponseller et al. 2001). Against this background, buffers of variable length (500 m, 1000 m, 2500 m, 5000 m) and width (25 m, 50 m, 100 m, 250 m, 500 m) upstream of a sampling site were created using ArcView (version 3.3). The proportion (%) of different land use types within buffers was calculated afterwards in ArcGIS (version 10). Hydromorphological variables were generated accordingly, considering the on-site information as well as buffers of different length upstream of a sampling site (500 m, 1000 m, 2500 m, 5000 m). The calculated values refer to the assessment scale for hydro-morphological parameters (assessment scale values 1 = ‘very good’ to 7 = ‘bad’, Länderarbeitsgemeinschaft Wasser 2000) and are given as means for different lengths upstream of the sampling site. The distance from the source and the altitude above sea level were used as additional parameters.

5.2.3 Model species

Species distribution and dispersal models were developed for ten benthic invertebrate species. The model species can be allocated to five taxonomic groups as follows: i) Gastropoda (*Anisus vortex*), ii) Trichoptera (*Brachycentrus subnubilus*, *Lepidostoma hirtum*), iii) Ephemeroptera (*Ephemera danica*, *Heptagenia sulphurea*, *Kageronia fuscogrisea*, *Paraleptophlebia submarginata*, *Serratella ignita*), iv) Odonata (*Calopteryx splendens*), and v) Coleoptera (*Orectochilus villosus*). The selection of the model species was based on ecological criteria and methodological requirements. Beside a minimum catchment-wide prevalence of $> 10\%$ (based on presence/absence species data), most model species are characterized by high ecological demands and react sensitive towards morphological and chemical degradation, resulting in a patchy distribution within the catchment. Except for the hololimnic freshwater snail *Anisus vortex* all model species are characterized merolimnic and represent different dispersal capabilities and dispersal modes.

5.2.4 Species distribution models

Species distribution models were applied to predict the present distribution of each model species within the catchment. Predictions refer to river sections of 100 m length, determined by the spatial resolution of the hydromorphological river survey of Schleswig-Holstein. Overall, predictions were derived for 1139 river sections. We applied the Boosted Regression Tree (BRT) method (De'ath 2007, Elith et al. 2008) to set up SDMs using the DISMO package version 1.0.3 (Hijmans and Elith 2015) and additional code provided by Elith et al. (2008). BRTs are an ensemble method based on the combination of classification and regression trees. The method integrates binary decision trees to determine the best possible classification of the data into species presences and absences using environmental predictors (i.e. regression trees). Instead of using a single decision tree, BRTs combine multiple decision trees resulting in an additive model in order to improve model performance (i.e. boosting). BRTs show a number of additional advantages compared to traditional statistical modeling techniques, including the robustness towards outliers, missing data, and variable collinearity (Leathwick et al. 2006, De'ath 2007, Elith et al. 2008).

Model optimization was achieved by adjusting three parameters: i) the learning rate (lr), indicating the contribution of each single model run for the additive model, ii) the tree complexity (tc), representing the number of nodes in each decision tree, and iii) the bag fraction (bf), determining the proportion of data selected for each cross-validation iteration (Elith et al. 2008, Elith and Leathwick 2015). Only models with a minimum number of 1000 trees were taken into account (Elith et al. 2008). While a high number of predictors often positively influence the proportion of explained deviance, the ecological interpretation of the model results becomes increasingly difficult at the same time. Against this background, we applied the function *gbm.simplify* (Elith and Graham 2009) to drop insignificant variables and to gradually reduce the number of predictors. The simplification process was performed in a backwards fashion, calculating models with 8, 7, 6, 5, 4, and 3 variables for each species, respectively. The model performance was evaluated using an internal 10-fold cross validation (CV) and the explained deviance for each model run (mean total deviance – mean residual deviance / mean total deviance). Within the CV process, the original dataset is randomly divided into ten equal-sized subsamples. While a single subsample was used as a validation data set for testing the model, the remaining nine subsamples were grouped and act as a training data set. The cross-validation is calculated for ten repetitions with each of the ten subsamples

used once as validation data. The accuracy of the model is measured by the area under the Receiver Operating Characteristic (ROC) curve and takes values between 0 and 1. To ensure acceptable model results, a minimum value of 0.75 is required, while models exceeding 0.9 are considered to represent excellent model performance (Swets 1988, Elith 2000). In addition, the relative importance for each predictor variable was determined in the best model run. Based on the best set of predictor variables, a species-specific probability of occurrence (values 0–1) was calculated for each river section within the catchment. BRTs determine a species-specific cut-off value indicating a species' potential presence or absence. If the respective cut-off value is exceeded, the species is interpreted as present. The predicted presences are used as potential source populations and serve as input data for the dispersal model. All calculations were performed using the software R version 2.15.1 (R Development Core Team 2013).

5.2.5 Dispersal modeling ('least-cost' modeling approach)

We applied a raster-based modeling technique, based on the least-cost algorithm in order to estimate the dispersal for each model species within the catchment. Least-cost models are widely applied in ecology, e.g. for terrestrial vertebrates (Adriaensen et al. 2003) and invertebrates (Koch and W. D. Smith 2008), as well as for aquatic organisms (Dedecker et al. 2007, Keller and Holderegger 2013, Sondermann et al. 2015). The algorithm identifies the lowest accumulated (friction) cost between a certain raster cell and the source raster cells (here: source populations of the model species) (Adriaensen et al. 2003, Dedecker et al. 2007). Overall, the model requires information on (i) the location of source populations, (ii) the species' dispersal abilities, (iii) the location and characteristics of terrestrial and aquatic landscape features and iv) the shape of the river network.

The location of source populations was set using two different approaches: i) based on present species records according to the biological data provided by the State Agency for Agriculture, Environment and Rural Areas (LLUR), Schleswig Holstein and ii) based on (corrected) source populations as identified by the SDMs. The correction relates to those river sections, where a species was predicted absent by the SDM, but has been already recorded according to the monitoring data. The modeling was performed separately for three dispersal modes: aerial dispersal (adult stage), aquatic upstream dispersal (larval stages) and aquatic downstream dispersal (larval stages). For merolimnic species, all three dispersal modes were considered,

whereas the model calculations for the freshwater snail *Anisus vortex* refer only to aquatic upstream and aquatic downstream movement. Catastrophic drift due to flood events as well as the transport of specimens by zoochorie was not taken into account as quantitative information about these processes are largely lacking in the literature. To account for the uncertainty in addressing the dispersal abilities and to consider general dispersal patterns (Macneale et al. 2004), two dispersal scenarios were modeled for each species: a progressive scenario, assuming a high dispersal capability, and a conservative scenario, assuming a low dispersal capability. Both scenarios reflect general distribution patterns of aquatic invertebrates as most individuals of a population are known to disperse within close proximity of a source population (conservative scenario) whereas only few specimens cover long distances (progressive scenario) (Stettmer 1996). The dispersal capability is defined as the distances (in meter) that a species can disperse throughout the catchment within one life cycle. Species-specific dispersal distances for each dispersal mode and scenario were assigned based on information from literature and on expert judgment (Table 19). The model runs refer to a time period of one year which reflects the life cycle duration of most model species. Intraspecific variability of dispersal distances and consecutive modeling over a longer time period was neglected as no conclusions about the establishment of meta-populations could be drawn which might act as source populations in a further modeling step.

Table 19: Maximal dispersal distances for each model species and dispersal mode. Estimations were based on expert opinion and literature.

Taxon	Conservative scenario (Distance in m)			Progressive scenario (Distance in m)			Literature
	Upstream	Downstream	Aerial	Upstream	Downstream	Aerial	
<i>Anisus vortex</i>	500	500	-	10000	10000	-	1-3
<i>Brachycentrus subnubilus</i>	50	100	500	150	365	3000	2-7
<i>Calopteryx splendens</i>	30	50	200	30	50	4000	3,4,8-13
<i>Ephemera danica</i>	182	365	500	365	1095	3000	2,4,5,14-16
<i>Kageronia fuscogrisea</i>	292	547	750	547	2930	5000	2,4,7,17-19
<i>Heptagenia sulphurea</i>	292	547	750	547	2930	5000	2,4,7,17-19
<i>Lepidostoma hirtum</i>	100	150	750	100	3000	5000	3-5,21,23-25
<i>Orectochilus villosus</i> Lv.	182	182	500	365	365	2000	2,26
<i>Paraleptophlebia submarginata</i>	182	255	500	255	547	2000	2-4,20,27,28
<i>Serratella ignita</i>	182	255	500	255	547	3000	2-4,15,29-31

1 = Kappes and Haase 2012, 2 = Bis and Usseglio-Polatera 2004, 3 = Vieira et al. 2006, 4 = Poff et al. 2006, 5 = Ehler 2009, 6 = Bagge 1995, 7 = Vinikour 1981, 8 = Carvalho and Uieda 2006, 9 = Dorier and Vaillant 1954, 10 = L. Ward and Mill 2007, 11 = Stettmer 1996, 12 = Chaput-Bardy et al. 2008, 13 = Chaput-Bardy et al. 2010, 14 = Dedecker et al. 2007, 15 = Roos 1957 in Russev (1973), 16 = Otto and Sjöström 1986, 17 = Elliott 1971, 18 = Thiele et al. 1998, 19 = Masters et al. 2007, 20 = Verrier 1953 in Russev (1973), 21 = Schilz 2012, 22 = Hoffmann 1991, 23 = Gellert 2011, 24 = Foerster and Gellert 2012, 25 = Wallace et al. 1991, 26 = Braasch 1994, 27 = Rawer-Jost et al. 1999, 28 = Lautenschläger 2005, 29 = Madsen et al. 1973, 30 = Cimmins, personal communication in Russev (1973), 31 = Harris 1952 in Russev (1973)

Beside the location of source populations, least-cost modeling requires species-

specific defined (friction) costs for terrestrial and aquatic landscape features (friction cost maps). For each species and dispersal mode, friction costs per meter were attributed to all relevant landscape features (Annex Table I) based on a set of five values (1; 2; 5; 10; 10000) according to the classification of Sondermann et al. (2015). The highest value (10000) was attributed to non-permeable barriers, while landscape elements that may hinder, but do not block a species dispersal were assigned intermediate values (2, 5, 10). Highly permeable elements like water surfaces (e.g. the stream corridor) were assigned the lowest friction cost (1). The a priori defined dispersal distances determine the ‘friction cost budget’ for a species to disperse through its environment (e.g. a species with an aerial dispersal distance of 1000 m can fly the same distance along the stream corridor (friction cost value = 1), but only for 200 m (1000/5) through forested areas (friction cost value = 5)). Once the budget for accumulated friction costs is exceeded, the species’ dispersal is stopped (for detailed information see Sondermann et al. (2015)). The assignment of friction costs for all landscape features was estimated primarily based on expert judgment and qualitative descriptions from literature. All terrestrial and aquatic landscape elements were extracted from the physical habitat survey of Schleswig-Holstein, a record of barriers (QUIS) and a fine scale land cover survey (5 m × 5 m).

The least-cost-modeling was implemented in ArcGIS (ESRI 167 Inc., Redlands, CA, version 10), using the tools *Cost Distance* (ESRI 2011b) and *Path Distance* (ESRI 2011c). Based on a friction cost map and respective source populations as starting points, the least-cost algorithm identifies the lowest accumulated friction cost for each raster cell for each species and dispersal mode. The output of the dispersal model is a raster map (least-cost map) displaying the maximum dispersal extent of a species for each of the three considered dispersal modes (aquatic upstream, aquatic downstream and aerial) within the catchment. The least-cost-maps were subsequently converted into binary maps and combined (using the tool *Combine*, ESRI 2011a) to indicate those raster cells in the river network that can be reached by any dispersal mode (see Figure 16 A & B). Their accumulative number was used as a comparable measure of colonization potential between species. The results were given as a percentage of reachable raster cells, dividing the number of reachable raster cells by the total number of cells.

In total, six model runs for each species were performed (Table 20), resulting in a total number of 60 calculations. For each dispersal scenario (conservative, progressive), the model runs divide into an i) approach where source populations

are based on present species findings (C_find, P_find), an ii) approach based on source populations predicted by the species distribution models (C_SDM, P_SDM), and iii) an approach based on present records combining SDM model results (C_comb, P_comb). In the latter approach, the percentage of reachable river network is limited by the number of suited stretches within the dispersal radius based on present species records.

Table 20: List of dispersal scenarios applied in the Treene catchment for all model species.

Scenario	Source populations	Potential distribution	Dispersal scenario
C_find	Present findings	All streams	Conservative
P_find	Present findings	All streams	Progressive
C_SDM	Suited stretches (SDM)	All streams	Conservative
P_SDM	Suited stretches (SDM)	All streams	Progressive
C_comb	Present findings	Suited stretches (SDM)	Conservative
P_comb	Present findings	Suited stretches (SDM)	Progressive

5.3 Results

5.3.1 Species distribution models

The SDM results showed distinct differences in model performance with excellent to moderate cross validated model result (0.97 to 0.72, Table 21) and explained deviance, ranging between 97 % for *Brachycentrus subnubilus* and 45 % for *Serratella ignita*. The number of predictor variables varied between eight for *Anisus vortex* and three for *Brachycentrus subnubilus* and *Lepidostoma hirtum*. For each species, a combination of land use and hydromorphological variables was determined for the best model run, with hydromorphological variables presenting the largest share for most species (Annex Table I). The proportion of wetlands (n = 6) and urban areas (n = 5) adjacent to the sampling site were the most frequently selected land use variables for final SDM models, whereas the distance to source (n = 5) and the proportion of sand on the river bottom (n = 5) were the most relevant hydromorphological variables, respectively. The identified number of potential source populations differed considerably between species. Prevalences (number of source populations based on 100 m river sections divided by the total number of 100 m river sections in the catchment) range from 36.6 % (417 presences) for *Anisus vortex*, while *Paraleptolebia submarginata* shows the lowest prevalence with 3.6 % (41 presences, Table 22). In contrast, prevalences based on actual species records (n = 77) take values

between 26 % (20 presences) for *Orectochilus villosus* Lv. and 55 % (42 presences) for *Anisus vortex*.

Table 21: Summary of SDM model settings and results for all model species in the Treene catchment. Abbreviations: bf = bag fraction, tc = tree complexity, lr = learning rate.

Taxon	Model settings				Model results			
	bf	tc	lr	No. of trees	Total deviance	Residuals	Deviance explained (%)	ROC Score
<i>Anisus vortex</i>	0.75	3	0.0025	1850	1.197	0.248	79.28	0.862
<i>Brachycentrus subnubilus</i>	0.75	3	0.0025	2400	1.241	0.027	97.82	0.973
<i>Calopteryx splendens</i>	0.75	3	0.0025	3450	1.296	0.026	97.99	0.93
<i>Ephemera danica</i>	0.75	3	0.0025	1450	1.22	0.247	79.75	0.912
<i>Heptagenia sulphurea</i>	0.75	3	0.001	2400	0.986	0.347	64.81	0.924
<i>Kageronia fuscogrisea</i>	0.75	3	0.001	2600	0.948	0.34	64.14	0.787
<i>Lepidostoma hirtum</i>	0.75	3	0.001	1650	1.146	0.561	51.05	0.843
<i>Orectochilus villosus</i>	0.75	3	0.001	2300	1.279	0.531	58.48	0.826
<i>Paraleptophlebia submarginata</i>	0.75	3	0.0025	1400	0.772	0.203	73.7	0.826
<i>Serratella ignita</i>	0.75	3	0.001	1650	1.197	0.648	45.86	0.716

Table 22: Number and prevalence of source populations for all model species based on present findings (find), referring to a total number of 77 sampling sites, and SDM predictions (SDM) referring to a total number of 1139 100 m model reaches within the catchment. The probability threshold indicates the species-specific threshold given by the SDM (0–1). A species is described as present for a selected river reach once threshold is exceeded.

Taxon	Source populations (find)		Source populations (SDM)		
	Number	Prevalence (%)	Number	Prevalence (%)	Probability threshold
<i>Anisus vortex</i>	42	55	417	37	0.456
<i>Brachycentrus subnubilus</i>	28	36	108	9	0.484
<i>Calopteryx splendens</i>	38	49	178	16	0.488
<i>Ephemera danica</i>	33	43	89	8	0.403
<i>Heptagenia sulphurea</i>	26	34	66	6	0.433
<i>Kageronia fuscogrisea</i>	25	32	83	7	0.418
<i>Lepidostoma hirtum</i>	29	38	104	9	0.362
<i>Orectochilus villosus</i>	20	26	136	12	0.459
<i>Paraleptophlebia submarginata</i>	38	49	41	4	0.358
<i>Serratella ignita</i>	33	43	286	25	0.392

5.3.2 Dispersal modeling

Least-cost modeling revealed that the colonization potential differed clearly between species and scenarios (Table 23). However, species showed a similar response for all model runs, leading to a distinct order among scenarios (Figure 14, Figure 15). Values were lowest for a combined conservative approach based on present species records (1.2 to 2.1 %, median = 1.9 %), whereas highest values were observed for the progressive scenario and source populations based on SDMs (33.8 to 89.9 %, median = 60.5 %). Consequently, the amount of reachable river network was increasing with maximum dispersal distance and number of source populations. Standard deviation between species showed higher values for models based on SDM source populations

for both the conservative and progressive dispersal approach (sd = 7.5 to 15.5) compared to models based on species records (sd = 3.3 to 11.5).

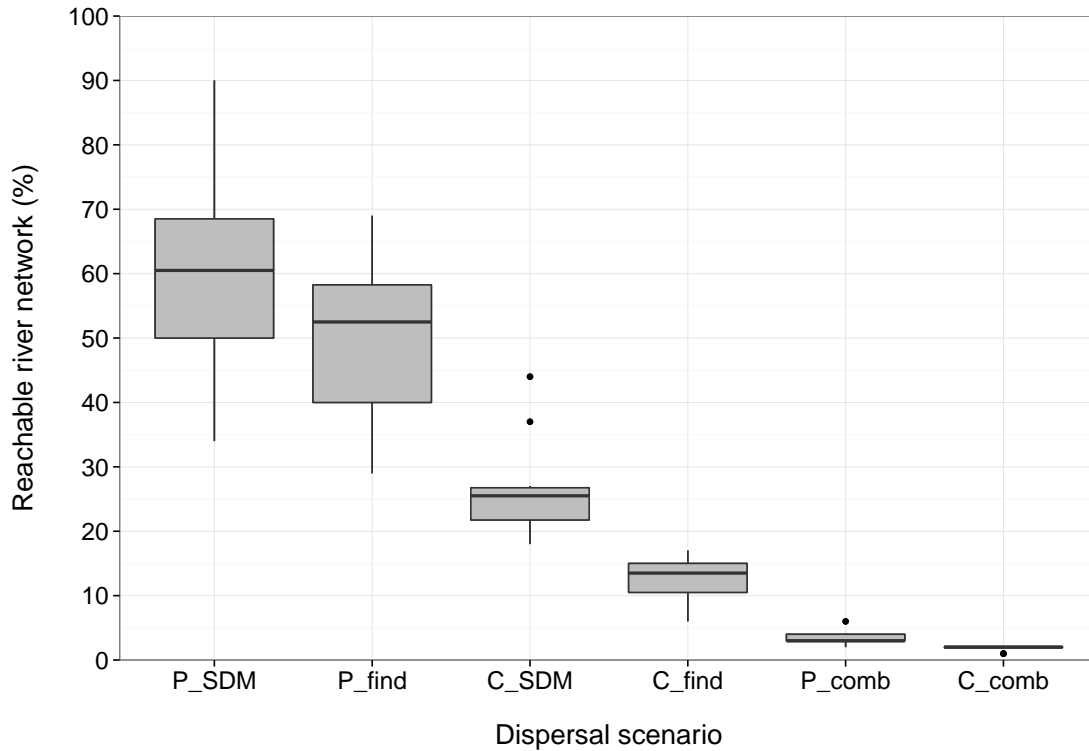


Figure 14: Percentage of reachable river network according to dispersal scenarios (Table 20) based on results for all model species.

An increase in source populations results in a higher colonization potential for both the conservative and progressive scenario. However, differences were more pronounced within the conservative scenario in which colonization potential based on SDMs was 4.1 to 34.0 percentage points higher among all model species compared to the model runs using species records as source populations. In the progressive scenario, differences were much lower with 1.1 to 20.9 percentage points. Differences across all species were tested significant for the conservative scenario (Asymptotic Wilcoxon Mann-Whitney Rank Sum Test, $P < 0.0001$, confidence interval = 0.95) while differences were not significant for the progressive approach (Asymptotic Wilcoxon Mann-Whitney Rank Sum Test, $P = 0.15$, confidence interval = 0.95).

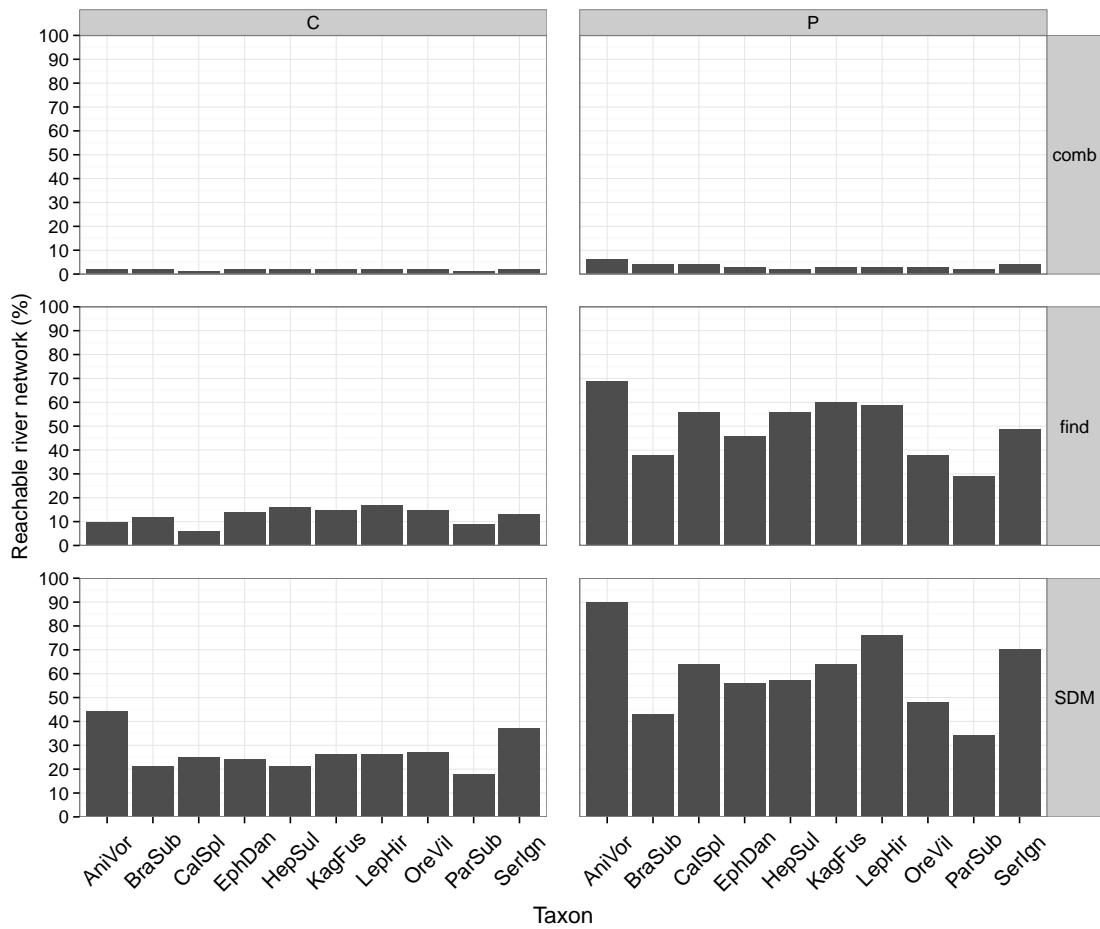


Figure 15: Results for the percentage of river network for each model species and dispersal scenario. Abbreviations: AniVor = *Anisus vortex*, BraSub = *Brachycentrus subnubilus*, CalSpl = *Calopteryx splendens*, EphDan = *Ephemera danica*, HepSul = *Heptagenia sulphurea*, KagFus = *Kageronia fuscogrisea*, LepHir = *Lepidostoma hirtum*, OreVil = *Orectochilus villosus*, ParSub = *Paraleptophlebia submarginata*, SerIgn = *Serratella ignita*. For abbreviations of dispersal scenarios see Table 20.

Table 23: Results for the percentage of reachable river network for each model species and dispersal scenario. For abbreviations of dispersal scenarios see Table 20. sd = standard deviation

Taxon	SDM		find		comb	
	P	C	P	C	P	C
<i>Anisus vortex</i>	89.9	44.1	68.9	10	1.7	6.4
<i>Brachycentrus subnubilus</i>	42.9	20.7	37.6	12.1	2	3.7
<i>Calopteryx splendens</i>	64.1	24.7	56.1	6.2	1.2	4.4
<i>Ephemera danica</i>	55.8	23.7	45.5	13.8	2.1	2.9
<i>Heptagenia sulphurea</i>	56.9	20.6	55.7	16.4	2.1	2.5
<i>Kageronia fuscogrisea</i>	64.2	26.5	59.5	15.1	1.7	3
<i>Lepidostoma hirtum</i>	75.7	26.5	58.8	17.3	2.1	2.8
<i>Orectochilus villosus</i>	48	27	38.5	15.2	2	3.2
<i>Paraleptophlebia submarginata</i>	33.8	18.4	29.5	9.2	1.2	1.8
<i>Serratella ignita</i>	69.7	37.3	49	13.1	1.8	4.3
median	60.5	25.6	52.4	13.4	1.9	3.1
sd	15.5	7.5	11.5	3.3	0.3	1.2

The ranking of the species according to their colonization potential differed significantly between dispersal scenarios and source population approaches (Table 24). The species order was only affected to a minor extent within the progressive scenario ($\pm 1-3$ ranks), with six species (*Anisus vortex*, *Brachycentrus subnubilus*, *Ephemera danica*, *Lepidostoma hirtum*, *Orectochilus villosus*, *Paraleptophlebia submarginata*) maintaining the same position in comparison. In contrast, the ranking of the species in the conservative scenario differed markedly, depending on which approach has been used to identify source populations ($\pm 1-7$ ranks).

Table 24: Ranking of model species according to the percentage of the maximum reachable amount of river sections under different scenarios. Rank deviation = Deviation of rank between the model runs based on present findings and SDM predictions. For abbreviations of dispersal scenarios see Table 20.

Taxon	C			P		
	find	SDM	Rank deviation	find	SDM	Rank deviation
<i>Anisus vortex</i>	1	8	7	1	1	0
<i>Brachycentrus subnubilus</i>	8	7	1	9	9	0
<i>Calopteryx splendens</i>	6	10	4	5	4	1
<i>Ephemera danica</i>	7	5	2	7	7	0
<i>Heptagenia sulphurea</i>	9	2	7	6	5	1
<i>Kageronia fuscogrisea</i>	4	3	1	4	3	1
<i>Lepidostoma hirtum</i>	5	1	4	2	2	0
<i>Orectochilus villosus</i>	3	4	1	8	8	0
<i>Paraleptophlebia submarginata</i>	10	9	1	10	10	0
<i>Serratella ignita</i>	2	6	4	3	6	3
Deviation rank sum			32			6

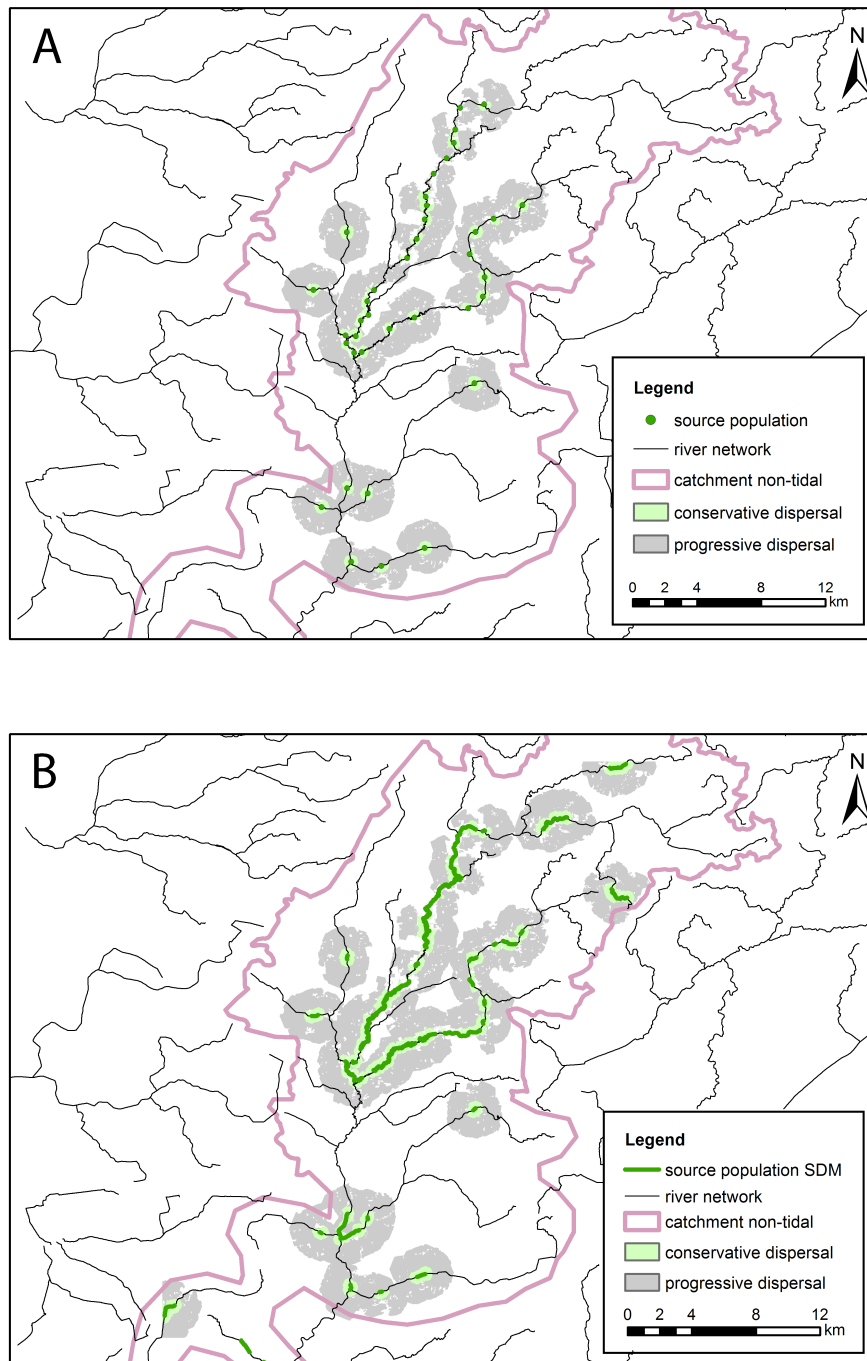


Figure 16: Example of a combined least-cost map for *Orectochilus villosus* within the Treene catchment based on source populations obtained from monitoring data (A) and SDM predictions (B).

5.4 Discussion

5.4.1 Methodological considerations

Both the identification of source populations and the subsequent dispersal modeling approach are subject to methodological limitations. In the following we would like to point out potential bottlenecks and suggest improvement.

5.4.2 Source populations based on present findings

The use of biological data compiled from state monitoring campaigns in SDMs suffers two major methodological drawbacks: i) the limited number of sampling sites and their distribution within a catchment and ii) the sampling technique applied. Regarding the first issue, species data is only patchily provided within the catchment and no conclusion can be drawn about a species presence or absence for the remaining parts of the river network. In addition, monitoring programs as implemented within the Water Framework Directive, often exclude sampling in head waters, i.e. streams of a catchment size $< 10 \text{ km}^2$. As a consequence, monitoring data of those species being naturally distributed in these river sections is largely missing and distributional patterns are thus reflected insufficiently. In our study, all model species however are predominantly distributed in the middle and lower river reaches according to their stream zonation preferences (Schmidt-Kloiber and Hering 2012, <http://www.freshwaterecology.info>). Only the mayflies *Serratella ignita*, *Paraleptophlebia submarginata* and *Ephemera danica* are known to colonize head waters to a lesser extent. Thus, potential populations located in the upper reaches and small tributaries may have been missed and source population numbers are likely underestimated. Secondly, all sampling sites are regular monitoring sites and have been sampled multiple times within the time period considered (1998 to 2010) using standard ‘Multi-Habitat-Sampling’ (MHS) (Meier et al. 2006b). It cannot, however, be concluded that a species is truly absent at a specific site. In this context, MacKenzie (2005) highlights the need to choose appropriate sampling methods to reduce the probability of reporting ‘false absences’ (i.e. a species was present at a specific site but remained undetected) that might in turn promote misleading species-environment inferences. Instead of using sampling techniques such as MHS which aim at acquiring a representative sample for a specific site, the application of a taxon-based approach considering species-specific habitat preferences may prove more suitable to correctly assess the presence or absence of a species,

respectively.

5.4.3 SDMs and source populations based on SDM predictions

Normally, SDMs are applied to identify areas of high conservation value for selected species based on presence-absence species data and environmental parameters as proxies (Elith et al. 2006, Elith and Leathwick 2009, Franklin 2010). Here, we used SDMs to identify areas within the river network that may act as potential source populations for subsequent dispersal modeling. In this context, the uneven and limited distribution of presence-absence data within the catchment may lead to SDMs being trained by data influenced by sampling bias (Kuemmerlen et al. 2014). Predictions of suitable habitat conditions may therefore be incomplete as species-environment gradients are only partially reflected in the input data (Pottier et al. 2013). In addition to the quality of presence-absence species data, predictions of potential habitats and model performance are subjected to the choice of algorithm and environmental predictors (Hernandez et al. 2006, Lütolf et al. 2006, Santika and Hutchinson 2009, Buckley et al. 2010).

Moreover, predicted suitable habitat conditions do not equate to actual species presences but rather to probabilities of such (Guisan and Thuiller 2005). We are thus aware that source population numbers are likely to be overestimated and do not reflect actual species population demographics or distributions. This effect might be, amongst other ecological factors, related to the presence of potential dispersal barriers, inter- and intraspecific competition and anthropogenic alterations within the catchment (Godsoe and Harmon 2012), all of which have not been considered in this study. However, the catchment-wide assessment of a species distribution based on SDMs provides a more suitable method to approximate potential source populations as opposed to a random determination. Analogous to our results, Kuemmerlen et al. (2014) discovered good SDM performances in the Treene catchment across different sets of environmental predictors. Optimal model results were achieved for an integrated model, including variables from various environmental fields. Even though we did not opt for an integrated model approach, the combination of land use and hydromorphological predictors reflects a variety of natural and stress variables and thus the suitability for source populations. Along with reliable model results, this assumption is supported by the fact that the distribution of species has been frequently linked to the land use in the catchment in previous studies and SDMs integrating land use parameters have proven to significantly improve model

performance (Schmalz et al. 2014).

In our study, however, model statistics significantly differed between species. While model runs for some species yielded excellent results, others performed relatively poor. These differences may be related to the diverse ecological spectrum reflected across all model species. SDM performance was assessed by applying an internal 10-fold cross validation as no independent validation dataset was available for the Treene catchment. Model performance, however, often improves using cross validation, so we generally recommend applying an external validation in addition, if possible, to correct for potential overestimation.

5.4.4 'Least-Cost' dispersal modeling

Both source population approaches were used separately as starting points for the subsequent dispersal modeling. In addition, dispersal modeling requires information about i) species-specific dispersal distances and ii) the permeability of terrestrial and aquatic landscape elements. Although dispersal of aquatic insects has been previously addressed in many studies (Bohonak and Jenkins 2003, R. F. Smith et al. 2009), empirical data on migration abilities and dispersal distances is still scarce (Kappes and Haase 2012).

Dispersal distances may be directly assessed using mark-recapture techniques (Stettmer 1996) or deduced indirectly within the scope of specific ecological research questions. For instance, Sundermann et al. (2011) found that the success of restoration measures significantly improved if source populations were located within a 5 km radius to a restoration site. They concluded that the majority of species are able to disperse within this radius, while greater distances presumably exceeded most species dispersal capacities. As opposed to this generalist approach, other studies rather focus on migration abilities of single or few species (Bergey and J. V. Ward 1989, Elliott 2003, Chaput-Bardy et al. 2010, Alexander et al. 2011). These studies usually differ fundamentally in experimental design and environmental setting, making general conclusions about dispersal capabilities increasingly difficult and comparisons between studies almost impossible. These constraints may contribute to the fact that information is rather given as rough estimates or categorical classifications of dispersal abilities for selected species or broader taxonomic units (Poff et al. 2006, Vieira et al. 2006). Contradicting information about dispersal distances may furthermore be attributed to intraspecific variation (Stettmer 1996). We attempted to address these problems by regarding two dispersal scenarios: i)

a conservative approach representative for individuals of a population dispersing within short distances of a source and ii) a progressive scenario, considering long-distances dispersers. We estimated dispersal distances based on literature and expert judgment. Dispersal distances used in our study should therefore be treated as approximate values, rather indicating general dispersal patterns as opposed to exact representations of dispersal distances.

We furthermore assume all species of a population to equally disperse within both dispersal scenarios (conservative, progressive). The diversity of species life cycles, individual life-history strategies, as well as the many factors influencing and triggering a species dispersal however stand opposed to these generalized assumptions and complicate the reliable simulation of a species dispersal within a catchment (R. F. Smith et al. 2009). Dispersal is, amongst other factors, influenced by intrinsic factors such as individual fitness, sex, body size and nutritional condition as well as by temporal synced reproductive features and mating behavior (e.g., fecundity, generation time, swarming). Dispersal is furthermore triggered and regulated by physical variations of the habitat, including changes in temperature, humidity, light intensity or wind direction and speed (Briers et al. 2002). Individual variability as well as spatial and temporal variation of physical factors and the stochasticity involved in these processes thus naturally limit the accuracy of dispersal models as proposed in our study. Despite the fact that we accounted for species-specific dispersal abilities, different landscape permeabilities and dispersal modes, our simulation nevertheless constitutes an oversimplification of a highly complex reality.

The assessment of friction costs for terrestrial and aquatic landscape features that may impede or even block the dispersal of a species constitutes another crucial step within the dispersal modeling process (Adriaensen et al. 2003, Dedecker et al. 2007). As it has been pointed out in previous studies (Dedecker et al. 2007, R. F. Smith et al. 2009, Sondermann et al. 2015), empirical data on the permeability of different landscape elements is largely lacking. However, qualitative descriptions and expert judgment may be used instead to assess potential impairing effects on species' dispersal. Sondermann et al. (2015) for example showed that the consideration of potential barriers significantly improved the overall predictions for selected species in a mountainous catchment. The authors concluded that models accounting for different landscape permeability reflect species specific dispersal patterns within a catchment more realistically.

5.4.5 Influence of source population numbers and dispersal scenarios on the colonization potential

In general, species showed a similar response for all model runs, leading to a distinct order among dispersal scenarios. The reachable river network increased with maximum dispersal distance and number of source populations. The results however indicated that the colonization potential most strongly depended on the scenario applied (conservative vs. progressive dispersal scenario) while the number of source populations affected the overall colonization potential to a lesser extent. These huge differences between scenarios point to the urgent need for fundamental research on the species and life cycle related dispersal abilities in order to describe the colonization potential of a species more accurately (Bohonak and Jenkins 2003). In particular, increased scientific efforts aiming at investigating and quantifying dispersal abilities will contribute to assess the success of restoration measures or species' vulnerability towards climate change.

As expected, the colonization potential for both the conservative and progressive dispersal scenario increased with a higher number of source populations. Our results however indicated that along with the assumption of high dispersal distances (progressive scenario), differences in reachable river sections due to a higher number of source populations become less apparent as opposed to the conservative dispersal approach. Under the progressive model approach it can therefore be assumed that most parts of the river network can already be reached based on populations documented in the state monitoring; the additional consideration of modeled source populations leads only to a slight increase in reachable river sections. For the conservative model approach, we assumed much lower maximum distances. Consequently, many parts of the river network were not reachable based on present species records. An increase in the number of source populations in the Treene catchment may therefore lead to a stronger increase of reachable river sections in general. Consequently, the creation of suitable habitat conditions which may act as potential source populations is of particular importance for species with limited dispersal capacities.

All model species were furthermore ordered according to their respective colonization potential. In general we assumed that the relative colonization potential between species remains constant within both dispersal scenarios, independently from the selected source population approach. We concluded that if ranks remain stable, no effect on the final assessment of the dispersal abilities is expected since it is only relational. However, we observed the ranking of species to significantly

change under conservative assumptions, whereas the ranking only slightly deviated within the progressive dispersal scenario. These differences may probably be related to an increased species-specific impact of instream and terrestrial barriers and the specific spatial arrangement of source populations in combination with low species dispersal capabilities (Tonkin et al. 2014).

However, dispersal might not be the limiting factor for model species in the Treene as opposed to the availability of suitable habitats. The colonization potential was largely dependent on the availability of suitable river stretches within the dispersal radius of a species. This observation was reflected in the combined dispersal approach, where we used actual species records as input for the dispersal model in combination with potential suitable habitats identified by the SDMs. Within this approach, the colonization potential was corrected for those river stretches that did not correspond to the ecological demands of the respective species and were thus assessed unsuitable for colonization. The results showed that only a fraction of the total river network may be colonized considering this limitation. This finding relates to the patchy distribution of macroinvertebrates in general but stresses the fact that information about the colonization potential of a species only proves useful when creating the preconditions for successful establishment of species.

Although the colonization potential is assessed considerably lower when assuming low dispersal capacities, the establishment of persistent meta-populations within the river network is presumably more likely under conservative model assumptions as the establishment of viable populations largely depends on the number of individuals conquering at site. This is due to the fact that the probability of a species to colonize nearby river sections is generally assessed high, as most species of a population are known disperse within a small range from their source population (Stettmer 1996). Empirical data from Brederveld et al. (2011) supported the importance of nearby source populations to increase restoration success.

Given the large number of invertebrate taxa and the unique character of river catchments, studies aiming to identify dispersal capacities of single species may only prove useful for target species. Here, the combination of dispersal maps for several target species may provide an indication for restoration management to locate potential restoration measures to increase restoration success. Moreover, further investigations relating community response to dispersal (Sundermann et al. 2011) seem promising since changes in biological quality are often associated with the change of whole species community as opposed to the occurrence of single taxa.

6 Summary, conclusion and future prospects

6.1 Summary

The distribution of macroinvertebrates in freshwaters constitutes a complex process governed by factors operating on different spatial scales. The response of macroinvertebrates towards environmental conditions is reflected on the individual level, as well as on the reach and catchment scale.

Against this background, the present thesis focused on the following three main objectives:

- (i) The characterization of *habitat preferences* to describe how macroinvertebrate species associate to changes in environmental conditions on the individual (and community) level
- (ii) The application of a reach-scale *habitat model* based on prior investigated habitat preferences to test how changes in abiotic habitat conditions are reflected on the community level
- (iii) The development and application of a *species distribution* and *dispersal model* to estimate the (re-)colonization potential for selected species within a catchment, depending on the availability of source populations and species-specific dispersal capacities

The individual components are part of an integrated modeling framework developed within the IMPACT research project (Developing an integrated model to predict abiotic habitat conditions and biota of rivers for application in climate change research and water management). The present thesis is divided into four main chapters associated to the prior delineated objectives. Background information and main results for the individual chapters are summarized in the following paragraphs.

Chapter 2: Substratum associations of benthic invertebrates in lowland and mountain streams

In the past, several compilations classified substrate preferences of species or higher taxonomic units to better understand how benthic invertebrates associate with bottom substrate composition and respond to habitat degradation. Most of these compilations, however, are based on literature analyses and expert knowledge as opposed to an analysis of original data. To support and enhance the knowledge of invertebrate substrate preferences, data on almost 1000 standardized substrate-specific samples was compiled and subjected to statistical analyses. The samples were taken from 18 streams in Germany, the Netherlands and Austria, comprising a total of 40 sampling sites and equally covering lowland and mountain streams. The main objectives were a) to derive substrate preferences of taxa in lowland and mountain streams, b) to compare obtained preferences with existing data, and c) to compare species' substrate preferences between lowland and mountain streams. For this purpose, a 'Multi-level pattern' analysis was applied, testing the strength and significance of the relationship between species and combinations of substrates or single substrate types.

The results indicated that the majority of taxa were significantly associated to a broad range of substrates while a subordinate amount was found to occur on single or very few substrate types only and thus may be described as habitat specialists. Of the 290 taxa analyzed, 'Multi-level pattern' analysis revealed significant substrate preferences for 188 taxa. Twenty-five taxa in lowland streams and 51 taxa in mountain streams prefer one or two substratum types (of nine substratum types considered in total) and may be classified as highly specialized. In contrast, 114 species (mountain streams $n = 84$, lowland streams $n = 28$) are associated with a broad range of substrates. Substrate preferences in both lowland and mountain streams were described for 25 species. The substrate preferences differed between the two stream groups for 18 species, including *Ancylus fluviatilis*, *Ephemera danica*, *Baetis vernus*, *Asellus aquaticus*, *Orthocladinae* Gen. sp., *Oulimnius tuberculatus* Ad. and *Limnius* sp. Lv. Of the 188 taxa that tested significant in 'Multi-level pattern' analysis in lowland and mountain streams, existing substrate classifications were available for 48 taxa. In general, the results support the existing classifications, with 34 taxa matching the classifications. However, classifications differed considerably for 14 species.

Chapter 3: Effects of salinity gradients on benthic invertebrate and diatom communities in a German lowland river

The estimated increase in salt pollution for freshwaters poses a severe threat to river biota. To analyze the effect of salt pollution on macroinvertebrate and diatom species, biological and chemical data were compiled from a publicly available database. The data refers to the Lippe, a German lowland river which has been heavily subjected to salt pollution in the past. Changes in the community composition due to increased salt concentrations were determined by Non-Metric Multidimensional Scaling. Indicator species and salinity thresholds for single species and communities were identified using the method TITAN (Threshold Indicator Taxa Analysis) and the results were compared to the literature and existing salinity classifications.

For both diatoms and benthic invertebrates, Non-Metric Multidimensional Scaling showed a clear split between samples of high and low salinities. Differences between samples of low and high salinity were tested significant for both groups and were considerably apparent for macroinvertebrates. Salinity thresholds varied considerably between species and were determined for 50 macroinvertebrate and 58 diatom species of which most taxa reacted sensitive to increased salinity loads. Twenty-three macroinvertebrate taxa (46%) and 18 diatom species (31%) were described as reliable indicators. Invasive species constituted the majority of salt-tolerant indicator organisms for macroinvertebrates, including the species *Corbicula fluminea*, *Potamopyrgus antipodarum*, *Dikerogammarus villosus*, *Gammarus tigrinus* and *Hypania invalida*. In addition to individual salinity thresholds, major changes in community composition for both organism groups were detected from a conductivity value exceeding 900 $\mu\text{S}/\text{cm}$. Salinity preferences for both organism groups were mostly consistent with salinity classifications obtained from literature. However, for some species, previous studies indicated deviating results.

Chapter 4: Simulating the effect of substratum composition on macroinvertebrate assessment metrics in two rivers

The biological effects of changes in composition and diversity of bottom substrates on the macroinvertebrate community have often been observed to be minor. Yet, little is known about how substrate composition needs to be changed in order to yield biological effects. Against this background, the effect of altered substrate composition on the macroinvertebrate community was investigated in two streams.

It was tested whether and to what extent changes in aquatic substrate conditions influence Water Framework Directive assessment metrics and ecological status for river reaches. For this purpose, substrate-specific macroinvertebrate samples were collected within a study reach for a German lowland river (Treene, N-Germany) and a mountain stream located in South-West France (Célé). Cluster techniques were applied to test for resembling macroinvertebrate assemblages between substrates and to identify key habitats. Subsequently, macroinvertebrate assemblages were simulated for predefined substrate compositions using a univariate model approach (Habitat Evaluation Tool, HET) which has been developed based on the results presented in Chapter 2.

Key habitats were identified for the Treene model reach: Here, the invertebrate assemblage on gravel patches varied substantially from assemblages associated to other substrate components and showed highest values by far for species richness, Shannon diversity and the number of sensitive taxa. For the Célé, no explicit key habitat was identified, as many substrate components supported equally diverse communities. Overall, substrate proportions significantly varied between different quality classes for assessment metrics. Even small amounts of gravel (5–10 %) contributed to an overall improved biological assessment in the Treene. For organic matter, the optimal amount ranged between 25 and 40 %. In comparison, the maintenance of substrate diversity seems to be crucial for the Célé model reach as a low coverage of different lentic habitats such as fine roots, coarse organic material and deadwood indicated a positive influence on the overall assessment. However, core-metrics (i.e. metrics used for assessment systems) and ecological status only showed minor to moderate variations under different substrate scenarios overall.

Chapter 5: Coupling Species Distribution Models and Dispersal models: the effect of source populations on the colonization potential for 10 riverine macroinvertebrates

Both the regional species pool and species-specific dispersal capacities have been highlighted to determine the distribution of riverine macroinvertebrates within a catchment. However, the interactions between these factors are poorly understood and models targeting the species' niche and its dispersal patterns have not yet been combined. Against this background, the study aimed to investigate, how number and distribution of source populations in combination with different dispersal capacities affect species distribution patterns. For this purpose, an approach to combine Species Distribution Models (SDMs) and dispersal models (least-cost modeling) was

developed and applied for ten macroinvertebrate species in the Treene catchment. Source populations were determined using biological monitoring data and SDM predictions derived from a predictor set of hydromorphological and land use variables and acted as starting points for the subsequent least-cost dispersal modeling. Dispersal distances for each species were defined using a progressive scenario, assuming a high dispersal capability, and a conservative scenario, assuming a low dispersal capability. In total, six dispersal scenarios based on combinations between SDMs and dispersal models were performed for each species, resulting in a total number of 60 models.

The results indicated, that the colonization potential most strongly depended on the scenario applied (conservative vs. progressive dispersal scenario) while the number of source populations affected the overall colonization potential to a lesser extent. The results however showed that along with the assumption of high dispersal distances (progressive scenario), differences in reachable river sections due to a higher number of source populations become less apparent as opposed to the conservative dispersal approach. In general, dispersal might not be the limiting factor for model species in the study catchment as the colonization potential was largely dependent on the availability of suitable river stretches within the dispersal radius of a species.

6.2 Conclusion and future prospects

The results obtained within this thesis will presumably contribute to a more comprehensive understanding about the distribution of riverine macroinvertebrates. Within the following paragraphs, main conclusions, as well as limitations and improvements of the present analyses are discussed. Furthermore suggestions for future research are made.

Chapter 2: Substratum associations of benthic invertebrates in lowland and mountain streams

Overall, the results present sound statistical evidence how macroinvertebrates associate to substrates and provide valuable results against the background of predominantly expert-based estimations. The results are particularly suitable to integrate in autecological databases like <http://www.freshwaterecology.info>, a database that is equally structured to the obtained results and describes preferences of macroinvertebrates based on a 10 point system. A deeper knowledge about the relation-

ship of macroinvertebrates to substrates may for example prove useful in restoration ecology, since the alteration of microhabitats (i.e. substrates) on the river bottom still constitutes one of the major principles in river restoration. Here, the creation of suitable habitat conditions appears to be especially important for specialized species which are highly dependent on the availability of certain substrates.

Despite the potential benefits gained from the analysis of habitat preferences in general and substrate preferences in particular, it is important to highlight potential limitations to ensure that the results obtained from the analyses are used and interpreted accordingly. Establishing a relationship between the frequency and abundance of species and a single environmental parameter naturally excludes additional factors which may influence and significantly alter species-environmental relationships. It is known that the association of macroinvertebrates towards substrates is subjected to inter- and intra-specific variability. The variation in the use of substrate types within individuals of the same species is attributed to individual fitness, inter- and intra-specific competition, different life cycle requirements and variation in other environmental conditions. This is partly reflected in the results as substrate preferences within individuals of the same species varied between river types (lowland vs. mountain streams). These differences are associated to the distinct distribution of substrates, e.g. dominance of larger stones and gravel in mountain stream while such components are rare or absent in lowland streams. It suggests that species preferences are to some extent context-dependent and that varying responses in preferences resulting from changing habitat availability are likely to be expected. In other words, the preference of a species for a particular substrate is conditional and dependent on the availability of all possible habitats to the individual species and may as well influenced by various additional intrinsic and environmental factors.

Against this background it appears to make sense to integrate additional information on the underlying data sources (e.g. personal observations, expert opinion, or empirical data) in existing autecological databases to increase the transparency of ecological information provided in respective databases. Future research should furthermore aim to describe substrate preferences on the species level as a substantial amount of information might go unnoticed in analyses of broad taxonomic resolution.

Chapter 3: Effects of salinity gradients on benthic invertebrate and diatom communities in a German lowland river

The statistical analyses indicated that salinity largely influences the distribution of macroinvertebrates in the river Lippe and may thus be regarded as overarching parameter, presumably limiting the distribution of species within the catchment. Compiling quantitative and statistically significant information about species-specific salinity thresholds and cumulative community response seems crucial in order to estimate the biological impact associated with the commonly predicted increase in salt pollution. Species-specific thresholds for example may prove useful to further delineate and describe the conservation value of single sensitive species. They provide an indication, as to whether and when species are likely to be affected by changing salinities. Especially community thresholds may prove useful for river management to link present conditions or predicted changes in salinity to community composition and thus adjust measures or prioritize areas of special conservation need. A reduction of the average salinity below the designated community thresholds may have positive effects on the overall species richness and the persistence of sensitive taxa in a catchment. The observed strong discrimination between samples of different salinity loads and the associated decrease in species richness and loss of sensitive taxa appears to be especially useful to consider in SDMs. Here, the integration of parameters such as electric conductivity might improve model performance and therefore contribute to more reliably identify areas of special conservation interest or source population of a species within a catchment.

While the observed results provide valuable information about how species might respond to changes in salinity, it is important to note that the identified thresholds may be subjected to confounding chemical and physical parameters such as water temperature, pH-value and lime content. These variables are likely to influence a species tolerance towards salinity and cause fluctuations in species and community salinity thresholds. It therefore seems advisable for future investigations to keep these interdependencies in mind in order to prevent false conclusions. It may furthermore be relevant for further research to account for potential co-varying environmental factors (e.g. catchment size, land use, additional nutrients, etc.) that may mask or confound the understanding about salinity thresholds. As the present study was conducted within a comparatively small area, the lack of consideration of these factors seems unlikely to strongly have biased the obtained results.

The consideration of co-varying factors however appears to be all the more neces-

sary for the application of such analyses in large catchments, given the most likely occurring catchment-wide variation of environmental variables. Within this context, future research efforts may for example aim at a) investigating how salinity thresholds respond across larger spatial scales to test for transferability between catchments, or b) investigating salinity thresholds for additional biological groups such as fish. The results may be used to adjust generalized assumptions of salt stress as they are given in the chemical guidelines implemented within the Water Framework directive.

Chapter 4: Simulating the effect of substratum composition on macroinvertebrate assessment metrics in two rivers

Knowledge about key habitats that may harbour a distinct number of sensitive species can be used to effectively adjust restoration measures and simulated changes in substrate composition can suggest how habitats need to be changed in order to gain biological effects. The applied analysis is, however, rather theoretical. This is due to the fact as it does not account for macroinvertebrate emigration from adjacent river reaches and excludes overarching environmental factors that may favor or mitigate a species occurrence on the local scale (e.g. nutrients). Thus, the conclusion can be drawn that diversity of benthic invertebrates is generally supported by substrate diversity, but substrate alterations alone do exert only limited influence on the overall ecological assessment and core-metric performance. Changes in composition and diversity of bottom substrates need to be supported by dispersing specimens colonizing the new habitats and the mitigation of pressures acting at larger scales.

Future research should therefore aim at linking habitat models to dispersal or metapopulation models. Furthermore, the here applied HET model presents a first approach to link macroinvertebrate species in a river reach to changes in bottom substrates and ultimately assess its effect on the biological assessment according to the WFD. Although associations between substrates and macroinvertebrates are well known and supported by statistical evidence (see Chapter 2), the model presents a rather simplistic approach given its univariate nature. It is therefore advisable to furthermore integrate parameters such as flow velocity or depth in order to increase the model performance as it has initially been tested by Kiesel et al. (2015).

Chapter 5: Coupling Species Distribution Models and Dispersal models: the effect of source populations on the colonization potential for 10 riverine macroinvertebrates

Overall, the results indicated that macroinvertebrate dispersal (least-cost modeling) and estimations about a species distribution within a catchment (Species Distribution Models) are subjected to high levels of uncertainty. Both processes are highly complex in reality and influenced by intrinsic biological and environmental factors. Against this background, it is generally agreed that models only represent simplifications of the natural environment and that they will never achieve to depict natural processes in its entirety without error.

SDMs and least-cost models, however, may be used and improved in order to *realistically* describe ecological processes. For this purpose, providing reliable input data is crucial. With respect to SDMs, model performance may improve by integrating further environmental variables in addition to the considered land use and hydromorphological variables in this study, which may include a) bioclimatic variables, b) hydrological variables, or c) water quality parameters. An external validation of SDMs is recommended to account for potential overestimation associated to internal model cross-validation. Predictions of species source populations were limited to 100 m river stretches due to the large spatial resolution of hydromorphological input variables. The spatial accuracy of predictions should be improved by increasing the spatial resolution to river network segments or grid cells of approximately 20 m.

In order to improve the reliability of dispersal models such as the least-cost modeling approach, a number of different options can be envisaged. Future research should predominantly focus on acquiring sound quantitative data on species dispersal distances, which are largely lacking to this day. This can potentially be achieved by a) an increased number in experimental field work using mark-recapture techniques, b) long-time monitoring of newly created or extensively restored river reaches, and/or by c) genetic analyses of variations in metapopulations within a river catchment. Describing the species dispersal for single taxa however seems to be of limited value. This is related to the fact that relevant measurable biological changes are rather associated to changes of whole communities as opposed to single taxa. Here, trait-based approaches using physical and life cycle related features (e.g. body size, sex, wing length/width, duration of generation cycle, duration of flight period, fecundity) may present a useful alternative for future investigations, as species exhibiting similar traits can be combined and assessed accordingly with respect to their dispersal capabilities.

7 Zusammenfassung

7.1 Hintergrund

Die Besiedlung eines Fließgewässerabschnittes durch Gewässerinsekten und weitere benthische Wirbellose – in ihrer Gesamtheit als Makrozoobenthos bezeichnet – wird von verschiedenen Belastungen auf unterschiedlichen räumlichen Skalen beeinträchtigt und durch eine Vielzahl von abiotischen und biotischen Faktoren bestimmt (Feld und Hering 2007).

Natürliche Faktoren innerhalb eines Einzugsgebietes wie Geologie, Geomorphologie und Ökoregion beeinflussen maßgeblich die jeweils charakteristische Ausprägungen von Fließgewässern und ihrer Lebensgemeinschaften. Darüber hinaus zählen punktuelle und diffuse Verschmutzungsquellen (Cao et al. 1997), Veränderungen der Gewässermorphologie und der gewässernahen Landnutzung (Larsen und Ormerod 2010), sowie hydrologische Veränderungen (Dunbar et al. 2010, Poff und Zimmerman 2010) zu den wichtigsten anthropogenen Parametern, die zur Degradation von Fließgewässern beitragen. Die Zerstörung aquatischer und terrestrischer Lebensräume und die Beeinträchtigung ihrer natürlichen Lebensgemeinschaften sind die Folge. Die Veränderung der aquatischen und terrestrischen Umwelt und die Verminderung der longitudinalen Durchgängigkeit eines Fließgewässers durch Wanderhindernisse (z.B. Wehre, Dämme) führen des Weiteren zur Fragmentierung von Populationen einer Art und erschweren (Wieder-)Besiedlungsprozesse innerhalb eines Einzugsgebietes (Cortes et al. 1998). Zusätzlich bestimmen artspezifische Habitatpräferenzen und biologische Interaktionen (z.B. intra- und interspezifische Konkurrenz) die Verbreitung von Arten innerhalb eines Fließgewässerabschnittes. Infolge der vielfältigen natürlichen und anthropogenen Einflüsse kann die Besiedlung eines Gewässerabschnittes als eine Kombination aus multiplen Faktoren verstanden werden und bildet in ihrer jeweiligen Ausprägung die Gesamtheit aus aktuellen und historischen Belastungen ab.

Um die verschiedenen relevanten Belastungsfaktoren für die Besiedlung eines Fließgewässerabschnittes zusammenzuführen und zu bewerten, wurde das Projekt IMPACT (Developing an integrated model to predict abiotic habitat conditions and

biota of rivers for application in climate change research and water management) im Jahr 2010 initialisiert. Ziel des Gesamtprojektes war die Entwicklung und Erprobung eines integrierten Modellansatzes zur Prognose abiotischer Habitatbedingungen, um u.a. limitierende Faktoren für die Besiedlung des Makrozoobenthos in einem Fließgewässerabschnitt zu identifizieren. Der Modellansatz basiert auf den Untersuchungen von Kiesel et al. (2009) und beinhaltet die Kopplung unterschiedlicher Modelle (Abbildung 17). Zur Anwendung der Modellkette wurde jeweils ein naturnaher Gewässerabschnitt (Modellabschnitt) in einem sandgeprägten Tieflandfluss (Treene, Nord-Deutschland) und einem grobmaterialreichen Mittelgebirgsfluss (Célé, Süd-West-Frankreich) ausgewählt.

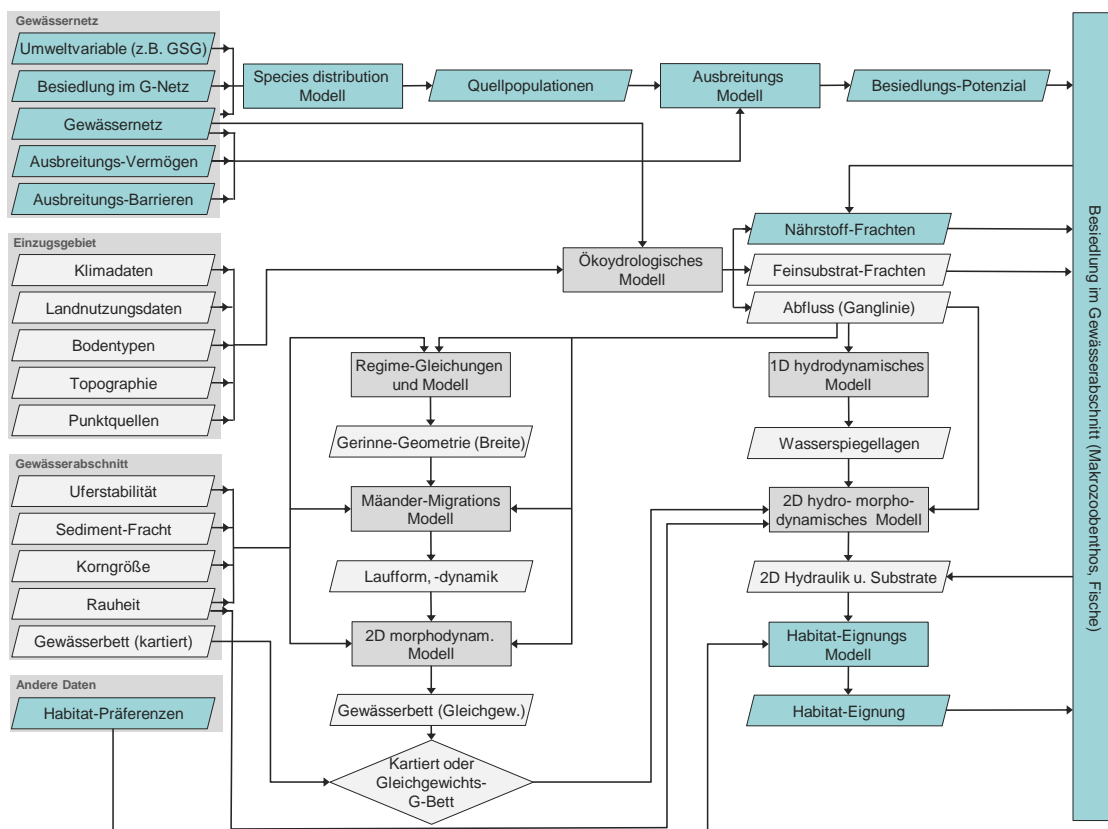


Abbildung 17: Konzeptuelle Übersicht des integrierten Modellansatzes in Anlehnung an Kail et al. (2015)

Die vorliegende Arbeit wurde im Rahmen des IMPACT-Projekts entwickelt und beschäftigt sich schwerpunktmäßig mit der Entwicklung und Anwendung von Teilkomponenten innerhalb der gesamten Modellkette (siehe blau hinterlegte Modellkomponenten, Abbildung 17). Gemäß des allgemeinen Modellierungsschemas wird die Besiedlung eines Fließgewässerabschnittes bestimmt durch a) artspezifische Anforderungen (*Habitatpräferenzen*) von Makrozoobenthos-Arten an ihren Lebensraum

(z.B. Substratverfügbarkeit, Wasserqualität), b) die Verfügbarkeit von geeigneten Habitaten im jeweiligen Gewässerabschnitt (*Habitateignung*) sowie c) von der Möglichkeit, die geeigneten Fließgewässerabschnitte ausgehend von *Quellpopulationen* im Einzugsgebiet über aquatische oder terrestrische Ausbreitungsmechanismen zu erreichen (*Besiedlungspotenzial*). Die vorliegende Arbeit widmet sich demnach der Bearbeitung der folgenden Teilaspekte:

- *Statistische Untersuchung von Habitatpräferenzen von Makrozoobenthos-Arten*
Vor dem Hintergrund vornehmlich expertenbasierter Einschätzungen zu Habitatpräferenzen von Makroinvertebraten wurden Substratpräferenzen und Salinitätspräferenzen über die statistische Auswertung empirischer Daten abgeleitet. Die allgemeine Analyse von Substratpräferenzen dient als Grundlage für die Entwicklung eines Habitateignungsmodells. Salinitätspräferenzen liefern zusätzliche Informationen die zukünftig zur genaueren Prognose des Artvorkommens im Treene-Einzugsgebiet herangezogen werden können.
- *Entwicklung und Anwendung eines Habitateignungsmodells für Makrozoobenthos-Arten*
Die Entwicklung und Anwendung eines Habitateignungsmodells basiert auf den statistischen Erkenntnissen zu Substratpräferenzen für Makrozoobenthos-Arten, die in einem ersten Schritt ermittelt wurden. Das Modell wurde angewendet, um die Abundanz und das Vorkommen von Makrozoobenthos-Arten innerhalb eines Fließgewässerabschnittes auf Grundlage abiotischer Rahmenbedingungen (Substratverteilung in einem Gewässerabschnitt) zu simulieren. Basierend auf der prognostizierten Artgemeinschaft kann abschließend eine biologische Bewertung mittels Anwendung von Standard-Bewertungsprogrammen für Makrozoobenthos-Arten vorgenommen werden.
- *Entwicklung und Anwendung eines Verbreitungs- und Ausbreitungsmodells für ausgewählte Makrozoobenthos-Arten*
Um das Vorkommen von ausgewählten Makrozoobenthos-Arten flächendeckend für ein gesamtes Einzugsgebiet zu modellieren und Quellpopulationen einer Art zu identifizieren, wurden sogenannte Species Distribution Models (SDMs) entwickelt. Das durch die SDMs prognostizierte Vorkommen der Arten wird in einem zweiten Modellierungsschritt neben tatsächlichen Fundpunkten aus biologischen Monitoringdaten als Ausgangsbasis für eine anschließende GIS-basierte Ausbreitungsmodellierung herangezogen ("Least-Cost"-Modellierung). Ziel der

Modellierung ist es, Aussagen über das Wiederbesiedlungspotenzial einzelner Arten zu formulieren und ihre Bedeutung für das jeweilige Einzugsgebiet abzuschätzen.

7.2 Methoden und Ergebnisse

Die Arbeit gliedert sich in Anlehnung an die oben genannten Teilaspekte in vier Hauptkapitel. Die jeweiligen Kapitel stellen individuelle Manuskripte dar und werden in den nachfolgenden Absätzen kurz zusammengefasst:

Kapitel 2: Analyse von Substratpräferenzen von Makrozoobenthos-Arten in Tiefland- und Mittelgebirgsflüssen

In diesem Kapitel werden Substratpräferenzen von Makroinvertebraten analysiert und klassifiziert (Substratspezialisten, Substratgeneralisten) sowie Indikatorarten für bestimmte Substrate bzw. Substratkombinationen abgeleitet. Es wird untersucht, inwiefern die Ergebnisse der statistischen Auswertung mit bestehenden, größtenteils expertenbasierten Klassifikationen von Substratpräferenzen übereinstimmen, und sich Substratpräferenzen für Individuen der gleichen Art in Mittelgebirgs- und Tieflandgewässern unterscheiden.

Um bestehende Annahmen zur Substratpräferenz von Makroinvertebraten zu validieren und zusätzliche, statistisch abgesicherte Informationen zu generieren, wurde ein Datensatz von fast 1000 substratspezifischen Makrozoobenthos-Proben erstellt. Die Daten wurden im Rahmen von Projekten und Abschlussarbeiten erhoben und umfassen Proben aus 18 Mittelgebirgs- und Tieflandgewässern aus Deutschland, den Niederlanden und Österreich. Insgesamt wurden 40 Probestellen berücksichtigt. Der Datensatz wurde mittels Anwendung einer “Multi-Level-Pattern“-Analyse ausgewertet, um die Stärke und Signifikanz des Zusammenhangs zwischen Arten und einzelnen Substraten und Substratgruppen zu testen und Indikatorarten zu identifizieren.

Gemäß der Ergebnisse zeigt der überwiegende Anteil der Arten eine signifikante Beziehung zu mehreren Substraten an, während ein geringerer Anteil als Substratspezialisten klassifiziert werden konnte und vornehmlich mit einem einzigen oder maximal zwei Substraten assoziiert war. Von 290 in der Analyse berücksichtigten Taxa wurden für 188 Taxa signifikante Substratpräferenzen nachgewiesen. In Tiefland- und Mittelgebirgsflüssen wurden 25, respektive 51 Taxa als Substratspe-

zialisten klassifiziert. Im Gegensatz dazu zeigen 114 Arten (Mittelgebirgsflüsse = 84 Taxa, Tieflandflüsse = 28 Taxa) signifikante Beziehungen zu einer Vielzahl von Substraten. Für 25 Taxa konnten Substratpräferenzen sowohl in Mittelgebirgs- und Tieflandgewässern beschrieben werden. Im Vergleich beider Gewässertypen zeigten 18 Arten unterschiedliche Substratpräferenzen (z.B. *Ancylus fluviatilis*, *Ephemera danica*, *Baetis vernus*, *Asellus aquaticus*, *Orthocladinae* Gen. sp., *Oulimnius tuberculatus* Ad. und *Limnius* sp. Lv). Die abgeleiteten Substratpräferenzen wurden für 48 Taxa bestehenden Angaben aus Literatur und autökologischen Datenbanken gegenübergestellt. Der Vergleich zeigt übereinstimmende Präferenzen für insgesamt 34 Arten, während für 14 Arten Substratpräferenzen deutlich voneinander abweichen.

Kapitel 3: Analyse von Salinitätspräferenzen für Makrozoobenthos- und Diatomeen-Arten entlang eines Salz-Gradienten in einem deutschen Tieflandfluss

In einem weiteren Kapitel werden Salztoleranzen für Makrozoobenthos- und Diatomeen-Arten untersucht und Schwellenwerte für einzelne Arten und Artgemeinschaften ermittelt. Salztolerante und salzsensitive Arten werden identifiziert (Indikatorarten) und ihre Reaktionen mit bestehenden Salinitätspräferenzen aus der Literatur abgeglichen.

Zur Untersuchung von Salinitätspräferenzen für Makrozoobenthos- und Diatomeen-Arten wurden biologische und chemische Daten aus dem Mittellauf der Lippe aus einer öffentlich zugänglichen Datenbank zusammengestellt. Die Lippe zählt zu den durch salzhaltige Grubenwässer stark beeinträchtigten deutschen Tieflandgewässern und zeigt in ihrem Verlauf deutliche Änderungen des Salzgehaltes an. Veränderungen der Lebensgemeinschaften entlang des Salinitäts-Gradienten wurden mit Hilfe einer Non-Metric Multidimensional Scaling (NMDS) untersucht. Indikatorarten und Salinitäts-Grenzwerte für einzelne Arten und Artgemeinschaften wurden mittels der TITAN-Methode (Threshold Indicator Taxa Analysis) identifiziert.

Das Ergebnis der NMDS zeigte sowohl für Makrozoobenthos- als auch für Diatomeen-Gemeinschaften eine signifikante Trennung zwischen Proben hoher und niedriger Salinität an. Die Unterschiede waren besonders deutlich für Makrozoobenthos-Gemeinschaften. Salinitäts-Grenzwerte unterscheiden sich deutlich zwischen Arten und konnten für insgesamt 50 Makrozoobenthos- und 58 Diatomeen-Arten identifiziert werden. Der überwiegende Anteil der Arten reagierte sensitiv gegenüber einem Anstieg der Salinität. Insgesamt konnten 23 Makrozoobenthos-Arten (46 %) und 18 Diatomeen-Arten (36 %) als verlässliche Indikatoren herausgestellt werden. Invasi-

ve Arten stellten den Großteil an salztoleranten Indikatorarten dar (z.B. *Corbicula fluminea*, *Potamopyrgus antipodarum*, *Dikerogammarus villosus*, *Gammarus tigrinus* und *Hypania invalida*). Deutliche Unterschiede in der Artzusammensetzung konnten sowohl für das Makrozoobenthos als auch für Diatomeen-Gemeinschaften ab einem Leitfähigkeitswert von 900 $\mu\text{S}/\text{cm}$ festgestellt werden. Die abgeleiteten Salinitätspräferenzen stimmen weitestgehend mit bestehenden Klassifikationen überein.

Kapitel 4: Auswirkungen simulierter Substratverteilungen auf Bewertungs-Metricen für Makroinvertebraten und ökologischen Status in zwei Gewässerabschnitten

Änderungen von Substratheterogenität und Substratverfügbarkeit zeigen meist keinen oder nur einen geringen Effekt auf die Makrozoobenthos-Gemeinschaft in einem Fließgewässerabschnitt. Es ist jedoch nur wenig darüber bekannt, inwieweit die Zusammensetzung bodenbedeckender Substrate in einem Fließgewässerabschnitt geändert werden muss, um potentielle biologische Effekte zu erzielen. Ziel war es daher, zu untersuchen, ob und inwiefern Veränderungen der Substratverfügbarkeit innerhalb eines Gewässerabschnitts Bewertungs-Metricen und den allgemeinen ökologischen Zustand (wie er im Rahmen des biologischen Monitoring der Wasserrahmenrichtlinie erhoben wird) beeinflussen.

Zu diesem Zweck wurden insgesamt 160 substratspezifische Makrozoobenthos-Proben in zwei Modellabschnitten für einen deutschen Tieflandfluss (Treene) und einen Mittelgebirgsfluss in Süd-West-Frankreich (Célé) erhoben. In einem ersten Schritt wurden Clusteranalysen durchgeführt um ähnlich besiedelte Substrate zu identifizieren. Substrat-Cluster wurden im Anschluss hinsichtlich ihrer Lebensgemeinschaften ökologisch charakterisiert, um u.a. ökologisch bedeutsame Schlüsselhabitate in den jeweiligen Fließgewässerabschnitten herauszustellen. Im Anschluss wurde die Makrozoobenthos-Gemeinschaft innerhalb des jeweiligen Fließgewässerabschnittes unter Annahme unterschiedlicher Substratverteilungen mit Hilfe eines univariaten Habitateignungsmodells simuliert.

Unterschiedliche Substratkompositionen zeigten insgesamt einen geringen bis moderaten Einfluss auf Bewertungs-Metricen und den allgemeinen ökologischen Zustand für beide Fließgewässerabschnitte. Im Fließgewässerabschnitt der Treene konnte Kies als Schlüsselhabitat herausgestellt werden. Die Lebensgemeinschaft auf Kies unterscheidet sich grundlegend von übrigen Substratkomponenten und zeigte höchste Werte für Artenreichtum, Shannon-Diversität und Anzahl sensitiver Taxa. Für den Fließgewässerabschnitt des Célé zeigten Clusteranalysen nur wenige Substrate mit

ähnlicher Besiedlung an. Charakteristische Schlüsselhabitats fehlen und viele Substrate beherbergen gleichwertig wertvolle Artgemeinschaften. In der Treene war ein optimales Bewertungsergebnis mit geringen Anteilen von Kies (5–10 %) und einem gleichzeitig hohem Anteil organischer Substrate assoziiert. Im Vergleich dazu scheint die Erhaltung der Substratdiversität entscheidend für den Célé-Modellabschnitt zu sein, da selbst geringe Anteile lenitischer Habitats wie uferständige Feinwurzeln, grob partikuläres organisches Material und Totholz einen positiven Effekt auf das allgemeine Bewertungsergebnis ausüben.

Kapitel 5: Kopplung von Verbreitungs- und Ausbreitungsmodellen in einem Tiefland-Einzugsgebiet: Einfluss von Quellpopulationen auf das Wiederbesiedlungspotenzial für 10 Makrozoobenthos-Arten

Sowohl der regionale Artenpool (Quellpopulationen) als auch das artspezifische Ausbreitungsvermögen bestimmen die Verbreitung einer Art im Einzugsgebiet. Um zu untersuchen, wie Anzahl von Quellpopulationen und Ausbreitungsvermögen das Wiederbesiedlungspotenzial einer Art im Einzugsgebiet beeinflussen können, wurden Verbreitungsmodelle (SDMs) und Ausbreitungsmodelle („Least-Cost“-Modelle) im Treene-Einzugsgebiet gekoppelt.

Das Wiederbesiedlungspotenzial für eine Art wurde definiert über die Fließgewässerstrecke im Einzugsgebiet, die über die Kombination von drei Ausbreitungswegen (aquatisch aktiv, aquatisch passiv, Flugverbreitung) erreicht werden kann. Das prognostizierte Artvorkommen durch SDMs auf Basis von hydromorphologischen Parametern und Landnutzungsvariablen sowie tatsächliche Fundpunkte aus biologischen Monitoringdaten dienen hierbei als Quellpopulationen und fungieren als Startpunkte für eine anschließende Ausbreitungsmodellierung. Insgesamt wurden für jede Art zwei Szenarien modelliert: ein progressives Modell unter Annahme einer maximal möglichen Ausbreitungsdistanz und ein konservatives Modell mit einer geringeren Ausbreitungsdistanz. Insgesamt wurden basierend auf Kombinationen von SDMs und unterschiedlichen Ausbreitungsdistanzen pro Art sechs Szenarien modelliert (60 Modellläufe insgesamt).

Der Anteil der erreichbaren Fließgewässerstrecke nimmt erwartungsgemäß mit der maximalen Distanz für eine Art und mit der Anzahl der Quellpopulationen zu. Die erreichbare Fließgewässerstrecke zeigt die niedrigsten Werte für das konservative Szenario basierend auf aktuellen Funden und erreicht Maximalwerte unter progressiven Annahmen für Quellpopulationen aus den SDMs. Es wird dabei auch deutlich, dass

weniger die Berücksichtigung weiterer Quellpopulationen für die Maximierung des Wiederbesiedlungspotenzials relevant ist, sondern dass sich die Unterschiede in der erreichbaren Fließgewässerstrecke vornehmlich aus den unterschiedlichen Annahmen für die Maximaldistanzen der Arten ergeben. Mit der Annahme höherer Maximaldistanzen (progressives Szenario) wird deutlich, dass sich die Unterschiede in der erreichbaren Fließgewässerstrecke bedingt durch eine höhere Anzahl von Quellpopulationen zunehmend aufheben. Unter konservativen Annahmen treten diese Unterschiede hingegen deutlicher hervor. Generell ist davon auszugehen, dass die Arten im progressiven Szenario bereits auf Grundlage des aktuellen Vorkommens den größten Teil des Fließgewässernetzes abdecken. Eine zusätzliche Berücksichtigung weiterer Quellpopulationen führt unter diesen Bedingungen nur zu einer geringen Erhöhung der erreichbaren Fließgewässerstrecke. Im konservativen Szenario hingegen werden deutlich geringere Maximaldistanzen zurückgelegt, ein Großteil der Fließgewässerstrecke liegt demnach außerhalb der Besiedlungsreichweite. Die Berücksichtigung weiterer Quellpopulationen kann daher zu einer stärkeren Erhöhung der erreichbaren Fließgewässerstrecke beitragen. Insgesamt scheint die Ausbreitung für die untersuchten Modellarten in der Treene jedoch nicht der limitierende Faktor zu sein, da das Wiederbesiedlungspotenzial vor allem von der Verfügbarkeit geeigneter Habitats innerhalb der erreichbaren Fließgewässerabschnitte anhängig ist.

7.3 Schlussfolgerungen und Ausblick

Die im Rahmen dieser Arbeit erzielten Ergebnisse tragen zu einem besseren Verständnis der Verbreitung von Makroinvertebraten in Fließgewässern bei. In den folgenden Paragraphen werden für die unterschiedlichen Kapitel der Arbeit die wichtigsten Schlussfolgerungen zusammengefasst, Einschränkungen aufgezeigt und Verbesserungen diskutiert. Darüber hinaus werden Vorschläge für zukünftige Forschungsvorhaben formuliert.

Kapitel 2: Analyse von Substratpräferenzen von Makrozoobenthos-Arten in Tiefland und Mittelgebirgsflüssen

Die Analyse substratspezifischer Abundanzdaten aus Tiefland und Mittelgebirge liefert umfassende, statistisch abgesicherte Ergebnisse zur Substratpräferenz aquatischer Makroinvertebraten in Fließgewässern. Die generierten Substratpräferenzen können in autökologische Datenbanken für aquatische Organismen (z. B. [http:](http://)

//www.freshwaterecology.info) implementiert werden, sofern diese – analog zu den vorliegenden Ergebnissen – Substratpräferenzen von Makroninvertebraten basierend auf einem 10-Punkte-System beschreiben. Besonders in der Renaturierungsökologie ist ein vertieftes Wissen zu Substratpräferenzen von Makroinvertebraten von Nutzen, da die flussabschnittsbasierte Umgestaltung und Schaffung von Mikrohabitaten (= Substraten) nach wie vor das grundlegende Prinzip von Renaturierungsmaßnahmen darstellt. Insbesondere für Arten, deren Vorkommen an die Verfügbarkeit bestimmter Substrate gekoppelt ist, sind Informationen zur Substratpräferenz besonders wertvoll.

Um eine adäquate Nutzung und Interpretation der Ergebnisse zu gewährleisten, ist es jedoch wichtig, auf mögliche Einschränkungen, die mit der angewandten Auswertungsmethode verbunden sind, hinzuweisen. Die Untersuchung des statistischen Zusammenhangs zwischen der Häufigkeit und Abundanz einer Art und einem einzigen Umweltparameter schließt die Berücksichtigung weiterer Umweltfaktoren naturgemäß aus. Die Assoziation einer Art mit einem Substrat oder einer Gruppe von Substraten unterliegt zudem intra- und interspezifischen Einflussfaktoren. Die individuelle physische Konstitution (z.B. Ernährungszustand), intra- und interspezifische Konkurrenz, lebenszyklusabhängige Anforderungen einer Art an ihre Umwelt, als auch die Substratverfügbarkeit in den untersuchten Gewässern können substratspezifische Besiedlungsmuster und demzufolge auch die Substratpräferenz einer Art beeinflussen. Diese Beobachtung spiegelt sich u.a. in den vorliegenden Ergebnissen wider, da Substratpräferenzen von Individuen einer Art zwischen Mittelgebirgs- und Tieflandflüssen teilweise deutlich differieren. Diese Unterschiede sind mit der grundlegend verschiedenen Substratverfügbarkeit in den jeweiligen Gewässern zu erklären (grobmaterialreiche Mittelgebirgsflüsse im Vergleich zu feinsedimentreichen Tieflandflüssen mit hohen Anteilen organischer Substrate). Substratpräferenzen von Individuen einer Art sind demnach zu einem bestimmten Grad kontextabhängig und werden von intrinsischen Faktoren und zusätzlichen Umweltparametern beeinflusst.

Generalisierte Annahmen, die mit der Ableitung artspezifischer Präferenzen einhergehen, sollten daher stets mit Blick auf die zugrundeliegende Datenbasis interpretiert werden. Vor diesem Hintergrund erscheint es sinnvoll, zusätzliche Informationen hinsichtlich der Herkunft und Art der verwendeten Daten (z.B. persönliche Beobachtungen, Expertenmeinungen, empirische Daten) in autökologischen Datenbanken zu vermerken. Zudem ist es ratsam, zukünftige Untersuchungen von Substratpräferenzen auf Artniveau durchzuführen, da Substratpräferenzen häufig artspezifisch

sind. Diese zwischenartliche Variabilität kann durch Auswertungen von Daten höherer taxonomischer Auflösung nicht erfasst werden.

Kapitel 3: Analyse von Salinitätspräferenzen für Makrozoobenthos- und Diatomeen-Arten entlang eines Salz-Gradienten in einem deutschen Tieflandfluss

Die Ergebnisse zeigen, dass der Salzgehalt eines Gewässers die Zusammensetzung von Makrozoobenthos- und Diatomeen-Artgemeinschaften deutlich beeinflussen kann. Informationen zu artspezifischen Salinitätspräferenzen und Grenzwerten sind besonders vor dem Hintergrund der zunehmenden anthropogenen Salzbelastung von Gewässern hilfreich.

Artspezifische Grenzwerte können dazu dienen, die Gefährdung einzelner Arten und ihre Schutzwürdigkeit besser zu bewerten. Insbesondere Grenzwerte für Artgemeinschaften liefern wichtige Informationen, um aktuelle oder zukünftige Belastungen auch auf Gemeinschaftsebene abzuschätzen, Gegenmaßnahmen umzusetzen und Gebiete erhöhter Schutzwürdigkeit zu definieren. Eine Reduktion der durchschnittlichen Leitfähigkeitswerte unter die ermittelten Artgemeinschafts-Grenzwerte kann positive Effekte auf den Artenreichtum und das Auftreten sensibler Taxa im Untersuchungsgebiet nach sich ziehen. Aufgrund der deutlichen Trennung von Artgemeinschaften basierend auf Proben hoher und niedriger Salzgehalte und der damit einhergehenden Beeinträchtigung vieler sensibler Arten erscheint es sinnvoll, Salinitätsparameter in Verbreitungsmodellen (SDMs) für Makroinvertebraten zu integrieren. Die Berücksichtigung von Parametern wie z.B. elektrischer Leitfähigkeit könnte die Vorhersagekraft von Modellen verbessern und dazu beitragen, Gebiete erhöhter Schutzwürdigkeit oder Quellpopulationen einer Art präziser zu identifizieren.

Die ermittelten Grenzwerte stellen jedoch keine fixen Werte dar und können durch Parameter wie Wassertemperatur, pH-Wert und Kalkgehalt beeinflusst werden. Weiterhin erscheint es sinnvoll, mit dem Salzgehalt potentiell korrelierende Umweltfaktoren (z.B. Größe des Einzugsgebietes, Landnutzung, Nährstoffe) in zukünftigen Auswertungen zu berücksichtigen. Dies erscheint besonders wichtig in großen Einzugsgebieten, die oftmals eine hohe Variabilität hinsichtlich verschiedener Umweltfaktoren aufweisen. Vor diesem Hintergrund wäre es sinnvoll, zukünftig zu untersuchen, wie sich Salinitätsgrenzwerte auf größeren räumlichen Skalen verhalten, und ob sich Grenzwerte auf andere Einzugsgebiete übertragen lassen können. Die Ermittlung von Grenzwerten für weitere biotische Komponenten (z.B. Fische) kann zudem

dazu beitragen, generalisierte Angaben zu Orientierungswerten von Salzgehalten in Fließgewässern zu überprüfen und anzupassen.

Kapitel 4: Auswirkungen simulierter Substratverteilungen auf Bewertungs-Metricen für Makroinvertebraten und ökologischen Status in zwei Gewässerabschnitten

Informationen zu Schlüsselhabitaten und Erkenntnisse zum Einfluss simulierter Substratzusammensetzungen auf Bewertungs-Metricen innerhalb eines Gewässerabschnittes können zu einer verbesserten Durchführung von Renaturierungsmaßnahmen in Fließgewässern beitragen. Die Ergebnisse zeigen, dass die Substratverfügbarkeit in einem Gewässerabschnitt die Zusammensetzung von Makrozoobenthos-Artgemeinschaften beeinflusst, Substratveränderungen allein jedoch nur begrenzt zu einer Änderung bewertungsrelevanter Metricen beitragen. Die Einwanderung von Organismen aus angrenzenden Gewässerabschnitten und der Einfluss großräumiger Umweltparameter (z.B. Landnutzung, Nährstoffe) muss zwingend für eine umfassende Abschätzung zur Besiedlung eines Gewässerabschnittes berücksichtigt werden.

Zukünftige Studien sollten daher darauf ausgerichtet sein, Habitateignungsmodelle mit Ausbreitungsmodellen zu kombinieren. Das im Rahmen der Studie verwendete Modell ist zudem lediglich ein erster Versuch, Änderungen der Artgemeinschaft auf Basis veränderter abiotischer Habitatbedingungen mit Bewertungs-Metricen zu koppeln und verfügt in seiner jetzigen Version nur über eine univariate Anwendungsmöglichkeit (Substrate). Obschon Beziehungen von Makroinvertebraten und Substraten bereits vielfach untersucht wurden und für viele Arten eine statistisch signifikante Beziehung zu bestimmten Substraten nachgewiesen werden konnte (siehe Kapitel 2), stellt das Modell lediglich einen stark simplifizierten Modellierungsansatz dar. Die Integration weiterer Parameter (z. B. Fließgeschwindigkeit und Tiefe) ist für zukünftige Untersuchungen sinnvoll.

Kapitel 5: Kopplung von Verbreitungs- und Ausbreitungsmodellen in einem Tiefland-Einzugsgebiet: Einfluss von Quellpopulationen auf das Wiederbesiedlungspotenzial für 10 Makrozoobenthos-Arten

Die Ergebnisse zeigen, dass sowohl die Vorhersage des Vorkommens von Arten mit Hilfe von SDMs als auch die Ausbreitungsmodellierung und das damit verbundene Wiederbesiedlungspotenzial einer Art im Einzugsgebiet mit hohen Unsicherheiten verbunden sind. Beide Modellansätze können die realen Begebenheiten nicht in ihrer Vollständigkeit abbilden und stellen daher nur grobe Vereinfachungen natürlicher,

in Realität hochkomplexer Prozesse dar. Zukünftige Verbesserungen von SDMs und “Least-Cost”-Modellen können jedoch dazu beitragen, die Güte der Modelle zu verbessern.

Vor diesem Hintergrund ist die Akquise geeigneter, hochauflösender Daten von großer Bedeutung. Beispielsweise könnte die zusätzliche Berücksichtigung physikalisch-chemischer Parameter sowie bioklimatischer und hydrologischer Variablen zu den hier verwendeten hydromorphologischen Variablen und Landnutzungsparametern die Vorsagefähigkeit der SDMs verbessern. Bedingt durch die Verwendung hydromorphologischer Variablen bezieht sich die Prognose für das Vorkommen einer Art auf eine Gewässerabschnittslänge von 100 m. In diesem Zusammenhang ist es sinnvoll, die Prognose für eine räumlich präzisere Darstellung auf eine Abschnittslänge oder Rasterzellenkantenlänge von 20–50 m zu skalieren.

Eine Verbesserung von Ausbreitungsmodellen (“Least-Cost”-Modelle) für Makroinvertebraten ist in vielerlei Hinsicht denkbar. Zukünftige Forschungsvorhaben sollten schwerpunktmäßig darauf ausgerichtet sein, derzeit nur begrenzt verfügbare quantitative Daten zu Ausbreitungsdistanzen von Makroinvertebraten entlang von Fließgewässern zu ermitteln. Denkbar wäre in diesem Zusammenhang a) eine vermehrte Durchführung experimenteller Studien (z. B. Markierung-Wiederfang-Methoden), b) langfristig angelegte biologische Untersuchungen von neu angelegten oder umfassend renaturierten Gewässerabschnitten sowie c) genetische Vergleiche von Metapopulationen in einem Untersuchungsgebiet.

Bibliography

- Adriaensen, F., Chardon, J. P., de Blust, G., Swinnen, E., Villalba, S., Gulinck, H., and Matthysen, E. (2003). The application of ‘least-cost’ modelling as a functional landscape model. *Landscape and Urban Planning*, 64 (4): 233–247.
- Albertson, L. K., Cardinale, B. J., Zeug, S. C., Harrison, L. R., Lenihan, H. S., and Wydzga, M. A. (2011). Impacts of channel reconstruction on invertebrate assemblages in a restored river. *Restoration Ecology*, 19: 627–638.
- Alexander, L. C., Hawthorne, D. J., Palmer, M. A., and Lamp, W. O. (2011). Loss of genetic diversity in the North American mayfly *Ephemerella Invaria* associated with deforestation of headwater streams. *Freshwater Biology*, 56: 1456–1467.
- Allan, J. D. (1995). *Stream ecology: structure and function of running waters*. Springer.
- (2004). Landscapes and riverscapes: The influence of land use on stream ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, 35: 257–284.
- Allouche, O., Steinitz, O., Rotem, D., Rosenfeld, A., and Kadmon, R. (2008). Incorporating distance constraints into species distribution models. *Journal of Applied Ecology*, 45: 599–609.
- Amsler, M. L., Blettler, M. C. M., and Ezcurra De Drago, I. (2009). Influence of hydraulic conditions over dunes on the distribution of the benthic macroinvertebrates in a large sand bed river. *Water Resources Research*, 45: W06426.
- Araújo, M. B. and Williams, P. H. (2000). Selecting areas for species persistence using occurrence data. *Biological Conservation*, 96 (3): 331–345.
- ASTERICS (2013). ASTERICS, Version 4 - Deutsches Bewertungssystem auf Grundlage des Makrozoobenthos. URL: http://www.fliessgewaesserbewertung.de/downloads/ASTERICS%5C_Softwarehandbuch%5C_Version4.pdf (visited on 04/04/2015).
- Bagge, P. (1995). Emergence and upstream flight of lotic mayflies and caddisflies (Ephemeroptera and Trichoptera) in a lake outlet, central Finland. *Entomologica Fennica*, 6: 91–97.

- Baguette, M., Blanchet, S., Legrand, D., Stevens, V. M., and Turlure, C. (2013). Individual dispersal, landscape connectivity and ecological networks. *Biological Reviews*, 88: 310–326.
- Baker, M. E. and King, R. S. (2010). A new method for detecting and interpreting biodiversity and ecological community thresholds. *Methods in Ecology and Evolution*, 1: 25–37.
- Barbour, M. T., Gerritsen, J., Snyder, B. D., and Stribling, J. B. (1998). Rapid bioassessment protocols for use in streams and wadeable rivers: periphyton, benthic macroinvertebrates and fish, Second Edition. URL: <http://water.epa.gov/scitech/monitoring/rs1/bioassessment/index.cfm> (visited on 04/04/2015).
- Barnes, A. D. and Chapman, H. M. (2014). Dispersal traits determine passive restoration trajectory of a Nigerian montane forest. *Acta Oecologica*, 56: 32–40.
- Bäthe, J. and Coring, E. (2011). Biological effects of anthropogenic salt-load on the aquatic Fauna: A synthesis of 17 years of biological survey on the rivers Werra and Weser. *Limnologica - Ecology and Management of Inland Waters*, 41 (2): 125–133.
- Beauger, A., Lair, N., Reyes-Marchant, P., and Peiry, J.-L. (2006). The distribution of macroinvertebrate assemblages in a reach of the River Allier (France), in relation to riverbed characteristics. *Hydrobiologia*, 571: 63–76.
- Becker, G. (1994). Food preference by five trichopteran scrapers. *Hydrobiologia*, 273: 171–178.
- Beisel, J.-N., Peltre, M.-C., and Usseglio-Polatera, P. (2011). Einfluss der Salzbelastung auf die aquatische Biozönose der Mosel. Abschlussbericht des Labors LIEBE im Auftrag der IKSMS. URL: <http://www.iksms-cipms.org/servlet/is/411/Einfluss%20der%20Salzbelastung.pdf?command=downloadContent%5C&filename=Einfluss%20der%20Salzbelastung.pdf> (visited on 04/04/2015).
- Beisel, J.-N., Usseglio-Polatera, P., and Moreteau, J.-C. (2000). The spatial heterogeneity of a river bottom: a key factor determining macroinvertebrate communities. *Hydrobiologia*, 422/423: 163–171.
- Beisel, J.-N., Usseglio-Polatera, P., Thomas, S., and Moreteau, J.-C. (1998). Stream community structure in relation to spatial variation: the influence of mesohabitat characteristics. *Hydrobiologia*, 389 (1): 73–88.
- Benjamini, Y. and Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B*, 57: 289–300.

- Benke, A. C., van Arsdall Jr., T. C., Gillespie, D. M., and Parrish, F. K. (1984). Invertebrate productivity in a subtropical blackwater river: The importance of habitat and life history. *Ecological Monographs*, 54: 25–63.
- Benke, A. C. and Wallace, J. B. (2003). Influence of wood on invertebrate communities in streams and rivers. *American Fisheries Society Symposium*, 37: 149–177.
- Berezina, N. A. (2002). Tolerance of freshwater invertebrates to changes in water salinity. *Russian Journal of Ecology*, 34 (4): 261–266.
- Bergey, E. A. and Ward, J. V. (1989). Upstream-downstream movements of aquatic invertebrates in a Rocky Mountain stream. *Hydrobiologia*, 185: 71–82.
- Bernhardt, E. S., Palmer, M. A., Allan, J. D., Alexander, G., Barnas, K., Brooks, S., Carr, J., Clayton, S., Dahm, C., Follstad-Shah, J., Galat, D. L., Gloss, S., Goodwin, P., Hart, D., Hassett, B., Jenkinson, R., Katz, S., Kondolf, G. M., Lake, P. S., Lave, R., Meyer, J. L., O'Donnell, T. K., Pagano, L., Powell, B., and Sudduth, E. (2005). Synthesizing U.S. river restoration efforts. *Science*, 308: 636–637.
- Bertin, A., Alvarez, E., Gouin, N., Gianoli, E., Montecinos, S., Lek, S., Gascoin, S., and Lhermitte, S. (2015). Effects of wind-driven spatial structure and environmental heterogeneity on high-altitude wetland macroinvertebrate assemblages with contrasting dispersal modes. *Freshwater Biology*, 60 (2): 297–310.
- Besse-Lototskaya, A., Coste, M., Verdonschot, P. F. M., and Schmidt-Kloiber, A. (2007). Diatom Indicator Database. Euro-limpacs project, Workpackage 7 - Indicators of ecosystem health, Task 4, www.freshwaterecology.info, version 5.0. URL: <http://www.freshwaterecology.info> (visited on 04/04/2015).
- Bis, B. and Usseglio-Polatera, P. (2004). Standardisation of river classifications. Species traits analysis. URL: http://www.eu-star.at/pdf/Deliverable_N2.pdf (visited on 04/04/2015).
- Blakely, T. J., Harding, J. S., McIntosh, A. R., and Winterbourn, M. J. (2006). Barriers to the recovery of aquatic insect communities in urban streams. *Freshwater Biology*, 51: 1634–1645.
- Bogan, M. T. and Boersma, K. S. (2012). Aerial dispersal of aquatic invertebrates along and away from arid-land streams. *Freshwater Science*, 31: 1131–1144.
- Böhmer, J., Rawer-Jost, C., and Zenker, A. (2004). Multimetric assessment of data provided by water managers from Germany: assessment of several different types

- of stressors with macrozoobenthos communities. *Hydrobiologia*, 516 (1-3): 215–228.
- Bohonak, A. J. and Jenkins, D. G. (2003). Ecological and evolutionary significance of dispersal by freshwater invertebrates. *Ecology Letters*, 6: 783–796.
- Borcard, D., Gillet, F., and Legendre, P. (2011). *Numerical Ecology* with R. Springer.
- Bournaud, M., Tachet, H., Berly, A., and Cellot, B. (1998). Importance of microhabitat characteristics in the macrobenthos microdistribution of a large river reach. *Annales de Limnologie - International Journal of Limnology*, 34: 83–98.
- Boyero, L. (2003). The effect of substrate texture on colonization by stream macroinvertebrates. *Annales de Limnologie - International Journal of Limnology*, 39: 211–218.
- Braasch, D. (1994). Zum Auftreten des Bachtaumelkäfers (*Orectochilus villosus*, MÜLLER) in Brandenburg (Insecta, Coleoptera, Gyrinidae). *Entomologische Nachrichten und Berichte*, 39: 125–128.
- Braukmann, U. and Böhme, D. (2011). Salt pollution of the middle and lower sections of the river Werra (Germany) and its impact on benthic macroinvertebrates. *Limnologica*, 41: 113–124.
- Brederveld, R. J., Jähnig, S. C., Lorenz, A. W., Brunzel, S., and Soons, M. B. (2011). Dispersal as a limiting factor in the colonization of restored mountain streams by plants and macroinvertebrates. *Journal of Applied Ecology*, 48: 1241–1250.
- Briers, R. A., Cariss, H. M., and Gee, J. H. R. (2002). Dispersal of adult stoneflies (Plecoptera) from upload streams draining catchments with contrasting land-use. *Archiv für Hydrobiologie*, 155: 627–644.
- Brüggemeier, F.-J. (1994). A nature fit for industry: the environmental history of the Ruhr basin, 1840 - 1990. *Environmental History Review*, 18: 35–54.
- Brujjs, M. C. M., Kelleher, B., van der Velde, G., and de Vaate, A. B. (2001). Oxygen consumption, temperature and salinity tolerance of the invasive amphipod *Dikerogammarus villosus*: indicators of further dispersal via ballast water transport. *Archiv für Hydrobiologie*, 152: 633–646.
- Buckley, L. B., Urban, M. C., Angilletta, M. J., Crozier, L. G., Rissler, L. J., and Sears, M. W. (2010). Can mechanism inform species' distribution models? *Ecology Letters*, 13: 1041–1054.
- Buffagni, A., Erba, S., Cazzola, M., and Kemp, J. L. (2004). The AQEM multimetric system for the southern Italian Apennines: assessing the impact of water quality

- and habitat degradation on pool macroinvertebrates in Mediterranean rivers. *Hydrobiologia*, 516: 313–329.
- Buss, D. F., Baptista, D. F., Nessimian, J. L., and Egler, M. (2004). Substrate specificity, environmental degradation and disturbance structuring macroinvertebrate assemblages in neotropical streams. *Hydrobiologia*, 518: 179–188.
- Cañedo-Argüelles, M., Boersma, K. S., Bogan, M. T., Olden, J. D., Phillipsen, I., Schriever, T. A., and Lytle, D. A. (2015). Dispersal strength determines meta-community structure in a dendritic riverine network. *Journal of Biogeography*, 42: 778–790.
- Cañedo-Argüelles, M., Kefford, B. J., Piscart, C., Prat, N., Schäfer, R. B., and Schulz, C.-J. (2013). Salinisation of rivers: An urgent ecological issue. *Environmental Pollution*, 173: 157–167.
- Cao, Y., Bark, A. W., and Williams, W. P. (1997). Analysing benthic macroinvertebrate community changes along a pollution gradient: A framework for the development of biotic indices. *Water Research*, 31: 884–892.
- Carvalho, E. M. and Uieda, V. S. (2006). Colonization routes of benthic macroinvertebrates in a stream in southeast Brazil. *Acta Limnologica Brasiliensa*, 18: 367–376.
- Cassini, M. H. (2011). Ecological principles of species distribution models: the habitat matching rule. *Journal of Biogeography*, 38: 2057–2065.
- Chakona, A., Phiri, C., Magadza, C. H. D., and Brendonck, L. (2008). The influence of habitat structure and flow permanence on macroinvertebrate assemblages in temporary rivers in northwestern Zimbabwe. *Hydrobiologia*, 607: 199–209.
- Chambers, J. M. and Hastie, T. (1992). *Statistical models in S*. Wadsworth & Brooks / Cole.
- Chapman, M. G. and Underwood, A. J. (1999). Ecological patterns in multivariate assemblages: information and interpretation of negative values in ANOSIM tests. *Marine Ecology Progress Series*, 180: 257–265.
- Chaput-Bardy, A., Grégoire, A., Baguette, M., Pagano, A., and Secondi, J. (2010). Condition and phenotype-dependent dispersal in a damselfly, *Calopteryx splendens*. *PLoS ONE*, 5 (5): e10694.
- Chaput-Bardy, A., Lemaire, C., Picard, D., and Secondi, J. (2008). In-stream and overland dispersal across a river network influences gene flow in a freshwater insect, *Calopteryx splendens*. *Molecular Ecology*, 17 (15): 3496–3505.

- Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, 18: 117–143.
- Clarke, K. R. and Gorley, R. N. (2006). *PRIMER v6: User Manual/Tutorial*. PRIMER-E.
- Clarke, K. R. and Warwick, R. M. (2001). *Change in marine communities: an approach to statistical analysis and interpretation*, 2nd edition. PRIMER-E.
- Coe, H. J., Kiffney, P. M., Pess, G. R., Kloehn, K. K., and McHenry, M. L. (2009). Periphyton and invertebrate response to wood placement in large pacific coastal rivers. *River Research and Applications*, 25: 1025–1035.
- Collier, K. J. (2014). Wood decay rates and macroinvertebrate community structure along contrasting human pressure gradients (Waikato, New Zealand). *New Zealand Journal of Marine and Freshwater Research*, 48: 97–111.
- Collier, K. J. and Halliday, J. N. (2000). Macroinvertebrate-wood associations during decay of plantation pine in New Zealand pumice-bed streams: stable habitat or trophic subsidy? *Journal of the North American Benthological Society*, 19: 94–111.
- Cornell, H. V. and Lawton, J. H. (1992). Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology*, 61: 1–12.
- Cortes, R. M. V., Ferreira, M. T., Oliveira, S. V., and Godinho, F. (1998). Contrasting impact of small dams on the macroinvertebrates of two Iberian mountain rivers. *Hydrobiologia*, 389: 51–61.
- Coulson, S. J., Hodkinson, I. D., and Webb, N. R. (2003). Aerial dispersal of invertebrates over a high-Arctic glacier foreland: Midtre Lovénbreen, Svalbard. *Polar Biology*, 26: 530–537.
- Crosa, G., Froebrich, J., Nikolayenko, V., Stefani, F., Galli, P., and Calamari, D. (2006). Spatial and seasonal variations in the water quality of the Amu Darya River (Central Asia). *Water Research*, 40 (11): 2237–2245.
- Cuffney, T. F., Brightbill, R. A., May, J. T., and Waite, I. R. (2010). Responses of benthic macroinvertebrates to environmental changes associated with urbanization in nine metropolitan areas. *Ecological Applications*, 20: 1384–1401.
- Cuffney, T. F., Kashuba, R., Qian, S. S., Alameddine, I., Cha, Y. K., Lee, B., Coles, J. F., and McMahon, G. (2011). Multilevel regression models describing regional patterns of invertebrate and algal responses to urbanization across the USA. *Journal of the North American Benthological Society*, 30: 797–819.

- Culp, J. M., Walde, S. J., and Davies, R. W. (1983). Relative importance of substrate particle size and detritus to stream benthic macroinvertebrate microdistribution. *Canadian Journal of Fisheries and Aquatic Sciences*, 40 (10): 1568–1574.
- Cummins, K. W. and Lauff, G. H. (1969). The influence of substrate particle size on the microdistribution of stream macrobenthos. *Hydrobiologia*, 34: 145–181.
- Dallas, H. F. (2007). The influence of biotope availability on macroinvertebrate assemblages in South African rivers: Implications for aquatic bioassessment. *Freshwater Biology*, 52: 370–380.
- De Cáceres, M. and Legendre, P. (2009). Associations between species and groups of sites: Indices and statistical inference. *Ecology*, 90: 3566–3574.
- De Cáceres, M., Legendre, P., and Moretti, M. (2010). Improving indicator species analysis by combining groups of sites. *Oikos*, 119: 1674–1684.
- De'ath, G. (2007). Boosted trees for ecological modeling and prediction. *Ecology*, 88: 243–251.
- Dedecker, A. P., van Melckebeke, K., Goethals, P. L. M., and De Pauw, N. (2007). Development of migration models for macroinvertebrates in the Zwalm river basin (Flanders, Belgium) as tools for restoration management. *Ecological Modelling*, 203: 72–86.
- Dell'Uomo, A. (2004). L'indice diatamico di eutrofizzazione/polluzione (EPI-D) nel monitoraggio delle acque correnti. Linee Guida. APAT Agenzia per la protezione dell'ambiente e Servizi tecnici.
- Dewson, Z. S., James, A. B. W., and Death, R. G. (2007). A review of the consequences of decreased flow for instream habitat and macroinvertebrates. *Journal of the North American Benthological Society*, 26: 401–415.
- Dick, J. T. A. and Platvoet, D. (2000). Invading predatory crustacean *Dikerogammarus villosus* eliminates both native and exotic species. *Proceedings of the Royal Society B: Biological Sciences*, 267: 977–983.
- Doeg, T. J., Marchant, R., Douglas, M., and Lake, P. S. (1989). Experimental colonization of sand, gravel and stones by macroinvertebrates in the Acheron River, southeastern Australia. *Freshwater Biology*, 22: 57–64.
- Dolédec, S., Statzner, B., and Bournard, M. (1999). Species traits for future biomonitoring across ecoregions: patterns along a human-impacted river. *Freshwater Biology*, 42: 737–758.

- Domisch, S., Jähnig, S. C., and Haase, P. (2011). Climate-change winners and losers: stream macroinvertebrates of a submontane region in Central Europe. *Freshwater Biology*, 56: 2009–2020.
- Dorier, A. and Vaillant, F. (1954). Observations et expériences relatives à la résistance au courant de divers invertébrés aquatiques. Extrait de la Laboratoire de Hydrobiologie et Pisciculture Grenoble, 45: 9–31.
- Downes, B. J. (2010). Back to the future: little-used tools and principles of scientific inference can help disentangle effects of multiple stressors on freshwater ecosystems. *Freshwater Biology*, 55: 60–79.
- Drury, D. M. and Kelso, W. E. (2000). Invertebrate colonization of woody debris in coastal plain streams. *Hydrobiologia*, 434: 63–72.
- Duan, X., Wang, Z., Xu, M., and Zhang, K. (2009). Effect of streambed sediment on benthic ecology. *International Journal of Sediment Research*, 24: 325–338.
- Dufrêne, M. and Legendre, P. (1997). Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs*, 67: 345–366.
- Dunbar, M. J., Pedersen, M. L., Cadman, D., Extence, C. A., Waddingham, J., Chadd, R. P., and Larsen, S. E. (2010). River discharge and local-scale physical habitat influence macroinvertebrate LIFE scores. *Freshwater Biology*, 55: 226–242.
- Dunlop, J. E., Horrigan, N., McGregor, G., Kefford, B. J., Choy, S. C., and Prasad, R. (2008). Effect of spatial variation on salinity tolerance of macroinvertebrates in Eastern Australia and implications for ecosystem protection trigger values. *Environmental Pollution*, 151: 621–630.
- Dunlop, J. E., McGregor, G., and Horrigan, N. (2005). Potential impacts of salinity and turbidity in riverine ecosystems. National Action Plan for Salinity and Water Quality Technical Report Series.
- Ehlert, T. (2009). Flugaktivität, Eiablage und Habitatbindung von Köcherfliegen (Trichoptera) an Fließgewässern. Westarp Wissenschaftenverlagsgesellschaft.
- Elith, J. (2000). Quantitative methods for modeling species habitat: Comparative performance and an application to Australian plants. In: *Quantitative Methods for Conservation Biology*, pp. 39–58.
- Elith, J. and Graham, C. H. (2009). Do they? How do they? WHY do they differ? on finding reasons for differing performances of species distribution models. *Ecography*, 32: 66–77.
- Elith, J., Graham, C. H., Anderson, R. P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R. J., Huettmann, F., Leathwick, J. R., Lehmann, A., Li, J., Lohmann,

- L. G., Loiselle, B. A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J. M., Peterson, A. T., Phillips, S. J., Richardson, K., Scachetti-Pereira, R., Schapire, R. E., Soberón, J., Williams, S., Wisz, M. S., and Zimmermann, N. E. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29 (2): 129–151.
- Elith, J. and Leathwick, J. R. (2009). Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, 40: 677–697.
- (2015). Boosted Regression Trees for ecological modeling. URL: <http://cran.r-project.org/web/packages/dismo/vignettes/brt.pdf> (visited on 04/04/2015).
- Elith, J., Leathwick, J. R., and Hastie, T. (2008). A working guide to boosted regression trees. *Journal of Animal Ecology*, 77: 802–813.
- Elliott, J. M. (1971). Upstream movements of benthic invertebrates in a Lake District Stream. *The Journal of Animal Ecology*, 40 (1): 235–252.
- (2003). A comparative study of the dispersal of 10 species of stream invertebrates. *Freshwater Biology*, 48: 1652–1668.
- Entrekin, S. A., Tank, J. L., Rosi-Marshall, E. J., Hoellein, T. J., and Lamberti, G. A. (2009). Response of secondary production by macroinvertebrates to large wood addition in three Michigan streams. *Freshwater Biology*, 54: 1741–1758.
- Erman, D. C. and Erman, N. A. (1984). The response of stream macroinvertebrates to substrate size and heterogeneity. *Hydrobiologia*, 108: 75–82.
- ESRI (2011a). Combine (Spatial Analyst). URL: <http://help.arcgis.com/en/arcgisdesktop/10.0/help/index.html%5C#/Combine/009z0000007r000000/> (visited on 04/04/2015).
- (2011b). Cost Distance (Spatial Analyst). URL: <http://help.arcgis.com/en/arcgisdesktop/10.0/help/index.html%5C#//009z00000018000000.htm> (visited on 04/04/2015).
- (2011c). Path Distance (Spatial Analyst). URL: <http://help.arcgis.com/en/arcgisdesktop/10.0/help/index.html%5C#//009z0000001q000000.htm> (visited on 04/04/2015).
- Feld, C. K. (2013). Response of three lotic assemblages to riparian and catchment-scale land use: implications for designing catchment monitoring programmes. *Freshwater Biology*, 58: 715–729.
- Feld, C. K., Birk, S., Bradley, D. C., Hering, D., Kail, J., Marzin, A., Melcher, A., Nemitz, D., Pedersen, M. L., Pletterbauer, F., Pont, D., Verdonschot, P. F. M.,

- and Friberg, N. (2011). From natural to degraded rivers and back again: a test of restoration ecology theory and practice. *Advances in Ecological Research*, 44: 119–209.
- Feld, C. K., de Bello, F., and Dolédec, S. (2014). Biodiversity of traits and species both show weak responses to hydromorphological alteration in lowland river macroinvertebrates. *Freshwater Biology*, 59: 233–248.
- Feld, C. K. and Hering, D. (2007). Community structure or function: effects of environmental stress on benthic macroinvertebrates at different spatial scales. *Freshwater Biology*, 52 (7): 1380–1399.
- Figuerola, J. and Green, A. J. (2002). Dispersal of aquatic organisms by waterbirds: a review of past research and priorities for future studies. *Freshwater Biology*, 47 (3): 483–494.
- Foerster, J. and Gellert, G. (2012). Das Makrozoobenthos der Lippe nach Renaturierung: die Zusammensetzung der Makrozoobenthosfauna in ausgewählten Abschnitten der Lippe als Folge von ökologischen Umbaumaßnahmen. *Natur in NRW*, 37: 38–40.
- Franklin, J. (2010). Mapping species distributions: spatial inference and prediction. Vol. 1. Cambridge University Press.
- Fritz, S. C. (2007). Salinity and climate reconstruction from diatoms in continental lakes. In: *Encyclopedia of Quaternary Science*, Vol. 1. Ed. by S. A. Elias. Elsevier, pp. 514–522.
- Gabriel, C. M., Clarke, K. D., and Campbell, C. E. (2010). Invertebrate communities in Compensation Creek, a man-made stream in boreal Newfoundland: The influence of large woody debris. *River Research and Applications*, 26: 1005–1018.
- Gayraud, S. and Philippe, M. (2003). Influence of bed-sediment features on the interstitial habitat available for macroinvertebrates in 15 French streams. *International Review of Hydrobiology*, 88: 77–93.
- Gellert, G. (2011). Bewegungsmuster und -dynamik der Makrozoobenthosfauna in der Lippeseemflut innerhalb eines Zeitraums von fünf Jahren. In: *Erweiterte Zusammenfassung der Jahrestagung der DGL 2010*. Eigenverlag der DGL.
- Gellert, G., Pottgiesser, T., and Euler, T. (2014). Assessment of the structural quality of streams in Germany - basic description and current status. *Environmental Monitoring and Assessment*, 186 (6): 3365–3378.

- Gerhard, M. and Reich, M. (2000). Restoration of streams with large wood: Effects of accumulated and built-in wood on channel morphology, habitat diversity and aquatic fauna. *International Review of Hydrobiology*, 85: 123–137.
- Gies, M., Sondermann, M., Hering, D., and Feld, C. K. (2015). Are species distribution models based on broad-scale environmental variables transferable across adjacent watersheds? A case study with eleven macroinvertebrate species. *Fundamental and Applied Limnology*, 186: 63–97.
- Giller, P. S. and Malmqvist, B. (1998). *The biology of streams and rivers*. Oxford University Press.
- Gillilan, S., Boyd, K., Hoitsma, T., and Kauffman, M. (2005). Challenges in developing and implementing ecological standards for geomorphic river restoration projects: A practitioner’s response to Palmer et al. (2005). *Journal of Applied Ecology*, 42: 223–227.
- Godsoe, W. and Harmon, L. J. (2012). How do species interactions affect species distribution models? *Ecography*, 35: 811–820.
- Gower, J. C. (1983). Comparing Classifications. In: *Numerical Taxonomy*. Springer, pp. 137–155.
- Grabowski, M., Bacela, K., and Konopacka, A. (2007). How to be an invasive gammarid (Amphipoda: Gammaroidea) - comparison of life history traits. *Hydrobiologia*, 590: 75–84.
- Gray, L. J. and Fisher, S. G. (1981). Postflood recolonization pathways of macroinvertebrates in a lowland Sonoran Desert stream. *American Midland Naturalist*, 106: 249–257.
- Grönroos, M., Heino, J., Siqueira, T., Landeiro, V. L., Kotanen, J., and Bini, L. M. (2013). Metacommunity structuring in stream networks: roles of dispersal mode, distance type, and regional environmental context. *Ecology and Evolution*, 3: 4473–4487.
- Guisan, A. and Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, 8 (9): 993–1009.
- Guse, B., Reusser, D. E., and Fohrer, N. (2014). How to improve the representation of hydrological processes in SWAT for a lowland catchment - temporal analysis of parameter sensitivity and model performance. *Hydrological Processes*, 28: 2651–2670.

- Haapala, A., Muotka, T., and Laasonen, P. (2003). Distribution of benthic macroinvertebrates and leaf litter in relation to streambed retentivity: Implications for headwater stream restoration. *Boreal Environment Research*, 8: 19–30.
- Haase, P., Hering, D., Jähnig, S. C., Lorenz, A. W., and Sundermann, A. (2013). The impact of hydromorphological restoration on river ecological status: a comparison of fish, benthic invertebrates, and macrophytes. *Hydrobiologia*, 704: 475–488.
- Haase, P., Lohse, S., Pauls, S., Schindehütte, K., Sundermann, A., Rolauffs, P., and Hering, D. (2004a). Assessing streams in Germany with benthic invertebrates: development of a practical standardised protocol for macroinvertebrate sampling and sorting. *Limnologia*, 34: 349–365.
- Haase, P., Pauls, S., Sundermann, A., and Zenker, A. (2004b). Testing different sorting techniques in macroinvertebrate samples from running waters. *Limnologia*, 34: 366–378.
- Halse, S. A., Ruprecht, J. K., and Pinder, A. M. (2003). Salinisation and prospects for biodiversity in rivers and wetlands of south-west Western Australia. *Australian Journal of Botany*, 51: 673–688.
- Hanski, I. (1998). Metapopulation dynamics. *NATURE*, 396: 41–49.
- Harris, J. R. (1952). *An angler's entomology*. Collins.
- Harrison, S. S. C., Pretty, J. L., Shepherd, D., Hildrew, A. G., Smith, C., and Hey, R. D. (2004). The effect of instream rehabilitation structures on macroinvertebrates in lowland rivers. *Journal of Applied Ecology*, 41: 1140–1154.
- Hart, B. T., Bailey, P., Edwards, R., Hortle, K., James, K., McMahon, A., Meredith, C., and Swadling, K. (1991). A review of the salt sensitivity of the Australian freshwater biota. *Hydrobiologia*, 210: 105–144.
- Hawkes, C. (2009). Linking movement behaviour, dispersal and population processes: Is individual variation a key? *Journal of Animal Ecology*, 78: 894–906.
- Heino, J. (2000). Lentic macroinvertebrate assemblage structure along gradients in spatial heterogeneity, habitat size and water chemistry. *Hydrobiologia*, 418: 229–242.
- (2013). The importance of metacommunity ecology for environmental assessment research in the freshwater realm. *Biological Reviews*, 88: 166–178.
- Heino, J., Louhi, P., and Muotka, T. (2004). Identifying the scales of variability in stream macroinvertebrate abundance, functional composition and assemblage structure. *Freshwater Biology*, 49: 1230–1239.

- Hering, D., Aroviita, J., Baattrup-Pedersen, A., Brabec, K., Buijse, T., Ecke, F., Friberg, N., Gielczewski, M., Januschke, K., Köhler, J., Kupilas, B., Lorenz, A. W., Muhar, S., Paillex, A., Poppe, M., Schmidt, T., Schmutz, S., Vermaat, J., Verdonschot, P. F. M., Verdonschot, R. C. M., Wolter, C., and Kail, J. (2015). Contrasting the roles of section length and instream habitat enhancement for river restoration success: a field study on 20 European restoration projects. Submitted.
- Hering, D., Buffagni, A., Moog, O., Sandin, L., Sommerhäuser, M., Stubauer, I., Feld, C. K., Johnson, R. K., Pinto, P., Skoulikidis, N., Verdonschot, P. F. M., and Zahrádková, S. (2003). The development of a system to assess the ecological quality of streams based on macroinvertebrates – Design of the sampling programme within the AQEM project. *International Review of Hydrobiology*, 88: 345–361.
- Hering, D., Gerhard, M., Kiel, E., Ehlert, T., and Pottgiesser, T. (2001). Review study on near-natural conditions of Central European mountain streams, with particular reference to debris and beaver dams: Results of the “REG meeting” 2000. *Limnologica*, 31: 81–92.
- Hering, D., Johnson, R. K., and Buffagni, A. (2006). Linking organism groups - major results and conclusions from the STAR project. *Hydrobiologia*, 566: 109–113.
- Hering, D., Meier, C., Rawer-Jost, C., Feld, C. K., Biss, R., Zenker, A., Sundermann, A., Lohse, S., and Böhmer, J. (2004a). Assessing streams in Germany with benthic invertebrates: Selection of candidate metrics. *Limnologica*, 34: 398–415.
- Hering, D., Moog, O., Sandin, L., and Verdonschot, P. F. M. (2004b). Overview and application of the AQEM assessment system. *Hydrobiologia*, 516 (1): 1–20.
- Hering, D. and Reich, M. (1997). Bedeutung von Totholz für Morphologie, Besiedlung und Renaturierung mitteleuropäischer Fließgewässer. *Natur und Landschaft*, 72: 383–390.
- Hernandez, P. A., Graham, C. H., Master, L. L., and Albert, D. L. (2006). The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography*, 29: 773–785.
- Hijmans, R. J. and Elith, J. (2015). Species distribution modeling with R. URL: <ftp://cran.r-project.org/pub/R/web/packages/dismo/vignettes/sdm.pdf> (visited on 04/04/2015).
- Hilderbrand, R. H., Lemly, A. D., Dolloff, C. A., and Harpster, K. L. (1997). Effects of large woody debris placement on stream channels and benthic macroinvertebrates. *Canadian Journal of Fisheries and Aquatic Sciences*, 939: 931–939.

- Hoffmann, A. (1991). Ökologische Untersuchungen an *Lasiocephala basalis* (Kole-nati) (Trichoptera, Lepidostomatidae) an einem Mittelgebirgsbach. Diploma the-sis. University of Marburg.
- (2000). The association of the stream caddisfly *Lasiocephala basalis* (Kol.) (Tri-choptera: Lepidostomatidae) with wood. *International Review of Hydrobiology*, 85 (1): 79–93.
- Hoffmann, A. and Hering, D. (2000). Wood-associated macroinvertebrate fauna in Central European streams. *International Review of Hydrobiology*, 85 (1): 25–48.
- Hofmann, G., Werum, M., and Lange-Bertalot, H. (2013). *Diatomeen im Süßwasser-Benthos von Mitteleuropa*. Koeltz Scientific Books.
- Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, 6: 65–70.
- Holomuzki, J. R., Feminella, J. W., and Power, M. E. (2010). Biotic interactions in freshwater benthic habitats. *Journal of the North American Benthological Society*, 29: 220–244.
- Horrigan, N., Choy, S. C., Marshall, J., and Recknagel, F. (2005). Response of stream macroinvertebrates to changes in salinity and the development of a salinity index. *Marine and Freshwater Research*, 56: 825–833.
- Horton, B. P., Corbett, R., Culver, S. J., Edwards, R. J., and Hillier, C. (2006). Modern saltmarsh diatom distributions of the Outer Banks, North Carolina, and the development of a transfer function for high resolution reconstructions of sea level. *Estuarine, Coastal and Shelf Science*, 69: 381–394.
- Hustedt, F. (1953). *Die Systematik der Diatomeen in ihren Beziehungen zur Geologie und Ökologie nebst einer Revision des Halobiensystems*. *Svensk Botanisk Tidskrift*, 47: 509–519.
- Illies, J. (1978). *Limnofauna Europaea*. A checklist of the animals inhabiting Euro-pean inland waters, with account of their distribution and ecology. Second revised and enlarged edition. G. Fischer Verlag.
- Jahn, R. and Schmid, A.-M. M. (2007). Revision of the brackish-freshwater diatom genus *Bacillaria* Gmelin (Bacillariophyta) with the description of a new variety and two new species. *European Journal of Phycology*, 42: 295–312.
- Jähnig, S. C., Brabec, K., Buffagni, A., Erba, S., Lorenz, A. W., Ofenböck, T., Ver-donschot, P. F. M., and Hering, D. (2010). A comparative analysis of restoration measures and their effects on hydromorphology and benthic invertebrates in 26 central and southern European rivers. *Journal of Applied Ecology*, 47: 671–680.

- Jähnig, S. C., Brunzel, S., Gacek, S., Lorenz, A. W., and Hering, D. (2009). Effects of re-braiding measures on hydromorphology, floodplain vegetation, ground beetles and benthic invertebrates in mountain rivers. *Journal of Applied Ecology*, 46: 406–416.
- Jähnig, S. C., Kuemmerlen, M., Kiesel, J., Domisch, S., Cai, Q., Schmalz, B., and Fohrer, N. (2012). Modelling of riverine ecosystems by integrating models: conceptual approach, a case study and research agenda. *Journal of Biogeography*, 39: 2253–2263.
- Jähnig, S. C. and Lorenz, A. W. (2008). Substrate-specific macroinvertebrate diversity patterns following stream restoration. *Aquatic Sciences*, 70 (3): 292–303.
- Jähnig, S. C., Lorenz, A. W., and Hering, D. (2008). Hydromorphological parameters indicating differences between single- and multiple-channel mountain rivers in Germany, in relation to their modification and recovery. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 18: 1200–1216.
- Johnson, W. C. (2002). Riparian vegetation diversity along regulated rivers: Contribution of novel and relict habitats. *Freshwater Biology*, 47: 749–759.
- Jones, J. I., Murphy, J. F., Collins, A. L., Sear, D. A., Naden, P. S., and Armitage, P. D. (2012). The impact Of fine sediment on macro-invertebrates. *River Research and Applications*, 28: 1055–1071.
- Jorde, K. (1996). Mindestwasserregelungen in Ausleitungsstrecken: Ein Simulation-smodell zur Beurteilung ökologischer und ökonomischer Auswirkungen. *Wasserwirtschaft*, 86 (6): 302–308.
- Kail, J. (2003). Influence of large woody debris on the morphology of six central European streams. *Geomorphology*, 51: 207–223.
- Kail, J., Arle, J., and Jähnig, S. C. (2012). Limiting factors and thresholds for macroinvertebrate assemblages in European rivers: Empirical evidence from three datasets on water quality, catchment urbanization, and river restoration. *Ecological Indicators*, 18: 63–72.
- Kail, J., Guse, B., Radinger, J., Schröder, M., Kiesel, J., Kleinhans, M., Schuurman, F., Fohrer, N., Hering, D., and Wolter, C. (2015). Coupling models in a modelling framework to assess the effect of pressures on abiotic habitat conditions and biota of rivers. Submitted to PLoS ONE.
- Kappes, H. and Haase, P. (2012). Slow, but steady: dispersal of freshwater molluscs. *Aquatic Sciences*, 74: 1–14.

- Kay, W. R., Halse, S. A., Scanlon, M. D., and Smith, M. J. (2001). Distribution and environmental tolerances of aquatic macroinvertebrate families in the agricultural zone of southwestern Australia. *Journal of the North American Benthological Society*, 20: 182–199.
- Kefford, B. J. (1998a). Is salinity the only water quality parameter affected when saline water is disposed in rivers? *International Journal of Salt Lake Research*, 7: 285–300.
- (1998b). The relationship between electrical conductivity and selected macroinvertebrate communities in four river systems of south-west Victoria, Australia. *International Journal of Salt Lake Research*, 7: 153–170.
- Kefford, B. J., Dalton, A., Palmer, C. G., and Nugegoda, D. (2004). The salinity tolerance of eggs and hatchlings of selected aquatic macroinvertebrates in south-east Australia and South Africa. *Hydrobiologia*, 517: 179–192.
- Kefford, B. J., Hickey, G. L., Gasith, A., Ben-David, E., Dunlop, J. E., Palmer, C. G., Allan, K., Choy, S. C., and Piscart, C. (2012a). Global scale variation in the salinity sensitivity of riverine macroinvertebrates: Eastern Australia, France, Israel and South Africa. *PLoS ONE*, 7 (5): e35224.
- Kefford, B. J., Marchant, R., Schäfer, R. B., Metzeling, L., Dunlop, J. E., Choy, S. C., and Goonan, P. (2011). The definition of species richness used by species sensitivity distributions approximates observed effects of salinity on stream macroinvertebrates. *Environmental Pollution*, 159: 302–310.
- Kefford, B. J., Nugegoda, D., Metzeling, L., and Fields, E. J. (2006). Validating species sensitivity distributions using salinity tolerance of riverine macroinvertebrates in the southern Murray–Darling Basin (Victoria, Australia). *Canadian Journal of Fisheries and Aquatic Sciences*, 63: 1865–1877.
- Kefford, B. J., Schäfer, R. B., and Metzeling, L. (2012b). Risk assessment of salinity and turbidity in Victoria (Australia) to stream insects' community structure does not always protect functional traits. *Science of the Total Environment*, 415: 61–68.
- Keller, D. and Holderegger, R. (2013). Damselflies use different movement strategies for short- and long-distance dispersal. *Insect Conservation and Diversity*, 6: 590–597.
- Kennedy, A. J., Cherry, D. S., and Currie, R. J. (2004). Evaluation of ecologically relevant bioassays for a lotic system impacted by a coal-mine effluent, using *Isonychia*. *Environmental Monitoring and Assessment*, 95: 37–55.

- Kiesel, J., Hering, D., Schmalz, B., and Fohrer, N. (2009). A transdisciplinary approach for modelling macroinvertebrate habitats in lowland streams. In: *Ecology of Surface and Groundwater Dependent Systems: Concepts, Methods and Recent Developments*. Vol. 328, pp. 24–33.
- Kiesel, J., Schröder, M., Hering, D., Schmalz, B., Hörmann, G., Jähnig, S. C., and Fohrer, N. (2015). A new model linking macroinvertebrate assemblages to habitat composition in rivers: development, sensitivity and univariate application. *Fundamental and Applied Limnology*, 186 (1-2): 117–133.
- King, R. S. and Baker, M. E. (2010). Considerations for analyzing ecological community thresholds in response to anthropogenic environmental gradients. *Journal of the North American Benthological Society*, 29: 998–1008.
- Koch, F. H. and Smith, W. D. (2008). Spatio-temporal analysis of *Xyleborus glabratus* (Coleoptera: Curculionidae: Scolytinae) invasion in eastern U.S. forests. *Environmental Entomology*, 37 (2): 442–452.
- Korte, T. (2010). Current and substratum preferences of benthic invertebrates in the rivers of the Hindu Kush-Himalayan region as indicators of hydromorphological degradation. *Hydrobiologia*, 651 (1): 77–91.
- Kramm, S. (2002). Vergleichende Untersuchung der Besiedlung von Hartsubstraten durch Makroinvertebraten in Sandbächen. Diploma thesis. University of Duisburg-Essen.
- Krisp, H. and Maier, G. (2005). Consumption of macroinvertebrates by invasive and native gammarids: a comparison. *Journal of Limnology*, 64: 55–59.
- Kubosova, K., Brabec, K., Jarkovsky, J., and Syrovatka, V. (2010). Selection of indicative taxa for river habitats: a case study on benthic macroinvertebrates using indicator species analysis and the random forest methods. *Hydrobiologia*, 651: 101–114.
- Kuemmerlen, M., Schmalz, B., Guse, B., Cai, Q., Fohrer, N., and Jähnig, S. C. (2014). Integrating catchment properties in small scale species distribution models of stream macroinvertebrates. *Ecological Modelling*, 277: 77–86.
- Lake, P. S., Bond, N., and Reich, P. (2007). Linking ecological theory with stream restoration. *Freshwater Biology*, 52: 597–615.
- Lamouroux, N., Dolédec, S., and Gayraud, S. (2004). Biological traits of stream macroinvertebrate communities: effects of microhabitat, reach, and basin filters. *Journal of the North American Benthological Society*, 23: 449–466.

- Länderarbeitsgemeinschaft Wasser (1997). Zielvorgaben zum Schutz oberirdischer Binnengewässer. Band 1. Kulturbuchverlag Berlin.
- (2000). Gewässerstrukturgütekartierung in der Bundesrepublik Deutschland: Verfahren für kleine und mittelgroße Fließgewässer. Länderarbeitsgemeinschaft Wasser.
 - (2014). Rahmenkonzeption Monitoring Teil B. Bewertungsgrundlagen und Methodenbeschreibungen. Arbeitspapier II: Hintergrund- und Orientierungswerte für physikalisch-chemische Qualitätskomponenten zur unterstützenden Bewertung von Wasserkörpern entsprechend EG-WRRL. Länderarbeitsgemeinschaft Wasser.
- Landesamt für Natur, Umwelt und Verbraucherschutz Land NRW (2015). ELWASWEB: Elektronisches wasserwirtschaftliches Verbundsystem für die Wasserwirtschaftsverwaltung in NRW. URL: <http://www.elwasweb.nrw.de> (visited on 04/04/2015).
- Landesamt für Vermessung und Geoinformation (2004). Automatisierte Liegenschaftskarte (ALK). In: Vermessungs- und Katasterverwaltung Schleswig-Holstein.
- Landres, P. B., Verner, J., and Thomas, J. W. (1988). Ecological uses of vertebrate indicator species: a critique. *Conservation Biology*, 2: 316–328.
- Langford, T. E. L., Shaw, P. J., Ferguson, A. J. D., and Howard, S. R. (2009). Long-term recovery of macroinvertebrate biota in grossly polluted streams: Recolonisation as a constraint to ecological quality. *Ecological Indicators*, 9: 1064–1077.
- Larsen, S. and Ormerod, S. J. (2010). Combined effects of habitat modification on trait composition and species nestedness in river invertebrates. *Biological Conservation*, 143: 2638–2646.
- Larson, M. G., Booth, D. B., and Morley, S. A. (2001). Effectiveness of large woody debris in stream rehabilitation projects in urban basins. *Ecological Engineering*, 18: 211–226.
- Lautenschläger, M. (2005). Anpassungen der Lebensgemeinschaft von Mittelgebirgs-Fließgewässern an urbane Überprägungen unter besonderer Berücksichtigung der Kriebelmücken (Diptera; Simuliidae). PhD thesis. University of Duisburg-Essen.
- Lawton, J. H. (2000). Community ecology in a changing world. *Excellence in Ecology Book 11*. International Ecology Institute.
- Leathwick, J. R., Elith, J., and Hastie, T. (2006). Comparative performance of generalized additive models and multivariate adaptive regression splines for statistical modelling of species distributions. *Ecological Modelling*, 199: 188–196.

- Lee, C. E. and Bell, M. A. (1999). Causes and consequences of recent freshwater invasions by saltwater animals. *Trends in Ecology and Evolution*, 14: 284–288.
- Lee, C. E., Moss, W. E., Olson, N., Chau, K. F., Chang, Y.-M., and Johnson, K. E. (2013). Feasting in fresh water: impacts of food concentration on freshwater tolerance and the evolution of food x salinity response during the expansion from saline into fresh water habitats. *Evolutionary Applications*, 6: 673–689.
- Lee, C. E. and Petersen, C. H. (2003). Effects of developmental acclimation on adult salinity tolerance in the freshwater-invading copepod *Eurytemora affinis*. *Physiological and biochemical zoology*, 76 (3): 296–301.
- Legendre, P. and Legendre, L. (2012). *Numerical ecology*, Third Edition. Elsevier.
- Lek, S., Scardi, M., Verdonschot, P. F. M., Descy, J.-P., and Park, Y.-S. (2005). *Modelling community structure in freshwater ecosystems*. Springer.
- Lemly, A. D. and Hilderbrand, R. H. (2000). Influence of large woody debris on stream insect communities and benthic detritus. *Hydrobiologia*, 421: 179–185.
- Lepori, F., Palm, D., and Malmqvist, B. (2005). Effects of stream restoration on ecosystem functioning: detritus retentiveness and decomposition. *Journal of Applied Ecology*, 42: 228–238.
- Leunda, P. M., Oscoz, J., Miranda, R., and Ariño, A. H. (2009). Longitudinal and seasonal variation of the benthic macroinvertebrate community and biotic indices in an undisturbed Pyrenean river. *Ecological Indicators*, 9: 52–63.
- Lobo, J. M., Jiménez-Valverde, A., and Hortal, J. (2010). The uncertain nature of absences and their importance in species distribution modelling. *Ecography*, 33: 103–114.
- Lorenz, A. W. and Feld, C. K. (2013). Upstream river morphology and riparian land use overrule local restoration effects on ecological status assessment. *Hydrobiologia*, 704 (1): 489–501.
- Lorenz, A. W., Hering, D., Feld, C. K., and Rolauffs, P. (2004). A new method for assessing the impact of hydromorphological degradation on the macroinvertebrate fauna of five German stream types. *Hydrobiologia*, 516: 107–127.
- Lorenz, A. W., Jähnig, S. C., and Hering, D. (2009). Re-meandering German lowland streams: qualitative and quantitative effects of restoration measures on hydromorphology and macroinvertebrates. *Environmental Management*, 44: 745–754.
- Lütolf, M., Kienast, F., and Guisan, A. (2006). The ghost of past species occurrence: improving species distribution models for presence-only data. *Journal of Applied Ecology*, 43: 802–815.

- Lyon, J. P., Nicol, S. J., Lieschke, J. A., and Ramsey, D. S. L. (2009). Does wood type influence the colonisation of this habitat by macroinvertebrates in large lowland rivers? *Marine and Freshwater Research*, 60 (5): 384–393.
- Mackay, R. J. (1992). Colonization by lotic macroinvertebrates: a review of processes and patterns. *Canadian Journal of Fisheries and Aquatic Sciences*, 49 (3): 617–628.
- MacKenzie, D. I. (2005). What are the issues with presence-absence data for wildlife managers? *Journal of Wildlife Management*, 69: 849–860.
- Macneale, K. H., Peckarsky, B. L., and Likens, G. E. (2004). Contradictory results from different methods for measuring direction of insect flight. *Freshwater Biology*, 49 (10): 1260–1268.
- Madsen, B. L., Bengtson, J., and Butz, I. (1973). Observations on upstream migration by imagines of some Plecoptera and Ephemeroptera. *Limnology and Oceanography*, 18: 678–681.
- Malmqvist, B. and Rundle, S. (2002). Threats to the running water ecosystems of the world. *Environmental Conservation*, 29 (2): 134–153.
- Masters, Z., Petersen, I., Hildrew, A. G., and Ormerod, S. J. (2007). Insect dispersal does not limit the biological recovery of streams from acidification. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 17: 375–383.
- McGill, B. J., Enquist, B. J., Weiher, E., and Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, 21: 178–185.
- Meier, C., Böhmer, J., Biss, R., Feld, C. K., Haase, P., Lorenz, A. W., Rawer-Jost, C., Rolauffs, P., Schindehütte, K., Schöll, F., Sundermann, A., Zenker, A., and Hering, D. (2006a). Weiterentwicklung und Anpassung des nationalen Bewertungssystems für Makrozoobenthos an neue internationale Vorgaben. Im Auftrag des Umweltbundesamtes. URL: http://www.fliessgewaesserbewertung.de/downloads/abschlussbericht%5C_20060331.pdf (visited on 04/04/2015).
- Meier, C., Haase, P., Rolauffs, P., Schindehütte, K., Schöll, F., Sundermann, A., and Hering, D. (2006b). Methodisches Handbuch Fließgewässerbewertung. Handbuch zur Untersuchung und Bewertung von Fließgewässern auf der Basis des Makrozoobenthos vor dem Hintergrund der EG-Wasserrahmenrichtlinie. URL: http://www.fliessgewaesserbewertung.de/downloads/abschlussbericht%5C_20060331%5C_anhang%5C_IX.pdf (visited on 04/04/2015).

- Mérigoux, S. and Dolédec, S. (2004). Hydraulic requirements of stream communities: A case study on invertebrates. *Freshwater Biology*, 49: 600–613.
- Merritt, R. W. and Cummins, K. W. (1995). An introduction to the aquatic insects of North America. 3rd edition. Kendall Hunt.
- Milhous, R. T., Wegner, D. L., and Waddle, T. (1984). User's guide to the physical habitat simulation system (PHABSIM). Instream flow information paper 11. Rev. B. Dept. of the Interior, U.S. Fish and Wildlife Service.
- Millennium Ecosystem Assessment (2005). Ecosystems and human well-being: wetlands and water. URL: <http://www.millenniumassessment.org/documents/document.358.aspx.pdf> (visited on 04/04/2015).
- Miller, S. W., Budy, P., and Schmidt, J. C. (2010). Quantifying macroinvertebrate responses to in-stream habitat restoration: Applications of meta-analysis to river restoration. *Restoration Ecology*, 18: 8–19.
- Minshall, G. W. (1967). Role of allochthonous detritus in the trophic structure of a woodland springbrook community. *Ecology*, 48 (1): 139–149.
- Minshall, J. N. (1967). Life history and ecology of *Epeorus pleuralis* (Banks) (Ephemeroptera: Heptageniidae). *American Midland Naturalist*, 78 (2): 369–388.
- Moller-Pillott, H. K. M. (1984). De larven der Nederlandse Chironomidae (Diptera). *Nederlandse Faunistische Mededelingen*, 1A + 1B.
- Monk, W. A., Wood, P. J., Hannah, D. M., Extence, C. A., Chadd, R. P., and Dunbar, M. J. (2012). How does macroinvertebrate taxonomic resolution influence ecohydrological relationships in riverine ecosystems. *Ecohydrology*, 5: 36–45.
- Moog, O. (1995). *Fauna Aquatica Austriaca*. Wasserwirtschaftskataster. Bundesministerium für Land- und Forstwirtschaft.
- Moss, B. R. (2010). *Ecology of freshwaters: a view for the twenty-first century*, 4th Edition. Wiley-Blackwell.
- Muotka, T. and Syrjänen, J. (2007). Changes in habitat structure, benthic invertebrate diversity, trout populations and ecosystem processes in restored forest streams: a boreal perspective. *Freshwater Biology*, 52: 724–737.
- Nakano, D. and Nakamura, F. (2006). Responses of macroinvertebrate communities to river restoration in a channelized segment of the Shibetsu River, Northern Japan. *River Research and Applications*, 22: 681–689.
- (2008). The significance of meandering channel morphology on the diversity and abundance of macroinvertebrates in a lowland river in Japan. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 18: 780–798.

- Negishi, J. N. and Richardson, J. S. (2003). Responses of organic matter and macroinvertebrates to placements of boulder clusters in a small stream of southwestern British Columbia, Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, 60: 247–258.
- Nhiwatiwa, T., Brendonck, L., Waterkeyn, A., and Vanschoenwinkel, B. (2011). The importance of landscape and habitat properties in explaining instantaneous and long-term distributions of large branchiopods in subtropical temporary pans. *Freshwater Biology*, 56: 1992–2008.
- Ormerod, S. J., Dobson, M., Hildrew, A. G., and Townsend, C. R. (2010). Multiple stressors in freshwater ecosystems. *Freshwater Biology*, 55: 1–4.
- Otto, C. and Sjöström, P. (1986). Behaviour of drifting insect larvae. *Hydrobiologia*, 131: 77–86.
- Palmer, M. A., Allan, J. D., Meyer, J., and Bernhardt, E. S. (2007). River restoration in the twenty-first century: Data and experiential knowledge to inform future efforts. *Restoration Ecology*, 15: 472–481.
- Palmer, M. A., Ambrose, R. F., and Poff, N. L. (1997). Ecological theory and community restoration ecology. *Restoration Ecology*, 5: 291–300.
- Palmer, M. A., Menninger, H. L., and Bernhardt, E. S. (2010). River restoration, habitat heterogeneity and biodiversity: A failure of theory or practice? *Freshwater Biology*, 55: 205–222.
- Pardo, I. and Armitage, P. D. (1997). Species assemblages as descriptors of mesohabitats. *Hydrobiologia*, 344: 111–128.
- Parker, M. S. (1989). Effect of substrate composition on detritus accumulation and macroinvertebrate distribution in a southern Nevada desert stream. *The Southwestern Naturalist*, 34: 181–187.
- Parkyn, S. M. and Smith, B. J. (2011). Dispersal constraints for stream invertebrates: setting realistic timescales for biodiversity restoration. *Environmental Management*, 48: 602–614.
- Pearson, R. G., Thuiller, W., Araújo, M. B., Martinez-Meyer, E., Brotons, L., McClean, C., Miles, L., Segurado, P., Dawson, T. P., and Lees, D. C. (2006). Model-based uncertainty in species range prediction. *Journal of Biogeography*, 33: 1704–1711.
- Pedersen, M. L., Kristensen, K. K., and Friberg, N. (2014). Re-meandering of lowland streams: will disobeying the laws of geomorphology have ecological consequences? *PLoS ONE*, 10 (3): e108558.

- Peeters, E. T. H. M., Gylstra, R., and Vos, J. H. (2004). Benthic macroinvertebrate community structure in relation to food and environmental variables. *Hydrobiologia*, 519: 103–115.
- Petersen, I., Masters, Z., Hildrew, A. G., and Ormerod, S. J. (2004). Dispersal of adult aquatic insects in catchments of differing land use. *Journal of Applied Ecology*, 41 (5): 934–950.
- Petersen, I., Winterbottom, J. H., Orton, S., Friberg, N., Hildrew, A. G., and Spiers, D. C. (1999). Emergence and lateral dispersal of adult Plecoptera and Trichoptera from Broadstone Stream, U.K. *Freshwater Biology*, 42: 401–416.
- Petruck, A. and Stöfler, U. (2011). On the history of chloride concentrations in the River Lippe (Germany) and the impact on the macroinvertebrates. *Limnologica - Ecology and Management of Inland Waters*, 41 (2): 143–150.
- Petty, J. T., Fulton, J. B., Strager, M. P., Merovich Jr, G. T., Stiles, J. M., and Ziemkiewicz, P. F. (2010). Landscape indicators and thresholds of stream ecological impairment in an intensively mined Appalachian watershed. *Journal of the North American Benthological Society*, 29: 1292–1309.
- Piscart, C., Bergerot, B., Laffaille, P., and Marmonier, P. (2010). Are amphipod invaders a threat to regional biodiversity? *Biological Invasions*, 12: 853–863.
- Piscart, C., Lecerf, A., Usseglio-Polatera, P., Moreteau, J.-C., and Beisel, J.-N. (2005a). Biodiversity patterns along a salinity gradient: The case of net-spinning caddisflies. *Biodiversity and Conservation*, 14: 2235–2249.
- Piscart, C., Manach, A., Copp, G. H., and Marmonier, P. (2007). Distribution and microhabitats of native and non-native gammarids (Amphipoda, Crustacea) in Brittany, with particular reference to the endangered endemic sub-species *Gammarus duebeni celticus*. *Journal of Biogeography*, 34: 524–533.
- Piscart, C., Moreteau, J.-C., and Beisel, J.-N. (2005b). Biodiversity and structure of macroinvertebrate communities along a small permanent salinity gradient (Meurthe River, France). *Hydrobiologia*, 551: 227–236.
- (2006a). Monitoring changes in freshwater macroinvertebrate communities along a salinity gradient using artificial substrates. *Environmental Monitoring and Assessment*, 116: 529–542.
- Piscart, C., Usseglio-Polatera, P., Moreteau, J.-C., and Beisel, J.-N. (2006b). The role of salinity in the selection of biological traits of freshwater invertebrates. *Archiv für Hydrobiologie*, 166: 185–198.

- Poff, N. L., Olden, J. D., Vieira, N. K. M., Finn, D. S., Simmons, M. P., and Kondratieff, B. C. (2006). Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. *Journal of the North American Benthological Society*, 25: 730–755.
- Poff, N. L. and Zimmerman, J. K. H. (2010). Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. *Freshwater Biology*, 55: 194–205.
- Potapova, M. and Charles, D. F. (2003). Distribution of benthic diatoms in U.S. rivers in relation to conductivity and ionic composition. *Freshwater Biology*, 48: 1311–1328.
- Pottgiesser, T. and Sommerhäuser, M. (2004). Fließgewässertypologie Deutschlands: Die Gewässertypen und ihre Steckbriefe als Beitrag zur Umsetzung der EU-Wasser-rahmenrichtlinie. In: *Handbuch der Limnologie*. 19. Ergänzungslieferung. Ed. by C. Steinberg, W. Calmano, R.-D. Wilken, and H. Klapper.
- Pottier, J., Dubuis, A., Pellissier, L., Maiorano, L., Rossier, L., Randin, C. F., Vittoz, P., and Guisan, A. (2013). The accuracy of plant assemblage prediction from species distribution models varies along environmental gradients. *Global Ecology and Biogeography*, 22: 52–63.
- Pretty, J. L. and Dobson, M. (2004). The response of macroinvertebrates to artificially enhanced detritus levels in plantation streams. *Hydrology and Earth System Sciences*, 8: 550–559.
- Qian, S. S., King, R. S., and Richardson, C. J. (2003). Two statistical methods for the detection of environmental thresholds. *Ecological Modelling*, 166: 87–97.
- R Development Core Team (2013). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. URL: <http://www.r-project.org> (visited on 04/04/2015).
- Rabeni, C. F., Doisy, K. E., and Galat, D. L. (2002). Testing the biological basis of a stream habitat classification using benthic invertebrates. *Ecological Applications*, 12 (3): 782–796.
- Rabeni, C. F. and Minshall, G. W. (1977). Factors affecting microdistribution of stream benthic insects. *Oikos*, 29: 33–43.
- Rawer-Jost, C., Kappus, B., Böhmer, J., Jansen, W., and Rahmann, H. (1999). Upstream movements of benthic macroinvertebrates in two different types of fishways in southwestern Germany. *Hydrobiologia*, 391: 47–61.

- Remane, A. and Schlieper, C. (1971). *Biology of brackish water*. Die Binnengewässer Series. Schweizerbart.
- Rempel, L. L., Richardson, J. S., and Healey, M. C. (2000). Macroinvertebrate community structure along gradients of hydraulic and sedimentary conditions in a large gravel-bed river. *Freshwater Biology*, 45 (1): 57–73.
- Resh, V. H. (1982). Age structure alteration in a caddisfly population after habitat loss and recovery. *Oikos*, 38: 280–284.
- Rinella, D. J. and Feminella, J. W. (2005). Comparison of benthic macroinvertebrates colonizing sand, wood, and artificial substrates in a low-gradient stream. *Journal of Freshwater Ecology*, 20: 209–220.
- Rolauffs, P. (2006). Modellierung ökologischer Zusammenhänge bei Mittelgebirgsbächen unter Berücksichtigung von Gewässermorphologie und Landnutzung im Hinblick auf die biozönotische Bewertung mittels Makroinvertebraten. PhD thesis. University of Duisburg-Essen.
- Roller, R. A. and Stickle, W. B. (1985). Effects of salinity on larval tolerance and early developmental rates of four species of echinoderms. *Canadian Journal of Zoology*, 63: 1531–1538.
- Roos, T. (1957). Studies on upstream migration in adult stream-dwelling insects. *Inst. Freshwater Res. Drottningholm*, 38: 167–193.
- Russev, B. K. (1973). Kompensationsflug bei der Ordnung Ephemeroptera. In: *Proceedings of the First International Conference on Ephemeroptera*. Ed. by W. L. Peters and J. G. Peters, pp. 132–142.
- Santika, T. and Hutchinson, M. F. (2009). The effect of species response form on species distribution model prediction and inference. *Ecological Modelling*, 220: 2365–2379.
- Saros, J. E. and Fritz, S. C. (2000). Nutrients as a link between ionic concentration/composition and diatom distributions in saline lakes. *Journal of Paleolimnology*, 23 (4): 449–453.
- Sarriquet, P. E., Bordenave, P., and Marmonier, P. (2007). Effects of bottom sediment restoration on interstitial habitat characteristics and benthic macroinvertebrate assemblages in a headwater stream. *River Research and Applications*, 23: 815–828.
- Schattmann, A. (2014). Ökologische Wirksamkeit von Renaturierungsmaßnahmen an einem Tieflandfluss - Reaktion von Hydromorphologie, Makrozoobenthos und Uferfauna. PhD thesis. University of Duisburg-Essen.

- Schaumburg, J., Schranz, C., Foerster, J., Gutowski, A., Hofmann, G., Meilinger, P., Schneider, S., and Schmedtje, U. (2004). Ecological classification of macrophytes and phytobenthos for rivers in Germany according to the water framework directive. *Limnologica*, 34: 283–301.
- Schilz, C. (2012). Herstellung der ökologischen Durchgängigkeit an der Orke. *Natur in NRW*, 37: 27–29.
- Schmalz, B., Kuemmerlen, M., Kiesel, J., Cai, Q., Jähnig, S. C., and Fohrer, N. (2014). Impacts of land use changes on hydrological components and macroinvertebrate distributions in the Poyang lake area. *Ecohydrology*, DOI: 10.1002/eco.1569.
- Schmedtje, U. and Colling, M. (1996). Ökologische Typisierung der aquatischen Makrofauna. Informationsberichte des Bayerischen Landesamtes für Wasserwirtschaft. Bayerisches Landesamt für Wasserwirtschaft.
- Schmidt-Kloiber, A., Graf, W., Lorenz, A., and Moog, O. (2006). The AQEM/STAR taxalist - a pan European macro-invertebrate ecological database and taxa inventory. *Hydrobiologia*, 566 (1): 325–342.
- Schmidt-Kloiber, A. and Hering, D. (2012). www.freshwaterecology.info - the taxa and autecology database for freshwater organisms, version 5.0. URL: <http://www.freshwaterecology.info> (visited on 04/01/2015).
- (2015). www.freshwaterecology.info – An online tool that unifies, standardises and codifies more than 20,000 European freshwater organisms and their ecological preferences. *Ecological Indicators*, 53: 271–282.
- Schröder, M., Kiesel, J., Schattmann, A., Jähnig, S. C., Lorenz, A. W., Kramm, S., Keizer-Vlek, H., Rolauuffs, P., Graf, W., Leitner, P., and Hering, D. (2013). Substratum associations of benthic invertebrates in lowland and mountain streams. *Ecological Indicators*, 30: 178–189.
- Schröder, M., Sondermann, M., Sures, B., and Hering, D. (2015). Effects of salinity gradients on benthic invertebrate and diatom communities in a German lowland river. Submitted to *Ecological Indicators*.
- Shaw, D. W. and Minshall, G. W. (1980). Colonization of an introduced substrate by stream macroinvertebrates. *Oikos*, 34: 259–271.
- Slooff, W. (1983). Benthic macroinvertebrates and water quality assessment: Some toxicological considerations. *Aquatic Toxicology*, 4: 73–82.
- Smith, R. F., Alexander, L. C., and Lamp, W. O. (2009). Dispersal by terrestrial stages of stream insects in urban watersheds: a synthesis of current knowledge. *Journal of the North American Benthological Society*, 28 (4): 1022–1037.

- Sommerhäuser, M., Lemmel, S., Eberhard, T., and Mählmann, S. (2009). Neozoen in der Lippe. *Natur in NRW*, 4/2009: 24–28.
- Sondermann, M., Gies, M., Hering, D., Schröder, M., and Feld, C. K. (2015). Modelling the effect of in-stream and terrestrial barriers on the dispersal of aquatic insect species: a case study from a Central European mountain catchment. *Fundamental and Applied Limnology*, 186 (1-2): 99–115.
- Soucek, D. J. and Kennedy, A. J. (2005). Effects of hardness, chloride, and acclimation on the acute toxicity of sulfate to freshwater invertebrates. *Environmental Toxicology and Chemistry*, 24: 1204–1210.
- Spänhoff, B., Alecke, C., and Meyer, E. (1999). The colonization of aquatic woody debris by Trichoptera, with special reference to the genus *Lype* (Psychomyiidae). *Proceedings of the 9th International Symposium on Trichoptera*: 349–358.
- Spänhoff, B., Alecke, C., and Meyer, E. I. (2000). Colonization of submerged twigs and branches of different wood genera by aquatic macroinvertebrates. *International Review of Hydrobiology*, 85: 49–66.
- Spänhoff, B., Reuter, C., and Meyer, E. I. (2006a). Epixylic biofilm and invertebrate colonization on submerged pine branches in a regulated lowland stream. *Archiv für Hydrobiologie*, 165: 515–536.
- Spänhoff, B., Riss, W., Jäkel, P., Dakkak, N., and Meyer, E. I. (2006b). Effects of an experimental enrichment of instream habitat heterogeneity on the stream bed morphology and chironomid community of a straightened section in a sandy lowland stream. *Environmental Management*, 37: 247–257.
- Sponseller, R. A., Benfield, E. F., and Valett, H. M. (2001). Relationships between land use, spatial scale and stream macroinvertebrate communities. *Freshwater Biology*, 46: 1409–1424.
- Šporka, F., Vlek, H. E., Bulánková, E., and Krno, I. (2006). Influence of seasonal variation on bioassessment of streams using macroinvertebrates. *Hydrobiologia*, 566: 543–555.
- Statzner, B. and Bêche, L. A. (2010). Can biological invertebrate traits resolve effects of multiple stressors on running water ecosystems? *Freshwater Biology*, 55: 80–119.
- Stettmer, C. (1996). Colonisation and dispersal patterns of banded (*Calopteryx splendens*) and beautiful demoiselles (*C. virgo*) (Odonata: Calopterygidae) in south-east German streams. *European Journal of Entomology*, 93: 579–593.

- Sundermann, A., Stoll, S., and Haase, P. (2011). River restoration success depends on the species pool of the immediate surroundings. *Ecological Applications*, 21: 1962–1971.
- Swets, J. A. (1988). Measuring the accuracy of diagnostic systems. *Science*, 240: 1285–1293.
- Testa III, S., Shields Jr, F. D., and Cooper, C. M. (2011). Macroinvertebrate response to stream restoration by large wood addition. *Ecohydrology*, 4: 631–643.
- Thiele, V., Mehl, D., Berlin, A., and Huijssoon, L. (1998). Untersuchungen zum Gegenstromwanderungsverhalten aquatischer und zum Gegenstromflug merolimnischer Evertebraten im Bereich von Fischaufstiegsanlagen in Mecklenburg-Vorpommern (Deutschland). *Limnologica*, 28: 167–182.
- Thompson, R. and Townsend, C. (2006). A truce with neutral theory: local deterministic factors, species traits and dispersal limitation together determine patterns of diversity in stream invertebrates. *Journal of Animal Ecology*, 75: 476–484.
- Tikkanen, P., Laasonen, P., Muotka, T., Huhta, A., and Kuusela, K. (1994). Short-term recovery of benthos following disturbance from stream habitat rehabilitation. *Hydrobiologia*, 273: 121–130.
- Timm, H., Käiro, K., Möls, T., and Virro, T. (2011). An index to assess hydromorphological quality of Estonian surface waters based on macroinvertebrate taxonomic composition. *Limnologica*, 41: 398–410.
- Tockner, K., Pusch, M., Borchardt, D., and Lorang, M. S. (2010). Multiple stressors in coupled river-floodplain ecosystems. *Freshwater Biology*, 55: 135–151.
- Tockner, K., Uehlinger, U., and Robinson, C. T. (2009). *Rivers of Europe*. Academic Press.
- Tonkin, J. D. and Death, R. G. (2012). Consistent effects of productivity and disturbance on diversity between landscapes. *Ecosphere*, 3: 108.
- Tonkin, J. D., Death, R. G., and Collier, K. J. (2012). Do productivity and disturbance interact to modulate macroinvertebrate diversity in streams? *Hydrobiologia*, 701: 159–172.
- Tonkin, J. D., Stoll, S., Sundermann, A., and Haase, P. (2014). Dispersal distance and the pool of taxa, but not barriers, determine the colonisation of restored river reaches by benthic invertebrates. *Freshwater Biology*, 59 (9): 1843–1855.
- Tronstad, L. M., Tronstad, B. P., and Benke, A. C. (2007). Aerial colonization and growth: rapid invertebrate responses to temporary aquatic habitats in a river floodplain. *Journal of the North American Benthological Society*, 26: 460–471.

- Usseglio-Polatera, P., Bournaud, M., Richoux, P., and Tachet, H. (2000). Biomonitoring through biological traits of benthic macroinvertebrates: how to use species trait databases? *Hydrobiologia*, 422/423: 153–162.
- van Dam, H., Mertens, A., and Sinkeldam, J. (1994). A coded checklist and ecological indicator values of freshwater diatoms from The Netherlands. *Netherlands Journal of Aquatic Ecology*, 28 (1): 117–133.
- van De Meutter, F., De Meester, L., and Stoks, R. (2007). Metacommunity structure of pond macroinvertebrates: Effects of dispersal mode and generation time. *Ecology*, 88: 1687–1695.
- Van Leeuwen, C. H. A., van der Velde, G., van Groenendael, J. M., and Klaassen, M. (2012). Gut travellers: Internal dispersal of aquatic organisms by waterfowl. *Journal of Biogeography*, 39: 2031–2040.
- Vandewalle, M., de Bello, F., Berg, M. P., Bolger, T., Dolédec, S., Dubs, F., Feld, C. K., Harrington, R., Harrison, P. A., Lavorel, S., da Silva, P. M., Moretti, M., Niemelä, J., Santos, P., Sattler, T., Sousa, J. P., Sykes, M. T., Vanbergen, A. J., and Woodcock, B. A. (2010). Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. *Biodiversity and Conservation*, 19: 2921–2947.
- Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R., and Cushing, C. E. (1980). The River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences*, 37: 130–137.
- Velásquez, S. M. and Miserendino, M. L. (2003). Habitat type and macroinvertebrate assemblages in low order Patagonian streams. *Archiv für Hydrobiologie*, 158: 461–483.
- Verberk, W. C. E. P., van Noordwijk, C. G. E., and Hildrew, A. G. (2013). Delivering on a promise: integrating species traits to transform descriptive community ecology into a predictive science. *Freshwater Science*, 32: 531–547.
- Verdonschot, P. F. M. (2006). Data composition and taxonomic resolution in macroinvertebrate stream typology. *Hydrobiologia*, 566: 59–74.
- Verrier, M. L. (1953). Le rhéotropisme et les larves d'éphémères. *Bull. Biol. Fr. Belg.* 87: 1–33.
- Viana, D. S., Santamaría, L., Michot, T. C., and Figuerola, J. (2013). Migratory strategies of waterbirds shape the continental-scale dispersal of aquatic organisms. *Ecography*, 36: 430–438.

- Vieira, N. K. M., Poff, N. L., Carlisle, D. M., Moulton II, S. R., Koski, M. L., and Kondratieff, B. C. (2006). A database of lotic invertebrate traits for North America. URL: <http://pubs.usgs.gov/ds/ds187/> (visited on 04/04/2015).
- Vinikour, W. S. (1981). Aquatic insect drift through a final-cut strip mine pit, with emphasis on drift distances. *Hydrobiologia*, 77 (3): 225–232.
- Vlek, H. E., Šporka, F., and Krno, I. (2006). Influence of macroinvertebrate sample size on bioassessment of streams. *Hydrobiologia*, 566: 523–542.
- Vlek, H. E., Verdonchot, P. F. M., and Nijboer, R. C. (2004). Towards a multimetric index for the assessment of Dutch streams using benthic macroinvertebrates. *Hydrobiologia*, 516: 173–189.
- Wallace, J. B. (1990). Recovery of lotic macroinvertebrate communities from disturbance. *Environmental Management*, 14: 605–620.
- Wallace, J. B., Huryn, A. D., and Lugthart, G. J. (1991). Colonization of a headwater stream during three years of seasonal insecticidal applications. *Hydrobiologia*, 211: 65–76.
- Wang, Z., Melching, C. S., Duan, X., and Yu, G. (2009). Ecological and hydraulic studies of step-pool systems. *Journal of Hydraulic Engineering*, 135: 705–717.
- Ward, J. V. (1975). Bottom fauna-substrate relationships in a northern Colorado trout stream: 1945 and 1974. *Ecology*, 56: 1429–1434.
- Ward, L. and Mill, P. J. (2007). Long range movements by individuals as a vehicle for range expansion in *Calopteryx splendens* (Odonata: Zygoptera). *European Journal of Entomology*, 104 (2): 195–198.
- Waringer, J. and Graf, W. (1997). Atlas der österreichischen Köcherfliegenlarven unter Einschluss angrenzender Gebiete. *Facultas Universitätsverlag*.
- Waterkeyn, A., Grillas, P., Vanschoenwinkel, B., and Brendonck, L. (2008). Invertebrate community patterns in Mediterranean temporary wetlands along hydroperiod and salinity gradients. *Freshwater Biology*, 53: 1808–1822.
- Wiens, J. J., Ackerly, D. D., Allen, A. P., Anacker, B. L., Buckley, L. B., Cornell, H. V., Damschen, E. I., Davies, T. J., Grytnes, J.-A., Harrison, S. P., Hawkins, B. A., Holt, R. D., McCain, C. M., and Stephens, P. R. (2010). Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters*, 13: 1310–1324.
- Wijnhoven, S., van Riel, M. C., and van der Velde, G. (2003). Exotic and indigenous freshwater gammarid species: physiological tolerance to water temperature in relation to ionic content of the water. *Aquatic Ecology*, 37: 151–158.

- Williams, D. D. and Williams, N. E. (1998). Aquatic insects in an estuarine environment: densities, distribution and salinity tolerance. *Freshwater Biology*, 39: 411–421.
- Williams, W. D. (1987). Salinization of rivers and streams: an important environmental hazard. *Ambio*, 16: 180–185.
- (1999). Salinisation: A major threat to water resources in the arid and semi-arid regions of the world. *Lakes and Reservoirs: Research and Management*, 4: 85–91.
- Wisz, M. S., Hijmans, R. J., Li, J., Peterson, A. T., Graham, C. H., and Guisan, A. (2008). Effects of sample size on the performance of species distribution models. *Diversity and Distributions*, 14: 763–773.
- Wohl, D. L., Wallace, J. B., and Meyer, J. L. (1995). Benthic macroinvertebrate community structure, function and production with respect to habitat type, reach and drainage basin in the southern Appalachians (USA). *Freshwater Biology*, 34: 447–464.
- Wolf, B. (2004). Datenbank zu den Metrics des Makrozoobenthos der Marschengewässer Niedersachsens. Im Auftrag der Hochschule Vechta.
- Wolf, B., Kiel, E., Hagge, A., Krieg, H. J., and Feld, C. K. (2009). Using the salinity preferences of benthic macroinvertebrates to classify running waters in brackish marshes in Germany. *Ecological Indicators*, 9: 837–847.
- Wolff, W. J. (2000). Recent human-induced invasions of fresh waters by saltwater animals? *Aquatic Ecology*, 34 (3): 319–321.
- Wood, P. J. and Armitage, P. D. (1997). Biological effects of fine sediment in the lotic environment. *Environmental Management*, 21: 203–217.
- Wood, P. J., Armitage, P. D., Cannan, C. E., and Petts, G. E. (1999). Instream mesohabitat biodiversity in three groundwater streams under base-flow conditions. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 9: 265–278.
- Ziemann, H. (1971). Die Wirkung des Salzgehaltes auf die Diatomeenflora als Grundlage für eine biologische Analyse und Klassifikation der Binnengewässer. *Limnologica*, 8: 505–525.
- Ziemann, H., Kies, L., and Schulz, C.-J. (2001). Desalinization of running waters. *Limnologica - Ecology and Management of Inland Waters*, 31 (4): 257–280.

Appendix

Appendices are available on the enclosed CD-ROM.

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Eidesstattliche Erklärungen

Erklärung:

Hiermit erkläre ich, gem. § 6 Abs. (2) f) der Promotionsordnung der Fakultäten für Biologie, Chemie und Mathematik zur Erlangung der Dr. rer. nat., dass ich das Arbeitsgebiet, dem das Thema “Explaining the distribution of riverine macroinvertebrates: from autecological preferences to a catchment-wide perspective” zuzuordnen ist, in Forschung und Lehre vertrete und den Antrag von Maria Schröder befürworte.

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Hiermit erkläre ich, gem. § 7 Abs. (2) d) + f) der Promotionsordnung der Fakultäten für Biologie, Chemie und Mathematik zur Erlangung des Dr. rer. nat., dass ich keine anderen Promotionen bzw. Promotionsversuche in der Vergangenheit durchgeführt habe und dass diese Arbeit von keiner anderen Fakultät abgelehnt worden ist.

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