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Disentangling environmental drivers of benthic invertebrate assemblages: The role of spatial scale and riverscape heterogeneity in a multiple stressor environment

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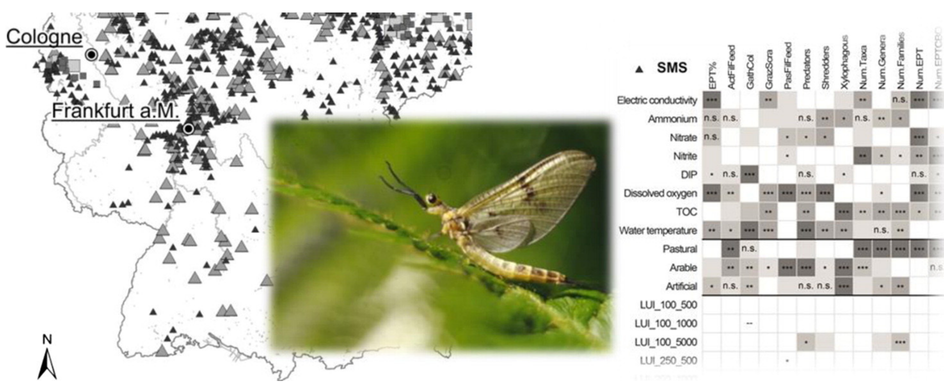
HIGHLIGHTS

- High impact factors controlling benthic invertebrate assemblages were identified.
- Relevant stressors varied across streams of different sizes and ecoregions.
- Land use was less relevant in large rivers compared to lower order streams.
- Mitigating effects of buffer strips might be overwhelmed by catchment-wide land use.
- Results enable more effective treatment of relevant stressors at appropriate scales.

GRAPHICAL ABSTRACT



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ABSTRACT

It is broadly acknowledged that freshwater ecosystems are affected by multiple stressors, but the relative importance of individual stressors in impairing riverine communities remains unclear. We investigated the impacts of multiple stressors, incorporating in-stream water quality, riparian and catchment land use and stream morphology, on riverine benthic invertebrate communities, while considering the spatial scales of factors and the heterogeneity of riverscapes. We performed a stepwise regression procedure linking 21 abiotic and 20 community metrics using Generalized Linear Models on data from 1018 river sites spread across Germany. High impact stressors (e.g., nutrients and water temperature) were identified for various community metrics. Both the combination of relevant stressors and their explanatory value differed significantly across streams of different sizes and ecoregions. In large rivers, the riparian land use was less important in determining community structure compared to lower order streams. Thus, possible mitigating effects of revegetated riparian buffer strips are likely to be overwhelmed by the influence of catchment-wide land use. Our results indicated substantial variability in stressors for the range of metrics studied, providing insight into potential target parameters for effective ecosystem management. To achieve long lasting successes in managing, protecting and restoring running waters, it is of vital importance to recognize the heterogeneity of riverscapes and to consider large-scale influences.

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1. Introduction

Stream biodiversity is severely threatened by anthropogenic activities such as catchment land use changes (Allan, 2004; Sala et al., 2000). The on-going intensification of both agriculture (Allan et al., 1997) and urban development (Walsh et al., 2005; Wenger et al., 2009) has led to degradation of aquatic habitats, in turn causing impoverished biological conditions in freshwater ecosystems worldwide. A suite of multiple stressors accompany these land use changes including increased organic matter, nutrients, contaminants, sediments and altered thermal regimes (Allan, 2004). Moreover, increased impervious areas in the catchment and river regulation alter the rivers' hydrology and cause deficiencies of in-stream hydromorphology (Allan et al., 1997; Sponseller et al., 2001). Ongoing climate change adds a novel and powerful driver of freshwater biodiversity change (Domisch et al., 2011; Palmer et al., 2009; Sala et al., 2000). However, the pathways of influence through which riverine communities are affected by multiple stressors and species' response characteristics are often unknown (Harding et al., 1998), with additional research needed to disentangle stress-induced change. Both research and application in water management inevitably involve the consideration of the following basic dimensions of complexity: first, the multiplicity of factors and their effects (i.e., multiple stressors; Munns, 2006); second, the spatial scales of influences (Wiens, 1989); and third, the heterogeneity of riverscapes across landscapes and ecoregions (see Rosgen, 1994).

1.1. Multiple stressors

Anthropogenic stressors often act simultaneously (multiple stressors) with possible interactive effects (Munns, 2006). The effects of multiple stressors on riverine benthic invertebrate communities have already been studied thoroughly in mesocosm experiments (Matthaei et al., 2010; Piggott et al., 2012, 2015; Wagenhoff et al., 2012), field surveys (Sundermann et al., 2013; Wagenhoff et al., 2011), and combinations of both (Townsend et al., 2008). Given the fact that species responses cannot be understood by examining stressors independently (Townsend et al., 2008), identifying the importance of stressors among a suite of potential influences is still a major focus of freshwater ecological research. For this purpose, analysing field data comes with the advantage that cause and effect relationships can be studied in-situ, with focus on a wide range of stressors and spatiotemporal scales. Yet, this requires comprehensive well replicated data and complex statistical analyses to disentangle the effects.

1.2. Spatial scales

Streams are organised hierarchically within the landscape (Frissel et al., 1986), and are controlled by factors operating at a range of spatial scales (Brosse et al., 2003; Mykrä et al., 2007). For instance, land use can exert control on stream communities from the riparian zone (local scale) through to the entire upstream catchment (catchment scale); in-stream habitat quality (i.e., hydromorphology) shapes assemblages on the local scale, whereas physico-chemical water quality at the local stream site is a function of catchment-scale processes (Allan et al., 1997; Roth et al., 1996; Sponseller et al., 2001).

The lack of success in river restoration projects with focus on enhancing local habitat diversity (Palmer et al., 2010) likely reflects the fact that physico-chemical water quality can override local improvements in habitat structure (Roni et al., 2008). However, whether land use activities and vegetative cover of the land immediately adjacent to the watercourse (riparian buffer strips) or of the whole catchment more strongly control the rivers' physico-chemical and ecological conditions remains uncertain and is widely discussed (Harding et al., 1998; Potter et al., 2005). Thus, water management practice requires further knowledge regarding the scale at which their efforts in managing, protecting and restoring running waters should be directed (see Hunsaker et al., 1990).

Riparian vegetation plays an important role in regulating stream temperature (shading) and water chemistry (e.g., reducing nutrient and sediment input), supplying food, energy and habitat and shaping channel morphology (Allan, 2004; Harding et al., 1998; Osborne and Kovacic, 1993; Potter et al., 2005; Vought et al., 1995). In fact, recent work has shown that riparian shading can indeed somewhat mitigate the impact of agricultural land use in the catchment (Burrell et al., 2014). However, some research suggests that there exists a more direct relationship between catchment-wide land use and the rivers' integrity (Kuemmerlen et al., 2014; Potter et al., 2005; Roth et al., 1996; Sliva and Williams, 2001; Wang et al., 1997; Weigel et al., 2000). This may be particularly the case for larger catchments (Johnson et al., 2001), where mitigating effects are possibly overwhelmed by catchment-scale processes. Consequently, clarification is needed on whether it is sufficient to preserve and revegetate the riparian zones in attempt to mitigate the impacts of catchment degradation.

1.3. Heterogeneity of riverscapes

Many methods of bioassessment are based on specific reference conditions, allowing comparisons between observed and expected community structures (Hawkins et al., 2010). This applies, for instance, to Europe's assessment system AQEM (Hering et al., 2004a; Nijboer et al., 2004), to the US Clean Water Act (Stoddard et al., 2006) and the Australian Water Reform Framework (Pardo et al., 2012). These various bioassessment approaches acknowledge the fact that lotic systems host differing communities depending on the natural abiotic gradients within the river continuum (Vannote et al., 1980) and, more generally, across different river types of separate ecoregions (Doledec et al., 1999). While investigating novel pressures originating from anthropogenic alteration, it is essential to account for this sort of natural variation (Tonkin, 2014). Lorenz et al. (2004b) showed that benthic invertebrate community composition differed strongly in respect of both catchment size (stream order) and ecoregion. Different stream types providing certain characteristics in habitat structure, energy flow, hydrology, chemistry and temperature regimes may thus induce specific communities with context-dependent biotic and abiotic interactions with their environment (Tonkin et al., 2015).

1.4. Research objectives

Given the uncertainty of the most important stressors and scales at which they operate, we investigated which physico-chemical stressors and catchment land uses exert the strongest influences on invertebrate community structure. To do this, we analysed a large and high-quality set of field-derived data from 1018 river sites (minus 9 outliers) spread across Germany with an average number of 49 ± 36 (SD) single recordings for each physico-chemical variable at each site. We correlated (1) local water chemistry data, (2) local hydromorphological quality data and (3) local-, regional- and catchment-scale land use data against 20 invertebrate metrics (i.e., composition, diversity, richness or sensitivity of the invertebrate fauna). Finally, we determined the similarity of individual results, which were calculated separately for different stream types. The following hypotheses were tested: (i) Relevant environmental stressors for shaping benthic invertebrate community assemblages differ in respect of catchment sizes and ecoregions, (ii) land use of the riparian zone is more relevant for biotic stream integrity for smaller rivers, whereas catchment-wide land use is more relevant for larger rivers.

Our findings will provide required knowledge for adapting current methods towards a future practice of management, enabling more effective treatment of relevant stressors at appropriate scales. The selection of restoration measures, sites and further actions in water management should be guided by these outcomes to enhance the restoration success and to overcome the frequently reported failures of hydromorphological river restoration projects. Lack of recovery is often observed for benthic invertebrate communities, probably as a combined result of accounting for the wrong stressors, implementing inappropriate methods, and the lack of attention to species pools, dispersal constraints and spatial scales (Bernhardt and Palmer, 2011; Haase et al., 2013; Jähnig et al., 2010; Palmer et al., 2010; Sundermann et al., 2011a,b; Tonkin et al., 2014).

2. Methods

2.1. Sample sites

In the present study, a total of 1018 river sites situated in nine Federal States of Germany were investigated (Fig. 1). The database comprises the full gradient of ecological conditions from near-natural to highly impaired. Catchment sizes range from 0.1 to 7125 km^2 at elevations of 1 to 711 m asl. The dataset was divided into four groups to account for different catchment properties (further referred to as stream type groups). Based on the findings of Lorenz et al. (2004b), who found clear separation in the composition of benthic communities between sites of these stream type groups, ecoregions (mountainous areas vs. lowlands) and catchment sizes (<100 km^2 vs. ≥100 km^2) were distinguished. Thus, the stream type groups were small and large mountain streams (SMS, LMS) and small and large lowland streams (SLS, LLS) with site numbers of 504, 219, 212 and 83, respectively.

2.2. Benthic invertebrate sampling

Benthic invertebrate samples of each site originated from routine surface water surveys according to the protocol for collecting samples in river monitoring programs to assess the ecological status of rivers in Germany (Haase et al., 2004, compare also European Standard EN 16150:2012). Samples were collected at each site from February to August in 2007 to 2010. The sampling method is based on sampling microhabitats according to their coverage at the sampling site (multi-habitat sampling). All microhabitats in a 100-m-long stream section that are represented with a minimum coverage of 5% are recorded in 5% coverage intervals, and each "sampling unit" (25 × 25 cm) is sampled using a handnet (mesh size: 0.5 mm) via the kick sampling method. A complete sample is comprised of 20 sampling units, which are pooled for further analysis (total sampling area of 1.25 square metres). The organisms are sorted from the sediments in the laboratory and identified according to the "Operational Taxalist for Running Waters in Germany" (Haase et al., 2006). The latter defines the minimum taxonomic level, the identification keys that have to be used and enables consistency in the identification work of involved laboratories.

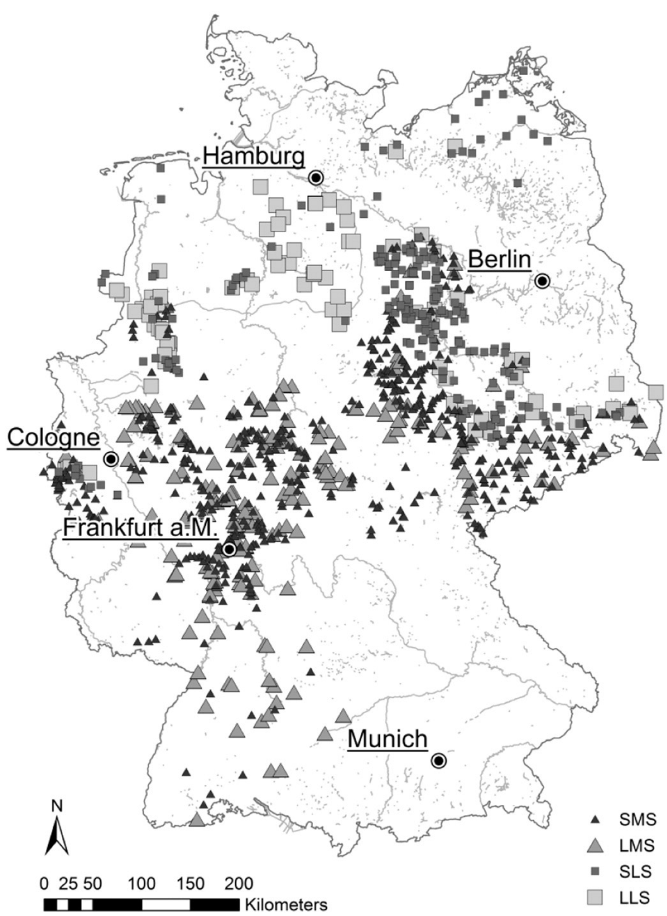


Fig. 1. Location of the 1018 sample sites in Germany. The classification into the four stream type groups is indicated by different symbols: small and large triangles show small and large mountain streams (SMS and LMS) and small and large squares show small and large lowland streams (SLS and LLS), respectively.

2.3. Community metrics

To describe the benthic invertebrate assemblages, 20 metrics were calculated for each site. These can be classified into four metric types: composition/abundance, richness/diversity, sensitivity/tolerance and percentage of functional groups (Hering et al., 2004b; Table 1). As the four sensitivity/tolerance metrics are not self-explanatory, they will be explained here. The stream type specific multi-metric index (MMI) is a German national metric that describes the general degradation of a site. For each river type, the MMI is the weighted mean value of three to five metrics scaled to values between zero (poor quality) and one (high quality) according to specific reference conditions (Böhmer et al., 2004). Among these metrics, the stream type specific German Fauna Index (indicating the hydromorphological degradation of the sites; see Lorenz et al., 2004a) accounts for 50% of the MMI. A full list of the included metrics is provided in the Supporting Information (Appendix A). The German Saprobic Index (GSI; see Friedrich and Herbst, 2004; Rolauffs et al., 2004), is one of many indices used in the European Union to assess the organic pollution of streams via the estimated oxygen demand of benthic invertebrate species (Sandin and Hering, 2004). The Biological Monitoring Working Party (BMWP) score equals the sum of the tolerance scores of all benthic invertebrate families in a sample, and a high BMWP score represents good water quality (Hawkes, 1998). The Average Score Per Taxon (ASPT) is the BMWP score of the sample divided by the number of scoring families that contributed to the BMWP score (Armitage et al., 1983). These metrics were calculated with the software ASTERICS, Version 3.01 (http://www.fliessgewaesserbewertung.de/download/berechnung).

2.4. Physico-chemical data

Data on the following physico-chemical variables were available for all investigated sites: electric conductivity, ammonium, nitrate, nitrite, dissolved inorganic phosphorous (DIP), dissolved oxygen and water temperature (for units, see Table 1). The variables were measured between the years 2004 and 2011 and an average of 49 ± 36 (SD) single recordings was performed for each variable at each site. The chemical status of each sample site was estimated by averaging single recordings, where a minimum number of eight recordings was required.

2.5. Land use data

To calculate upstream catchment land use, we used Corine Land Cover classes (CLC2000, www.eea.europa.eu; Keil et al., 2005) grouped into the following categories: (1) artificial surfaces (CLC class 1), (2) arable land and permanent crops (CLC classes 2.1 and 2.2) and (3) pastures and heterogeneous agricultural areas (CLC classes 2.3 and 2.4). The remaining cover is comprised of forest and other natural land cover (CLC classes 3–5). For use in the calculations, the percent coverages of the non-natural land use classes within the total catchment area were quantified. As the natural land cover builds a linear combination of the non-natural land use classes, including the natural land cover would not have added any statistical value. In addition, a Land Use Index was calculated according to Eq. (1) (Böhmer et al., 2004), using percentages of land use based on nine different sized buffer strips. These enclose adjoining areas upstream of the sample sites on both river banks. Widths of 100, 250 and 500 m and lengths of 500, 1000 and 5000 m were considered. As indicated in Table 1, LUI buffers has been named according to LUI_X_Y, with X and Y representing the buffer width and length, respectively.

$$\mathrm{LUI} = \text{pastural cover } [\%] + 2 \cdot \text{ arable cover } [\%] + 4 \cdot \text{ artificial cover } [\%] \quad (1)$$

2.6. Hydromorphological data

The river habitat survey method of LAWA (Kamp et al., 2007) was used to assess the local-scale habitat structure of a site. This method considers a 100-m-long stream section for which a total of 26 variables are investigated, such as erosion, flow diversity, bank stabilisation, constructions, substratum type, cross-section form (for details, see Kamp et al., 2007). The river habitat survey method uses a seven-step scale that defines the difference between actual and natural condition, so that each site can take integer values between 1 (undisturbed) and 7 (completely disturbed).

2.7. Calculations

All analyses were performed using R version 3.1.0 (R Core Team, 2014). The predictors were initially checked for collinearity using Spearman's rank correlation test (collinearity was assumed for $|\rho| \geq 0.7$; see Dormann et al., 2013). Subsequently, a multivariate outlier analysis according to McCune and Grace (2002) was performed, removing each site whose mean Euclidean Distance of the predictors to all other sample sites exceeded the total average by more than three times the respective standard deviation.

Multiple regression analyses were performed to model the invertebrate metrics using physico-chemical, hydromorphological and land use parameters as predictors. The analyses were repeated for each of the metrics and the four stream type groups, respectively. We applied Generalized Linear Models (GLM; Hardin and Hilbe, 2012), which is a statistically robust method, used frequently to model species occurrences and distributions (Guarino et al., 2012; McCarthy and Elith, 2002). All count data metrics were modelled with negative binomial distributed GLMs and the log link (see O'Hara and Kotze, 2010), using the R function glm.nb (MASS package; Ripley et al., 2012). The negative binomial has been demonstrated to be an appropriate distributional assumption to overcome common overdispersion in invertebrate density data (Gray, 2005). All other metrics were modelled with Gaussian distributed GLM and the identity link, while percentage metrics were logit transformed beforehand, according to Warton and Hui (2011).

Full GLM were built including all physico-chemical parameters, the catchment-wide percentage covers of pastoral, arable and artificial land use as well as one particular LUI buffer. Due to collinearity between single LUI buffers (Table 2), a simultaneous use of several buffers would have violated the multiple regressions' requirements. Hence, only the one LUI buffer was used, which was able to minimize the $\mathrm{AIC_c}$ in the full model. The $\mathrm{AIC_c}$ is the small-sample (second-order) bias adjusted AIC (Akaike Information Criterion; Burnham and Anderson, 2001).

A model selection procedure using backward elimination was applied, pruning the models while minimizing the $\mathrm{AIC_c}$ to find the most parsimonious model that adequately describes the data. Calculations were done using a modified version of the R function stepAIC (originally included in the MASS package; Ripley et al., 2012). The simplified models (further referred to as reduced models) were checked for

Table 1
Community metrics and environmental variables analysed. Metric types for community metrics (column 3) are coded as follows: C/A, composition and abundance; F, function; R/D, richness and diversity; S/T, sensitivity and tolerance. Units are specified in columns 4 and 7 (i, integer; n.i., non-integer). For explanation of the Land Use Index (LUI), see Eq. (1).

Community metrics				Environmental variables		
Full names	Short names	Metric types	Units	Full names	Short names	Units
Ephemeroptera, Plecoptera and Trichoptera; percentage of abundance	EPT%	C/A	Percentages	Electric conductivity		$\mathrm{mS\ m^{-1}}$
Percentage of active filter feeders	ActFilFeed	F	Percentages	Ammonium		$\mathrm{mg\ L^{-1}}$
Percentage of gatherers and collectors	GathCol	F	Percentages	Nitrate		$\mathrm{mg\ L^{-1}}$
Percentage of grazers and scrapers	GrazScra	F	Percentages	Nitrite		$\mathrm{mg\ L^{-1}}$
Percentage of passive filter feeders	PasFilFeed	F	Percentages	Dissolved inorganic phosphorus	DIP	$\mathrm{mg\ L^{-1}}$
Percentage of predators	Predators	F	Percentages	Total organic carbon	TOC	$\mathrm{mg\ L^{-1}}$
Percentage of shredders	Shredders	F	Percentages	Dissolved oxygen		$\mathrm{mg\ L^{-1}}$
Percentage of xylophagous taxa	Xylophagous	F	Percentages	Water temperature		$\mathrm{mg\ L^{-1}}$
Number of taxa	Num.Taxa	R/D	Count	Percentage of pastural land use	Pastural	Percentages
Number of genera	Num.Genera	R/D	Count	Percentage of arable land use	Arable	Percentages
Number of families	Num.Families	R/D	Count	Percentage of artificial land use	Artificial	Percentages
Number of Ephemeroptera, Plecoptera and Trichoptera	Num.EPT	R/D	Count	Land use index (LUI) for buffers of 100 × 500 m (length × width)	LUI_100_500	Index (0–400; n.i.)
Number of Ephemeroptera, Plecoptera, Trichoptera, Coleoptera, Bivalvia and Odonata	Num.EPTCBO	R/D	Count	LUI for buffers of 100 × 1000 m	LUI_100_1000	Index (0–400; n.i.)
Shannon-Wiener diversity index[a]	ShanWien	R/D	Index (positive; n.i.)	LUI for buffers of 100 × 5000 m	LUI_100_5000	Index (0–400; n.i.)
Simpson diversity index[b]	Simpson	R/D	Index (positive; n.i.)	LUI for buffers of 250 × 500 m	LUI_250_500	Index (0–400; n.i.)
Evenness[c]	Evenness	R/D	Index (positive; n.i.)	LUI for buffers of 250 × 1000 m	LUI_250_1000	Index (0–400; n.i.)
Biological Monitoring Working Party[d]	BMWP	S/T	Index (positive; i.)	LUI for buffers of 250 × 5000 m	LUI_250_5000	Index (0–400; n.i.)
Average Score per Taxon[d]	ASPT	S/T	Index (positive; n.i.)	LUI for buffers of 500 × 500 m	LUI_500_500	Index (0–400; n.i.)
German Saprobic Index[e]	GSI	S/T	Index (positive; n.i.)	LUI for buffers of 500 × 1000 m	LUI_500_1000	Index (0–400; n.i.)
Multi metric index[f]	MMI	S/T	Index (0–1; n.i.)	LUI for buffers of 500 × 5000 m	LUI_500_5000	Index (0–400; n.i.)
				Index of hydromorphological quality	Hydromorphology	Index (1–7; i.)

[a] Shannon and Weaver (1948).
[b] Simpson (1949).
[c] Pielou (1966).
[d] Armitage et al. (1983).
[e] Friedrich and Herbst (2004) and Rolauffs et al. (2004).
[f] Böhmer et al. (2004).

overall model significance through the χ^2-test and for predictor-specific significances using Wald tests (Wald, 1943). Moreover, percentages of deviance explained compared to the constant only model were calculated for the complete reduced model and for each included predictor individually (McCullagh and Nelder, 1989). Note that the latter do not add up to the total percentage of deviance explained.

In addition, a bootstrap approach (see Crowley, 1992) was applied to consider uncertainties of the model selection procedure due to sample composition. Each stepwise regression was repeated 1000 times, performing random resampling of the data (with replacement). Percentages of selections for each predictor were calculated for being included in the bootstrapped reduced models with a minimum significance level of 5%.

A final approach was performed to determine the similarity of individual model outcomes, which were calculated separately for different stream type groups. To do this, hierarchical cluster analyses were applied individually for each invertebrate metric. The predictor-specific percentages of deviance explained were tabulated for each of the four stream type-specific models of each single metric. In the case of missing predictors in a particular reduced model, percentages of zero were assumed. A distance matrix was calculated, comparing the four sets of values with Euclidean distances. Subsequently, the similarities of the models were assessed and significant clusters were identified. Both the clustering and an uncertainty assessment were performed using the pvclust package for R (Suzuki and Shimodaira, 2006), which calculates probabilities for clusters being significant (so-called approximately unbiased *P*-values) using bootstrap resampling techniques. Significance of a cluster was assumed for probability values larger than 95%.

3. Results

The mean number of taxa and individuals collected and identified from each sample was 31.2 ± 11.7 (SD) and 1145 ± 2230, respectively. Of these individuals, 33.2 ± 24.5% belonged to Ephemeroptera, Plecoptera and Trichoptera. Functional community composition was dominated by gatherers and collectors (GathCol), showing an average dominance of 25.1 ± 12.6%, whereas xylophagous taxa formed the least common feeding habit (0.15 ± 0.61% of the recorded individuals). The multimetric index (MMI) varied broadly from 0 to 0.98 with an average of 0.41 ± 0.26. Catchments were dominated by arable land use (42.5 ± 28%), followed by natural land use (34.3 ± 23.4%) and pastures (16 ± 14.3%). A comprehensive and stream type-specific summary of community and abiotic data is included in the Supporting Information (Appendix B).

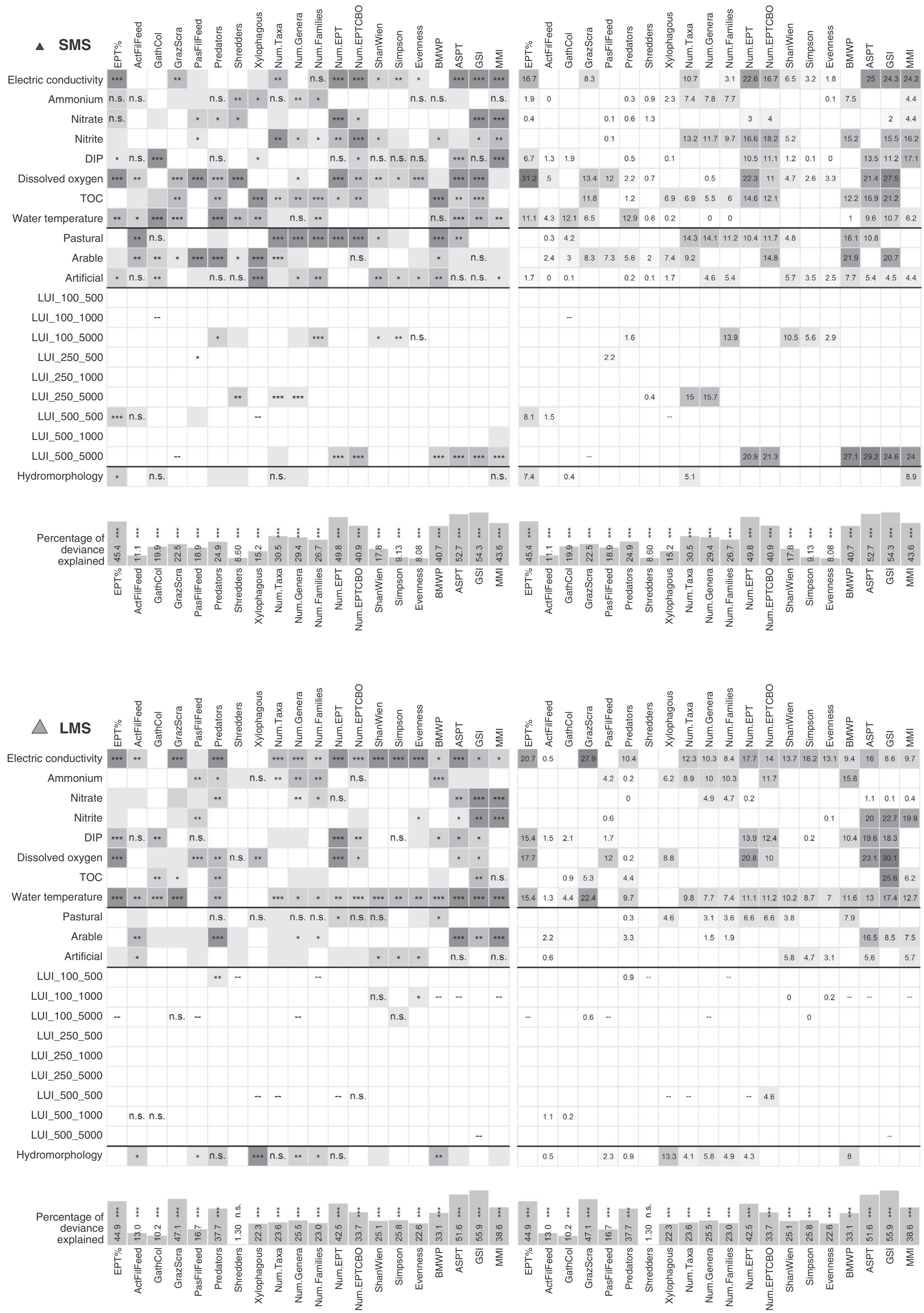
High collinearity ($\rho \geq 0.7$) occurred between land use parameters based on different sized buffer strips (Table 2), justifying the strategy to include not more than one of these predictors into individual GLMs. Nine sites were excluded from further analyses as they were identified as outliers due to extremely high pressure intensities. Subsequently, the number of sites available for calculations was reduced to 499, 218, 210 and 82 for the stream type groups SMS, LMS, SLS and LLS, respectively (for abbreviations, see Fig. 1).

3.1. Variable importance analysis

For the stepwise GLM regression procedures, full models comprising 13 predictors were pruned to reduced models with an average number of 5.8 remaining predictors (Figs. 2 and 3; detailed model results are available in the Supporting information, Appendix C). Apart from one exception (reduced model for shredders within LMS), all models were significant (Figs. 2 and 3). The outcomes of the bootstrapping procedure largely conformed to the predictor-specific significance levels (Figs. 2 and 3). Predictors with a high level of significance were normally included in the bootstrapped reduced models, indicating the model selection was relatively stable against the data's sample composition. Nevertheless, a high level of predictor specific significance was no guarantee for a high percentage of deviance explained by the same predictor.

Table 2
Spearman rank correlation coefficients (ρ) and levels of significance showing collinearity of the predictors. The presence of high collinearity ($\rho \geq 0.7$) is highlighted in grey. ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$ and n.s. $P \geq 0.05$. Land use index (LUI) buffers are named according to LUI_X_Y, with X and Y representing the buffer width and length, respectively.

	Electric conductivity	Ammonium	Nitrite	Nitrate	Dissolved oxygen	DIP	TOC	Water temperature	Artificial	Arable	Pastural	LUI_100_1000	LUI_100_500	LUI_100_5000	LUI_250_1000	LUI_250_500	LUI_250_5000	LUI_500_1000	LUI_500_500	LUI_500_5000	Hydromorphology
Electric conductivity		***	***	***	***	***	***	**	***	***	***	***	***	***	***	***	***	***	***	***	***
Ammonium	0.35		***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***
Nitrite	0.5	0.62		***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***
Nitrate	0.49	0.22	0.59		n.s.	***	*	n.s.	***	***	***	***	***	***	***	***	***	***	***	***	***
Dissolved oxygen	−0.31	−0.44	−0.31	0.05		*	***	***	n.s.	***	**	n.s.	n.s.	***	*	n.s.	***	*	*	***	**
DIP	0.36	0.4	0.67	0.43	−0.07		n.s.	***	***	***	*	***	***	***	***	***	***	***	***	***	***
TOC	0.41	0.41	0.24	0.08	−0.53	0.03		**	n.s.	***	***	**	**	***	**	**	***	***	**	***	**
Water temperature	0.1	0.19	0.26	0.04	−0.38	0.14	0.1		***	n.s.	***	***	***	***	***	***	***	***	***	***	***
Artificial	0.23	0.25	0.28	0.16	−0.04	0.28	0	0.35		n.s.	n.s.	***	***	***	***	***	***	***	***	***	***
Arable	0.69	0.37	0.46	0.55	−0.31	0.22	0.48	−0.02	0		***	***	***	***	***	***	***	***	***	***	***
Pastural	−0.47	−0.18	−0.25	−0.24	0.1	−0.06	−0.32	0.2	−0.04	−0.58		***	***	***	***	***	***	***	***	***	***
LUI_100_1000	0.29	0.2	0.28	0.22	−0.06	0.22	0.09	0.18	0.36	0.23	−0.23		***	***	***	***	***	***	***	***	***
LUI_100_500	0.3	0.2	0.27	0.23	−0.04	0.2	0.1	0.16	0.33	0.24	−0.24	0.94		***	***	***	***	***	***	***	***
LUI_100_5000	0.41	0.3	0.4	0.31	−0.13	0.28	0.13	0.21	0.47	0.38	−0.3	0.69	0.64		***	***	***	***	***	***	***
LUI_250_1000	0.3	0.21	0.29	0.24	−0.06	0.23	0.09	0.19	0.39	0.24	−0.24	0.97	0.93	0.7		***	***	***	***	***	***
LUI_250_500	0.31	0.21	0.28	0.24	−0.05	0.22	0.09	0.19	0.36	0.24	−0.24	0.94	0.97	0.65	0.96		***	***	***	***	***
LUI_250_5000	0.44	0.32	0.43	0.33	−0.15	0.3	0.15	0.23	0.5	0.41	−0.31	0.68	0.64	0.98	0.71	0.67		***	***	***	***
LUI_500_1000	0.34	0.22	0.33	0.27	−0.08	0.25	0.11	0.21	0.43	0.28	−0.25	0.91	0.86	0.72	0.96	0.92	0.75		***	***	***
LUI_500_500	0.33	0.21	0.31	0.26	−0.06	0.24	0.1	0.2	0.4	0.26	−0.24	0.9	0.9	0.67	0.95	0.96	0.7	0.97		***	***
LUI_500_5000	0.5	0.33	0.45	0.37	−0.17	0.32	0.2	0.25	0.51	0.46	−0.32	0.65	0.62	0.92	0.69	0.65	0.97	0.76	0.71		***
Hydromorphology	0.22	0.22	0.27	0.22	−0.09	0.17	0.09	0.24	0.28	0.23	−0.13	0.38	0.39	0.35	0.39	0.4	0.36	0.39	0.39	0.37	



SMS
LMS
EPT%
ActFilFeed
GathCol
GrazScra
PasFilFeed
Predators
Shredders
Xylophagous
Num.Taxa
Num.Genera
Num.Families
Num.EPT
Num.EPTCBO
ShanWien
Simpson
Evenness
BMWP
ASPT
GSI
MMI
Electric conductivity
Ammonium
Nitrate
Nitrite
DIP
Dissolved oxygen
TOC
Water temperature
Pastural
Arable
Artificial
LUI_100_500
LUI_100_1000
LUI_100_5000
LUI_250_500
LUI_250_1000
LUI_250_5000
LUI_500_500
LUI_500_1000
LUI_500_5000
Hydromorphology
Percentage of deviance explained

Conversely, predictors exhibiting a large amount of deviance explained were not necessarily assigned with a high level of significance.

The individual percentages of deviance explained varied strongly between metrics and stream type groups. On average, the best model results were achieved for GSI (average percentage of deviance explained: 50.2%), ASPT (41%), the number of EPT taxa (39.4%), MMI (37.8%), BMWP (34.6%) and for sensitivity/tolerance metrics in general (41.9%; Figs. 2 and 3). The weakest models were for Shannon's and Simpson's diversity metrics (17.7% and 14.8%, respectively), the percentage of active filter feeders (14.2%), the evenness (13.9%), the percentage of shredders (11%) and for functional and diversity metrics in general (20.1% and 15.5%, respectively). If included in the reduced model, each physico-chemical water quality parameter accounted for an average of 7.19% of the metrics' variance. The index of hydromorphological quality was included in 23 out of 80 models (28.8%) and accounted for an average of 4.56% of the explained deviance in these cases. The selected LUI buffer was part of the reduced model in 29 out of 40 small stream models (72.5%) but only in 14 out of 40 large stream models (35.0%), respectively. If included, the buffer accounted for 8.35% and 1.66% of the metrics' variances for small and large stream models, respectively. The catchment-wide land use categories pastoral, arable and artificial explained on average 6.4%, 7.19% and 3.05% of the small stream models and 3.08%, 5.61% and 3.92% of the large stream models, respectively.

3.2. Cluster analysis

The cluster analysis revealed significant clusters for 13 out of 20 metrics (Fig. 4; Euclidean distance values are available in the Supporting Information, Appendix D). A number of 47 reduced models (this corresponds to 58.8% of the reduced models) were not assigned to any significant cluster. Moreover, no significant clusters were detected for ActFilFeed, GathCol, PasFilFeed, Predators, Xylophagous, Num.Families and Num.EPT. Models of both lowland communities (SLS and LLS) were included in the same significant cluster in 12 cases, seven of which showing a clear dissimilarity to and between the mountain stream types (SMS and LMS). These were GrazScra, Num.Genera, Num.EPTCBO, ShanWien, ASPT, GSI and MMI.

4. Discussion

We took a comprehensive approach to examining the effects of multiple stressors on riverine benthic invertebrate communities in 1018 river sites (minus 9 outliers) across Germany. We found clear differences in the linkages between invertebrate community metrics and different scales of land use (i.e., local- to catchment-scale) and stream type groups (i.e., river sizes and ecoregions).

4.1. Multiple stressors

Many of the physico-chemical variables that characterize in-stream water quality contributed strongly to the explanation of benthic invertebrate responses. This infers that broad environmental in-stream gradients exist within the investigated rivers despite a high degree of development in German wastewater treatment (Eurostat, 2010) and major legislative efforts in pollution control (Salman and Bradlow, 2006; Zabel et al., 2001). Clearly, wide enough water quality gradients remain to exert a strong influence on instream biota (compare also Sundermann et al., 2015). In the case of mountain streams, community metrics were driven by a variety of physico-chemical parameters including nutrients and water temperature. Various factors can cause elevated water temperatures such as climate warming and intensive land use through, for instance, loss of shading from the removal of riparian vegetation. Contrarily, the selection of physico-chemical variables in lowland streams was rather focused, with a high relevance of electric conductivity (SLS) and ammonium load (LLS).

Additional explanatory value was provided by land use and, to some extent, the local hydromorphology. Thus, some community patterns exist, that cannot be predicted well by single physico-chemical water quality parameters. Among these patterns, indirect and synergistic effects between stressors may be particularly relevant, and might have been partly accounted for by riparian and catchment land use and local habitat structure.

Indirect effects: A high explanatory power does not necessarily mean benthic invertebrate communities are structured directly through the selected stressor (i.e. cause and effect). Along with physiological limitations due to the stressor variable itself, these may emerge through indirect relationships, such as via an altered food or habitat supply, or correlation with associated stressors other than that investigated. For instance, high nutrient loads might be representative of intensive land use (Carpenter et al., 1998), which also introduces the effects of altered hydrology and hydrodynamics (Fohrer et al., 2001), sedimentation (Wood and Armitage, 1997) and agrochemicals (Schulz and Liess, 1999; Schulz, 2001). Likewise, the explanatory power of some physico-chemical variables (e.g., electric conductivity and TOC) might imply the general effects of treated sewage effluents, containing industrial and household chemicals, pharmaceuticals and personal care products (DeBruyn and Rasmussen, 2002; Kelly et al., 2010).

Synergistic effects: To keep the regression outcomes of the present study meaningful but nonetheless simple and easily applicable, interaction terms were not included in the models. Yet, multiple stressors can operate in stream systems synergistically or antagonistically (Lange et al., 2014; Matthaei et al., 2010; Piggott et al., 2012; Piggott et al., 2015; Wagenhoff et al., 2011). However, since river regulation and land use practices alter physico-chemical water quality, interactive effects between single factors could somewhat be accounted for by including the more general land use and hydromorphological data. These variables integrate across the effects of multiple pathways of influence (e.g., solute loads, sediment inputs, thermal regimes, acid loads, altered hydrology, flow regimes and hydromorphological deficiencies) and consequently include both individual and interactive effects.

The investigated metrics responded in various manners and were not equally able to reflect the influence of multiple stressors on benthic invertebrate communities. For instance, the functional metrics describing feeding habits were often not able to be predicted well from the suite of environmental variables. Moreover, variability in responses indicated that increased stress often does not lead to consistent shifts towards a reduced or increased dominance of certain traits, even though shifts towards more tolerant and atypical communities were evident (i.e., declines in dominance and richness of sensitive EPT and EPTCBO taxa and changes in sensitivity and tolerance metrics). This complies with the findings of Feld et al. (2013) who, while detecting significant species turnover along a gradient of hydromorphological impairment, found no change in functional diversity. The authors concluded that species of certain guilds might be replaced by more tolerant species of the same guild.

Likewise, the model goodness for the diversity metrics was generally low. This matches Feld et al. (2013) and Sundermann et al. (2013) who concluded that a detected loss in taxon richness might not necessarily

Fig. 2. Results of the stepwise regression procedure for small mountain streams (SMS, upper figure) and large mountain streams (LMS, lower figure). The percentages of deviance explained by the reduced models are given below the figures and are visualized by bar plots. Asterisks indicate the levels of overall model significance. ****P* < 0.001, ***P* < 0.01, **P* < 0.05 and n.s. (not significant) *P* ≥ 0.05. For each metric (columns), the left halves of the figures give the levels of significance for each of the predictors (rows), which were included in the reduced model. Only one of the LUI buffers was included in the full model. Whenever this predictor was excluded during the procedure, this is indicated (− −). The results of the bootstrapping procedure are visualized by different shades of grey with dark colours representing predictors that were included in the bootstrapped reduced model more often (white: ≤25%; light grey: >25%–50%; medium light grey: >50%–75%; medium grey: >75%–90%; dark grey: ≥ 90%). Instead of levels of significance, the right halves of the figures give percentages of deviance explained by the individual predictors. This is visualized by a continuous colour shading with dark colours indicating high percentages.

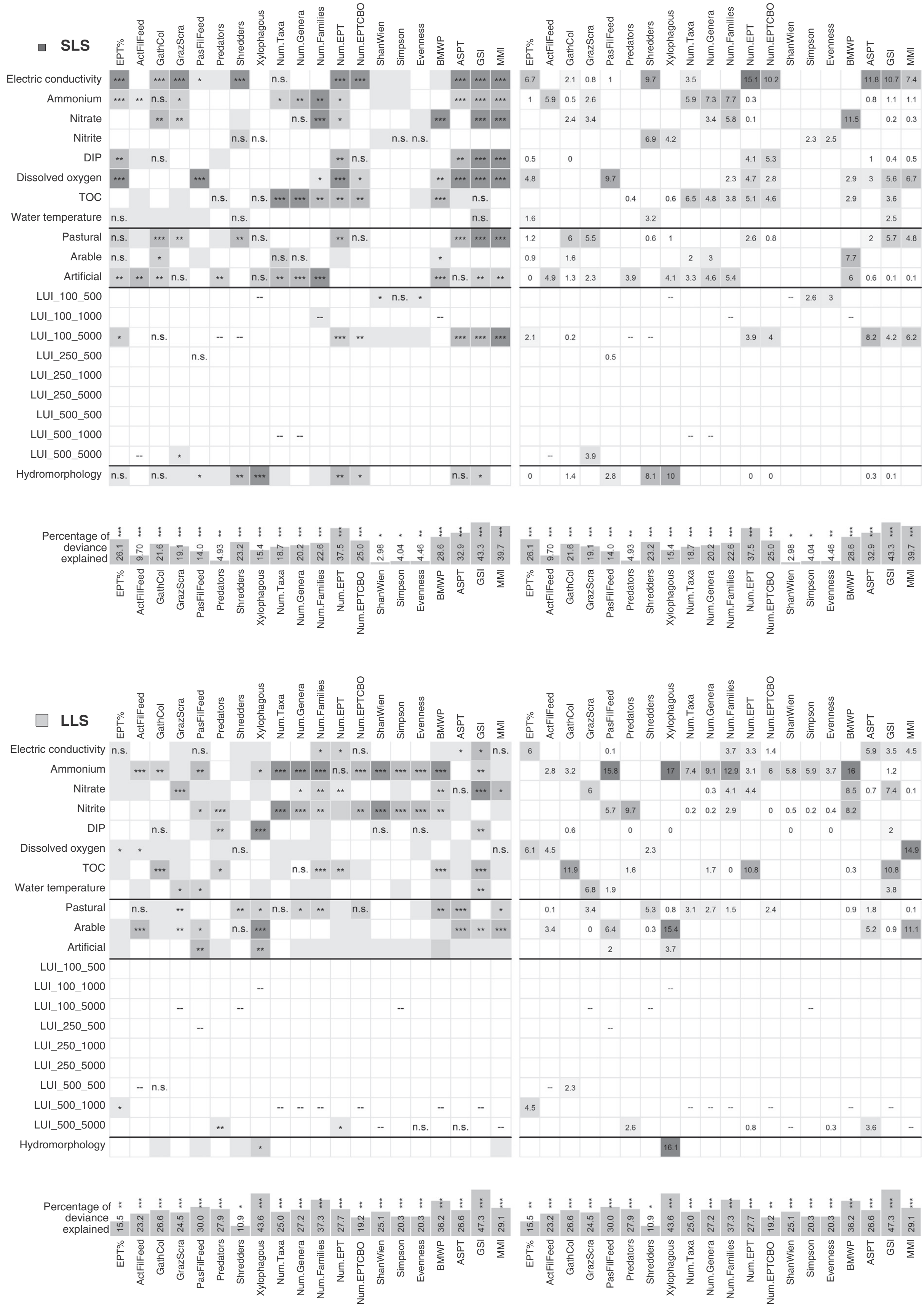


Fig. 3. Results of the stepwise regression procedure for small lowland streams (SLS, upper figures) and large lowland streams (LLS, lower figures). For full description see Fig. 2.

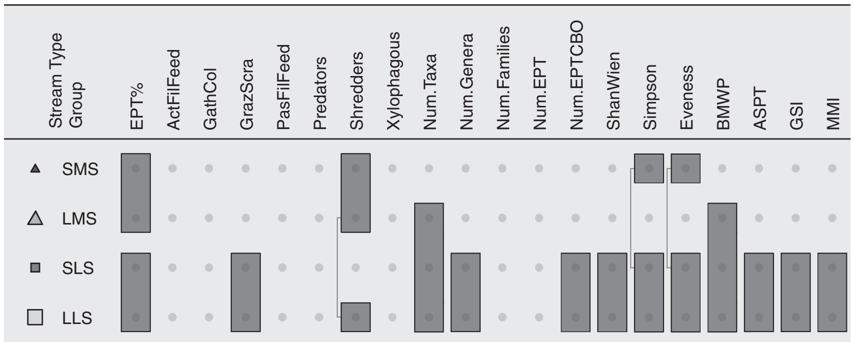


Fig. 4. Cluster analysis of the percentages of deviance explained by the reduced GLM models' predictors. Each circle represents one reduced model of the respective metric (column) and group (row). Rectangles enfold those models that were assigned to the same significant cluster and therefore indicate high similarity in stressor importance. Brackets connect elements of the same cluster, if these lie apart.

translate into changes in dominance structure and community composition. Biodiversity metrics may not be sufficient to reliably detect all changes within the community. Rather than generalizing across all community members, a more promising approach would be to focus on selected indicator taxa. This is done by the sensitivity and tolerance metrics investigated in the present study, which could be predicted well by a variety of different stressors. The greater performance of these metrics stems from the fact that they neither treat all individuals equally as the diversity indices do, nor do they focus only on specific taxon groups as EPT metrics do. Instead, these metrics use the full bandwidth of taxa, incorporating the environmental affinities of taxa (BMWP, ASPT and GSI) and the observed and expected community structure for certain stream types is considered (MMI).

4.2. Spatial scales

Our results demonstrate that local assemblages were primarily shaped by large-scale (catchment-scale) processes (i.e., physico-chemical variables and catchment-wide land use), rather than being controlled by local conditions (i.e., hydromorphology). Yet, this result clearly depends on the 26 variables used to describe the hydromorphology. Possibly, other non-measured hydromorphological variables might have influenced benthic invertebrate species at the local scale more than we were able to detect. According to our data, however, large-scale processes appear to have the potential to override local conditions. Correspondingly, catchment-wide land use was often able to explain a larger amount of the metrics' variance compared to the riparian zone represented by different sized buffer strips. The pattern was evident for many metrics, including the sensitivity and tolerance indices, which indicate the loss of sensitive taxa and show community shifts from those expected in natural conditions. This higher importance of catchment vs. riparian land use supports the findings of several previous studies, indicating a greater importance of catchment land use, and potentially demonstrating an inability of riparian buffer strips to prevent stream degradation associated with land use change (Death and Collier, 2010; Potter et al., 2005; Roth et al., 1996; Sliva and Williams, 2001; Wang et al., 1997; Weigel et al., 2000).

However, these scale-dependent influences do not apply equally to all river types and thus support our second hypothesis, based on Johnson et al. (2001), who expected the catchment-wide land use to be of higher relevance, especially in large catchments. In fact, land use buffers (i.e., land use in the riparian zone) were more relevant in small streams (catchment sizes up to 100 km^2), whereas the biotic integrity of larger rivers was better predicted by catchment-wide land use. Riparian zones of large rivers form only a minor proportion of their catchments, with much less direct contact with the aquatic environment (e.g., through overhead shading), and potential mitigating effects are likely to be overwhelmed by the background load of physico-chemical stress.

4.3. Heterogeneity of riverscapes

We expected communities in streams of different sizes and ecoregions to be controlled by specific sets of environmental stressors. This was supported by our results, with strong variation in model goodness, selected variables and explanatory power of individual predictors between stream type groups. In fact, the majority of the reduced models were not assigned to any significant cluster at all (e.g., models for ActFilFeed and Num.EPT).

Transitioning from the mountainous ecoregion to the lowlands not only comes with decreasing elevation and slope, but also with increased agriculture. Specifically, the percentage of arable land use increases from 35.9 ± 27.4% to 58.9 ± 22.2% ($P < 0.001$, Mann–Whitney U-test) at the expense of decreasing natural land uses (38.4 ± 23.3% in mountains vs. 24.1 ± 20.5% in lowlands; $P < 0.001$). Associated with this land use alteration, our results indicated a greater similarity in the interactions of communities in different lowland stream types with their environment, coupled with clear differences to and between the mountain stream types (SMS and LMS). Consequently, these lowland river communities may in turn be experiencing some form of biotic homogenisation (Olden and Rooney, 2006), which implies an increased degree of similarity between local populations. On both taxonomic and functional levels, biotic homogenisation and the positive selection of generalist taxa has been described for riverine benthic invertebrates as a response to anthropogenic stress (Johnson and Angeler, 2014; Mondy and Usseglio-Polatera, 2014). The higher degree of stress-induced homogenisation of taxa and traits in the lowlands might also be responsible for a homogenisation of cause and effect relationships.

Among others, this was evident for the German Saprobic Index (GSI) and the multi-metric index (MMI), which are used to classify river sites in the five ecological status classes according to European Union Water Framework Directive, WFD (Hering et al., 2004a; EU Commission, 2000). Given the WFD requires the ecological status of freshwaters to be at least of 'good' quality, a logical management strategy is to focus on stressors that cause decreasing values for GSI and MMI, implying an impairment of benthic invertebrate communities. Our outcomes clearly show that these critical stressors often vary with catchment size and ecoregion. Thus, adaptive management approaches will be needed, which consider the inherent variability in benthic invertebrate communities of different river types.

5. Implications for water management practice

For establishing successful water management schemes it is of vital importance to account for the multiplicity of stress factors, the spatial scales of influences and the heterogeneity of riverscapes while selecting measures and methods for monitoring, protecting and restoring running waters. Our study enabled the detection of stream type-specific key stressors that require attention in effective and problem-oriented river management, and mitigating the impacts of these stressors should benefit benthic invertebrate communities. We demonstrate, however, that this will not be effective unless the scope of these river management actions is widened to the full catchment scale and large scale processes of river impairment are answered by large-scale actions in water management. This applies particularly for high order streams, where the biotic status is controlled by in-stream conditions that are primarily controlled from upstream processes rather than the local zone. While riparian buffer zones are often restored to mitigate catchment degradation, our results indicate that this may be a promising approach in small catchments and headwater streams but is likely insufficient in larger rivers, potentially leading to failure of restoration. In general, small-scale local restoration may not have significant effects on riverine communities of higher order rivers subject to intensive upstream land use.

We encourage stream managers to reject generalised approaches and to establish a future practice considering running waters uniquely. These systems are embedded in catchments and ecoregions with specific characteristics, thus a multi-scale, catchment-specific approach should be a top priority. Incorporating the right spatial scales, appropriate stressors, and accounting for stream type-specific variability, should lead to a clear advancement of restoration practices.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.scitotenv.2015.07.083.

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