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BIOFRESH

Biodiversity of Freshwater Ecosystems: Status, Trends, Pressures, and Conservation Priorities

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D6.7: Manuscript on the effects of multiple stressors on freshwater biodiversity patterns

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Comments	**Draft manuscript versions** This report contains two draft manuscripts on the effects of land use and multiple stressors on freshwater biodiversity in various ecosystems. The content deviates from the descriptions made in the DoW (p. 37: Task 6.6 “Synthesis Report”) insofar that: • a focus had to be put on European data; the data used for this report were mainly derived from previous European research projects • a focus had to be put on land use, physico-chemical stressors and general human modification at the landscape scale, as only these stressor variables were consistently and reliably available for the ecosystems considered at the European scale

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PP	Restricted to other programme participants (including the Commission Services)	
RE	Restricted to a group specified by the consortium (including the Commission Services)	
CO	Confidential, only for members of the consortium (including the Commission Services)	

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Content

Chapter 1

Independent, overlapping and interacting effects of human land use and geo-climatic factors on European patterns of diversity in freshwater ecosystems

(submitted to Freshwater Biology, FWB-P-Apr-14-0217)

Abstract

Land use is considered one of the main stressors on biodiversity patterns of freshwater ecosystems, with up to 80% non-natural regional land cover in Europe. Consequently human impacts on freshwater biodiversity are numerous and wide-ranging.

Here, we address the impact of arable and urban landscapes, on the diversity of 11 organism groups encompassing vertebrates, invertebrates and plants, occurring in five freshwater ecosystems: rivers, floodplains, lakes, ponds and groundwater. In addition, nine geo-climatic variables (e.g. latitude, longitude, precipitation) were used to quantify the independent, overlapping and interacting effects of land use and natural descriptor variables. Biodiversity response was computed as taxon richness, Shannon diversity, taxon rareness and taxonomic distinctness.

The four biodiversity metrics were analysed using a variation partitioning scheme based on boosted regression trees (BRT) and subsequently with generalised linear modelling (GLM). The analyses sought: i) to partition the unique, shared and unexplained variation in the metrics explained by both groups of descriptor variables and ii) to quantify the contribution of each descriptor variable to biodiversity variation in the data.

Variation partitioning revealed the variation in biodiversity uniquely described by land use was consistently low across all ecosystems and organism groups. In contrast, the variation accounted for by both unique geo-climatic descriptors and the joint effects of both descriptor groups explained significantly more variance in the 39 biodiversity metrics tested. The GLM confirmed this and revealed significant interactions between geo-climatic descriptors and land use for roughly a third of the 33 GLM models. The interactions accounted for up to 17% of model deviance. With both BRT and GLM, however, no consistent patterns were observed related to the type of biodiversity metric and organism group considered.

Dividing the data according to the strongest geo-climatic gradient in each dataset was undertaken to reduce the strength of the respective natural descriptor variable and determine whether land use effects on biodiversity would increase in the data subsets. Results showed that data sub-setting can highlight land use effects on freshwater biodiversity, if geo-climatically more homogeneous datasets are analysed. However, the increased role of land use was not linked to the latitudinal or longitudinal extent of the data subsets, suggesting that the observed land use effects were not dependent upon the spatial extent of the subsets.

Our results confirm there are significant joint effects of, and interactions between, land use and natural environmental factors on freshwater biodiversity. This has three implications for biodiversity monitoring and assessment schemes. First, the combined analysis of anthropogenic stressors and geo-climatic factors is a prerequisite for the detection and quantification of human threats to biodiversity. Second, geo-climatically more homogeneous datasets can unmask the role of anthropogenic stressor variables in the analysis. And third, whole community-based biodiversity metrics reveal contrasting response directions and thus should be complemented by other metrics which account for taxon identity and turnover, to better address the loss of biodiversity in response to land use impacts and other stressors.

Introduction

Although freshwaters cover only 1% of the earth's surface, almost 10% of the world's species live in freshwater ecosystems (Loh & Wackernagel, 2004). Freshwater biodiversity is declining faster than marine and terrestrial biodiversity (Dudgeon et al., 2006), most likely because human life and many human activities rely on fresh water. This results in high population densities, intense land and water uses and modification and pollution hotspots in the vicinity of freshwater bodies. Consequently human impacts on freshwater biodiversity are numerous and wide ranging. Dudgeon et al. (2006) identify five major stressors of biodiversity which affect different freshwater ecosystem types to varying degrees: water i) overexploitation; ii) water pollution; iii) flow modification; iv) habitat degradation; and v) invasive species. While rivers are more affected by physical alterations (e.g. dams, impoundments, disconnection from the floodplain), lentic waters are more susceptible to nutrient enrichment (Wetzel et al., 2001; Schindler, 2006), with increasing adverse effects on lentic biota under climate change (Jeppesen et al., 2010; 2012).

Many of these stressors can be closely linked to land use, which may therefore be considered a composite (or proxy) stressor. Intensive agriculture, in particular, affects both lotic and lentic biodiversity through flow modification, pollution by fine sediment and pesticide fluxes (Allan, 2004; Feld, 2013), habitat degradation and eutrophication (Jeppesen et al., 2000). Urbanisation represents another intensive land use, with strong effects on freshwater biodiversity, resulting in "consistent declines in the richness of algal, invertebrate, and fish communities" (Paul & Meyer, 2001). In Europe, a very high share (up to 80%) of the land is intensively used for settlements, infrastructure and production systems (including agriculture and intense forestry (http://www.eea.europa.eu/themes/landuse/intro; accessed on 1 April 2014) and aquatic biodiversity is impoverished accordingly. Although point source pollution caused by intensive land use has decreased in recent decades due to enhanced waste water treatment, the legacy effects on biodiversity may be long-lasting, representing "the ghost of land use past" (Harding et al., 1998).

Anthropogenic stress intensity and thus its influence on biodiversity differs regionally, impacting large-scale biodiversity patterns, originally shaped by natural drivers. These natural drivers are considered in macro-ecological studies focusing on i) landscape energy/climate, ii) area/habitat heterogeneity and iii) history (e.g. Mittelbach et al., 2007; Leprieur et al., 2011; Oberdorff et al., 2011). The influence that landscape energy and climate have on biodiversity are primarily driven by temperature, precipitation or evapo-transpiration, all of which influence ecosystem energy supply and thus control or support biophysical processes operating within the system (Wright 1983; Hawkins et al., 2003; Evans et al., 2005; Mittelbach et al., 2007; Field et al., 2009). Area/habitat heterogeneity refers to the size and heterogeneity (habitat diversity) of an area under consideration, with the assumption that larger and more heterogeneous areas exhibit higher biodiversity (sensu Mc Arthur & Wilson, 1963; Guégan et al., 1998; Davies et al., 2007). Lastly, historical events (i.e. previous and often long-term events dating back for centuries or even millennia) may continue to shape contemporary biodiversity patterns (Mittelbach et al., 2007; Leprieur et al., 2011; Tisseul et al., 2012). The expansion of Pleistocene glaciers and their subsequent contraction followed by recolonisation, for example, are considered a key factor in explaining much of the variation in the distribution of contemporary biodiversity across Europe (Reyjol et al., 2007; Araujo et al., 2008; Baselga et al., 2012), with formerly glaciated regions (e.g. Scandinavia) generally exhibiting less diversity than non-glaciated regions (e.g. Mediterranean peninsula). Over more recent timescales land use practices dating back decades may continue to shape contemporary biodiversity even if land use has subsequently changed or been abandoned (Harding et al., 1998).

Both the natural drivers of freshwater biodiversity and multiple stressors resulting from human land and water uses have been addressed in a multitude of studies (see Stendera et al., 2012 for a recent summary of 368 papers), although few have considered these in an integrated way. Studies that investigate the combined effects of natural and anthropogenic descriptors are rare. Furthermore, Stendera et al. (2012) found that the majority of studies on natural drivers were rather broad-scale (continental and global), whereas studies on anthropogenic factors tend to focus on much finer (regional and local) spatial scales. The spatial resolution (grain size) also often differs, with the catchment 'grain' prominent in broad-scale studies, but single sites within one or several catchments foremost in fine-scale studies. Few studies addressed the impacts of both natural drivers and anthropogenic stressors on biodiversity and there remains a limited understanding of the synergies between both factors.

Brucet et al. (2013) suggest anthropogenic stressors have a minor role in shaping biodiversity patterns of lake fish assemblages in Europe compared to broad-scale climatic drivers. They found, for example, that the eutrophication gradient in their data was less significant than the natural temperature gradient. At the European scale however, these gradients (or drivers) are linked; eutrophication often results from intensive agriculture, the location of which is largely determined by recent and historic geo-climatic factors (e.g. altitude, mean annual temperature, annual precipitation, glaciation). As a result, intense row-crop agricultures (e.g. maize, rye, wheat) primarily occur in the temperate lowland regions of Central Europe (http://www.eea.europa.eu/data-and-maps/explore-interactive-maps/changing-face-of-europe-2014; accessed on 1 April 2014). Further, urbanisation, the second main composite stressor affecting freshwater biodiversity, is not independent from natural gradients; many large metropolitan areas in Europe (e.g. London, Paris, Cologne, Ruhr Metropolitan area, Berlin, Warsaw) are located between 50° and 52° N in lowland areas, i.e. within a narrow band of temperate climate conditions. Therefore, we expect strong interactions between land use and geo-climatic drivers and their impacts on freshwater biodiversity patterns. Both factors may interact in different ways: agriculture is least intensive in Scandinavia, where biodiversity is low due to the legacy of glaciation; urbanisation is strongest in Central Europe, away from the extremes of temperature and altitude. Intensive agriculture is most prominent in Central Europe and the Mediterranean region, yet the Mediterranean region in particular was not affected by Pleistocene glaciers and thus is one of the key biodiversity hotspots worldwide (Myers et al., 2000).

In this study, we developed a stepwise analysis to determine the independent, overlapping and interacting effects of anthropogenic land use and geo-climatic factors on the European biodiversity patterns of eleven organism groups in five lentic and lotic ecosystem types (rivers, lakes, floodplains, ponds and groundwater). First, we used a machine-learning technique to partition the variance and to quantify the independent and overlapping effects of both factors in each ecosystem. Second, we performed regression modelling including interactions of both factors and tested the significance of interaction terms. Eventually, to decrease the effect of the most influential geo-climatic variable in the regression models, we generated subsets of the data and quantified the proportion of variance attributable to land use separately for each subset. This is the first study to address the unique, shared and interacting effects of geo-climatic variables and land use on freshwater biodiversity patterns across numerous ecosystem types and organism groups.

Methods

Stressor variables

For all but groundwater ecosystems we used CORINE land cover data (European Environmental Agency; http://www.eea.europa.eu/publications/COR0-landcover) to calculate the proportion of arable and urbanised land within a catchment or the area directly surrounding a site (Table 1). The area considered differed between ecosystem types and was selected to match the scale of biological sampling. The CORINE land cover data are based on satellite imagery (Landsat 7, 25 x 25 m pixels), cover most countries in Europe (geometric accuracy: 100 m) and encompass land cover types with a minimum area of 25 ha. We used the land cover classes 'arable land' and 'urban land' (hereafter referred to as land use), which aggregate the CORINE level 3 types '2.1.1 Non-irrigated arable land' as 'arable land' and the level 2 types '1.1 Urban fabric' and '1.2 Industrial, commercial and transport units' as 'urban land'. We focused on these two land use types, because they are known to strongly affect aquatic biodiversity via numerous individual stressors (Paul & Meyer, 2001; Allan, 2004; Feld, 2013). For groundwater systems, we used the GlobCover land cover data (http://due.esrin.esa.int/globcover/) due to its comprehensive coverage of Eastern Europe. 'GlobCover Land Cover v2' is a global land cover map at a resolution of 10 arc seconds (or 300 m at the equator) and corresponds well with the CORINE land cover classification. Arable and urban land uses were derived from a grid-based scheme throughout Europe, with a grid size of 100 x 100 km (EDIT geoplatform; Sastre et al., 2009). The same grid was applied to generate the land use data for lakes using the CORINE land cover data. Proportions of different land use types were obtained by clipping the land use maps (either CORINE or GlobCover) with a layer containing the polygonal information from the targeted areas (Table 1) within a geographic information system (ESRI ArcGIS 10, Redlands, CA).

Geo-climatic descriptor variables

We used nine natural environmental descriptors covering geographical and climatic variables (hereafter referred to as geo-climatic variables, Supplementary Table S1). Latitude, longitude, altitude and catchment size were derived from digital maps using ArcGIS 10. Latitude and longitude were included as proxy geographical variables representing other potential natural drivers of biodiversity, such as historical climate and glaciation (Hortal et al., 2011; Stendera et al., 2012), but were excluded from the analysis if they were collinear with any of the other environmental descriptors. Altitude was included to account for the role of topography in shaping diversity patterns (e.g. Davies et al., 2006). Lake surface area was derived from the WISER lake database (Moe et al., 2013). Mean annual air temperature and annual precipitation were abstracted from the WorldClim database version 1.4 (Hijmans et al., 2005). WorldClim summarises measured data at weather stations between 1950 and 2000 as monthly mean values, interpolated by a thin-plate smoothing spline algorithm to fit a raster grid (grid size: 30 arc seconds, approximately 1 km at the equator). Mean annual air temperature was averaged from long-term yearly means, whereas a yearly mean was averaged from monthly means throughout a year. Annual precipitation was based on the sum of long-term monthly mean precipitation values. Actual and potential evapo-transpiration (AET, PET) were derived from the CGIAR-CSI Global-PET database (for details, see Zomer et al., 2008; http://www.cgiar-csi.org).

Biological data

Rivers

Site-specific river data were derived from the WISER river database (Moe et al., 2013), encompassing taxa lists of fish, macroinvertebrate and macrophyte communities and proportional catchment land use for up to 1,221 sites across Central Europe (Central/Western Mountains and Central/Western Plains ecoregions of France, Germany and Austria; Illies, 1978). Macroinvertebrate data were available for all sites, fish data for 590 sites and macrophyte data for 651 sites. The taxa lists originate from national monitoring surveys and followed the national monitoring standards defined for field sampling methodology and sample processing (see Dahm et al., 2012 and Feld, 2013 for details).

Prior to the calculation of biodiversity metrics, the raw taxa lists obtained from the WISER river database were manually adjusted to eliminate researcher-dependent bias, for example, caused by different taxonomic determination levels for macroinvertebrates (e.g. Oligochaeta, Diptera). Species-level identification was achieved for fish and macrophytes, while genus level was used for macroinvertebrates, as this is the standard determination level in France.

Lakes

Lake phytoplankton taxa lists from 836 lakes (surface area >0.5 km2) in 20 European countries were derived from the WISER lake database (Moe et al., 2013). The lakes are distributed among three major European regions: i) the Mediterranean region (145 lakes in Cyprus, Italy, Spain, Portugal and Romania), ii) the Central/Baltic region (373 lakes in Belgium, Germany, Estonia, France, Hungary, Lithuania, Latvia, the Netherlands and Poland) and iii) the Northern region (318 lakes in Denmark, Finland, Ireland, Norway, Sweden and the United Kingdom).

We chose samples taken between 2004 and 2010 to maximise the temporal comparability of samples. If multiple samples were available for a lake within this period, we selected the most recent sampling occasion to avoid a sample-density bias. For each sample, all stations within the same water body were combined by averaging to create a mean abundance for each lake. Taxa records from each country were harmonised for nomenclature (Phillips et al., 2012).

Ponds

We defined ponds as shallow lentic water bodies with surface area less than five hectares (0.05 km2) (De Meester et al., 2005). Pond taxa lists were obtained from 32 peer-reviewed publications indexed in the Web of Science and generated for amphibians, macrophytes and macroinvertebrates (Gastropoda, Odonata and Coleoptera only). Additional data were collated from Homes, Hering & Reich (1999), Nagorskaya et al. (2002), Sobkowiak (2003), Oertli et al. (2005), Sayer, Davidson & Jones (2010), Böhmer (2012), Moe et al. (2013), the

European Pond Conservation Network (http://campus.hesge.ch/epcn), N.J. Willby (University of Stirling, UK; unpubl.) and B.A. Lukács (Hungarian Academy of Sciences, HU; unpubl.).

Amphibian species were recorded once at 148 ponds in seven European countries. Macrophyte species records comprised 601 samples at 392 ponds in eight countries (genus level targeted for Chara sp. and Callitriche sp.; only hygrophytes, helophytes and hydrophytes with Ellenberg's moisture values ≥ 7 and stoneworts considered; Ellenberg et al., 1992). Macroinvertebrate taxa lists were collated using 189 samples from 176 ponds in twelve countries (species or genus level). Due to heterogeneous and thus incomparable sampling efforts, only binary data (i.e. presence/absence) were generated.

Floodplains

The floodplain database is based on publications of European datasets on plants, ground beetles and molluscs in riverine wetland ecosystems. A literature review was conducted using Web of Science, covering publications between 1990 and 2012. Altogether, 78 publications were reviewed in detail to generate three taxa lists (total number of sample sites: 565): 352 sites for floodplain vegetation, 132 sites for ground beetles and 81 sites for molluscs. Samples from distinct and separated habitat types within the same floodplain counted as different sites. The sites are located in 21 countries and on 51 river floodplains across Europe, with the majority of sites located in Central Europe: Poland: 99 sites, Germany: 98, France: 81, Belgium: 42, Switzerland: 29, the Netherlands: 25, Czech Republic: 7 and Denmark: 6.

Standardisation of species abundances among studies was impossible due to the lack of information on sampling effort in most studies. The bias in sampling effort was minimised by omitting studies with an extremely short or long field sampling period and those with strongly skewed or otherwise inconsistent data.

Groundwater

The European groundwater crustacean data set (EGCD) was assembled as part of the European BioFresh project (http://data.freshwaterbiodiversity.eu/metadb/bf_mdb_view.php? uid=5326d79b4af7b&code=60). It covers the whole of Europe, except Russia, and contains a total of 21,700 database records, which collectively represent 12 orders and 1,570 species and subspecies of obligate groundwater Crustacea. Records are from the European PASCALIS database (Deharveng et al., 2009), the hypogean crustacean recording scheme United Kingdom (Knight, 2012), the distributional checklist of the Italian fauna (Ruffo & Stoch, 2006), and the Berlin museum collection. They were complemented with occurrence data from an extensive literature search (i.e. 1,380 literature sources representing half of the records in the EGCD). Species names and distributions were checked by taxonomic experts and spurious occurrences were excluded from the data set. Occurrence data were projected onto the grid of 0.9° latitude cells provided by the EDIT geoplatform (Sastre et al., 2009). The area of cells in the grid was kept constant (10,000 km2) by adjusting the longitudinal divisions between adjacent cells in each latitudinal band. The final grid had 701 cells, 494 of which contained at least one species occurrence.

Calculation of biodiversity metrics

Biodiversity has many facets and, amongst others, encompasses compositional (structural), functional (trait) and phylogenetic aspects of assemblages. Given the mixture of binary (presence/absence) and continuous (abundance) data, the set of biodiversity metrics commonly calculable across all ecosystems was restricted here to total species richness, species rareness and taxonomic distinctness (i.e. phylogenetic diversity). With abundance data, we also calculated Shannon-Wiener diversity (referred to as Shannon diversity in the following). Species richness and Shannon diversity are among the most commonly-used indicators of aquatic biodiversity in Europe (see Birk et al., 2012 for a recent review of monitoring methodology). Taxon rareness (or endemicity) can be derived using the index of endemicity proposed by Crisp et al. (2001) and Linder (2001). The index describes the sum of relative frequencies of all taxa encountered at a site or within an area (grid) in relation to the overall number of sites or areas (grids) where the individual taxa have been observed. Hence, the index provides a measure of the summed relative frequencies of 'endemic' (or rare) taxa within a community, based on the overall frequency of the taxa in the entire dataset. Taxonomic distinctness refers to the mean taxonomic dissimilarity of any pair of taxa within a community along a Linnean phylogenetic tree (species, genus, family, order, class, phylum; Clarke & Warwick, 1998; 1999). For example, three species of the same genus are taxonomically less distinct than three species of different genera, orders or higher taxonomic entities, which is why taxonomic distinctness is also referred to as phylogenetic diversity. Taxonomic distinctness is applicable to binary taxa lists and adds a unique aspect of biodiversity, neither covered by taxon richness nor by taxon evenness (Gallardo et al., 2011; Feld et al., 2013).

Data analysis

We applied a stepwise analytical protocol for the multivariate analysis using Boosted Regression Tree analysis (BRT) and Generalised Linear Modelling (GLM).

STEP 1

Individual BRTs were run for each possible combination of organism group and biodiversity metric using all geo-climatic and land use descriptors (full model) to compare the effects of both descriptor groups. The major advantages of BRT analysis over classical regression modelling are its capacity to i) analyse collinear descriptor variables, ii) handle non-linear descriptors with missing values and iii) identify interactions between descriptors (Elith, Leathwick & Hastie, 2008).

The full BRT models allowed us to identify the contribution of each individual descriptor' to the overall variance explained in a biodiversity metric and the pairwise interactions between descriptor variables. Both were then used in GLM (see second step) to define the entry order of each descriptor variable in a model and the interaction terms (see below). Partial Dependence Plots (PDP) enabled the identification of the response patterns of biodiversity metrics along environmental descriptor gradients (Cutler et al., 2007). Accordingly, the PDPs identified potential thresholds along the geo-climatic gradients at which a biodiversity metric value either sharply increased or decreased (Clapcott et al., 2012; Feld, 2013a). Such thresholds may mark natural split points in the data, for example, geographical splits at a specific latitude, longitude or altitude, which then imply the presence of spatial patterns in the targeted biodiversity metric. We subsequently used these split points for the strongest geo-climatic descriptor in each BRT to divide each dataset (i.e. ecosystem type × organism group) into two subsets (see third step).

In addition to the full BRT models, we applied an additive partial regression scheme following Legendre & Legendre (1998, p. 531) to decompose the explained variation of the biodiversity metrics into four fractions: i) pure geo-climatic, ii) pure land use, iii) shared geo-climatic/land use and iv) unexplained. The shared fraction (iii) represents the variation that may be attributed to geo-climatic and land use descriptors together and is obtained additively in partial regression. As such, it is inherently different from non-additive interaction terms as introduced into the GLM (see next step). Differences in the variance explained were tested for significance using a Wilcoxon signed rank test.

STEP 2

GLM was applied individually to each combination of organism groups and three biodiversity metrics (Shannon's diversity excluded), and a set of geo-climatic and land use descriptors that excluded highly collinear variables, defined as those with a variance inflation factor >8 (Zuur, Ieno & Smith, 2007). We choose GLM for this step because of its flexibility in identifying the most parsimonious model (i.e. the best trade-off between model fit and complexity), including interactions between anthropogenic and geo-climatic descriptors. Adjusted goodness of fit (R2) and Akaike Information Criterion (AIC) were used as GLM quality indicators. The order of entry of each descriptor variable into a GLM model was based on the individual explanatory strength of the variable as identified in step 1 (i.e. the strongest descriptor entered a model first, followed by the second strongest, and so on). This procedure ensured a standardised and hence comparable analytical procedure for GLM models for all ecosystems.

We used Poisson regression for species richness and Gaussian regression for rareness/endemicity and taxonomic distinctness. If overdispersion was detected in Poisson regression, we used negative binomial distribution functions in GLM. Rareness and taxonomic distinctness were logit-transformed to better-fit Gaussian regression (Warton & Hui, 2011). The GLM model with the highest explained deviance (equivalent to R2 in Gaussian GLM), in combination with the lowest AIC obtained for each combination of organism group and biodiversity metric, was selected as the final model. A final model included borderline significant descriptors ($0.05<P<0.1$), if the explained deviance and/or AIC notably improved with the descriptors in the model.

STEP 3

The final analytical step repeated the procedure for step 2, but was applied to the data subsets. These subsets were defined using the split points of the most influential geo-climatic descriptor variable in each analysis. This was derived individually for each metric from the partial dependence plots of the BRTs (step 1). If necessary, the split points were slightly adjusted, to better achieve a balanced sample size of both data subsets. The objective of splitting the data according to the most influential geo-climatic descriptor variable was to control for the variance driven by the respective geo-climatic descriptor and thus to focus more on the role of land use.

All statistical analyses were run in R 2.15.3 (R Development Core Team, 2013). For BRTs, we used the packages ‘gbm’ (Ridgeway, 2013) and ‘dismo’ (Hijmans et al., 2013). GLMs were run with the package ‘MASS’ (Venables & Ripley, 2002).

Results

Partitioning the variance in biodiversity among geo-climatic and land use descriptors

Across all ecosystems, a total of 39 biodiversity metrics were calculated for eleven organism groups (Figure 1). Together, geo-climatic and land use descriptors explained between 20 and 93% (mean: 35%, SD: 18.7%) of the total variance in the full BRT models. On average, the explained variance was much higher for pond and floodplain biodiversity compared with the values obtained for the river, lake and groundwater models. No consistent metric driven differences across ecosystems and/or organism groups were detectable.

The variation partitioning scheme (BRT) revealed a consistently low proportion of variance attributable to pure land use effects for all metrics (Figure 1). Conversely, pure geo-climatic effects explained a relatively high proportion of the variance in river, lake and groundwater organisms and in pond amphibians and insects. This was irrespective of the biodiversity metric considered. Pure geo-climatic effects were significantly higher than pure land use effects (Wilcoxon signed rank test: $P<0.001$), i.e. geo-climatic descriptors were significantly more influential than human land use for the observed biodiversity patterns.

However, the proportion of variance jointly attributable to both descriptor groups was equally high in many cases and particularly pronounced with the floodplain and pond results (Figure 1). It accounted for as much as 19–87% of the total variance in the floodplain biodiversity metrics (ponds: 35–63%). It was also comparatively high for rivers (0.6–41%), but much lower for lakes and groundwater (<12 and <10%, respectively for all metrics). Nevertheless, the joint effects of land use and geo-climatic variables were significantly higher than the effects of land use alone. The findings suggest that both descriptor groups were intrinsically allied in many models, which rendered the separation of its unique effects on the response variables difficult.

Quantifying land use effects on biodiversity and interactions with geo-climatic descriptors

Similar as with the BRT results, land use descriptors alone accounted for less than 3% of the deviance (variation) in most GLM models (Table 2). Higher values (>10%) were found only for pond insect and floodplain carabid beetle richness and for river invertebrate and pond amphibian taxonomic distinctness. Both urban and agricultural land use performed similarly in the models and no general pattern was obvious regardless of the biodiversity metric considered.

Unexpectedly, however, we did not find a consistent decline in biodiversity in response to increasing land use intensity (Table 2). More often than not the sign of the relationship was positive, i.e. the biodiversity metrics value increased with increasing percentages of arable and urban areas. Irrespective of the biodiversity metric, organism group or ecosystem type, no consistent patterns were apparent.

Significant interactions of geo-climatic descriptors and land use were found for roughly a third of the 33 GLM models and accounted for up to 17% of model deviance (Table 3). The highest interactions (>10% explained deviance) were observed for floodplain carabid beetles and molluscs and for pond amphibians, but the majority of interaction terms accounted for less than were 5% of the deviance in the models. Land use interactions were strongest with longitude, latitude or annual precipitation, again highlighting the intrinsic co-dependence between land use and geo-climatic factors. Thus the land use patterns within these data were not independent of the geo-climatic patterns (or more specifically, the latitudinal and longitudinal location, respectively).

Controlling the influence of geo-climatic descriptors by data sub-setting

Latitude or longitude explained a considerable fraction of the variation in many biodiversity metrics, regardless of the analytical approach applied. For example, in 11 out of 33 BRT models, either latitude or longitude was the strongest geo-climatic descriptor, followed by temperature (9 models), altitude (5), river catchment/lake surface area (3) and precipitation (3) (Table 4). Temperature and precipitation, however, are also linked to latitude and longitude at the European scale. By splitting the datasets along one of these (mostly) geographical gradients the intention was to reduce the geographical extent of the derived data subsets and hence would decrease the role of geo-climatic descriptors relative to the role of land use in the data subsets.

Indeed, our findings confirm that data sub-setting can control the analysis of land use effects on freshwater biodiversity, yet apparently not necessarily through a reduction in the spatial extent of the obtained data subsets. With floodplain mollusc richness, for example, the deviance explained by one subset (annual precipitation ≤630 mm, see Table 4) was five times the deviance explained by the full data and accounted for 50% of the metric's total deviance in this subset. Likewise, the respective values doubled with floodplain carabid beetle and mollusc rareness/endemicity and achieved explained deviances between 40 and nearly 50% for one data subset (Figure 2, see Table 4 for the respective split points). In some cases, land use explained substantially more deviance in the biodiversity metrics in both subsets (e.g. groundwater crustacean richness and rareness/endemicity, Figure 2). However, all but one of these data subsets were obtained by splits along gradients of actual or potential evapo-transpiration, mean annual air temperature or altitude (Table 4).

More generally, the changes observed in the deviance explained by land use (including interaction terms) when analysing the data subsets were largely independent of the changes in the geographical extent within the subsets (Figure 3). Neither latitudinal nor longitudinal splits of the full data resulted in consistent and significant increases (or decreases) in the deviance explained by the GLM models.

Discussion

Pure and shared land use effects on freshwater biodiversity

Human land use, in particular urbanisation and intensified agriculture, are widely recognised as major threats to freshwater biodiversity worldwide (MEA, 2005; Dudgeon et al., 2006; Vörösmarty et al., 2010) and have been found to significantly impact the integrity of freshwater systems (e.g. Allan, 2004; Feld et al., 2011, Feld, 2013). However, the variation partitioning scheme applied in this study to quantify the role of land use in comparison to the natural drivers of biodiversity reveals a consistently low proportion of variation in biodiversity explained purely by land use at the European scale. This is irrespective of the ecosystem type, organism group and biodiversity metric considered. In contrast, the natural geo-climatic descriptors are much better correlates of diversity. This suggests both land use variables are less influential compared to the geo-climatic gradients at the ecoregional and continental scales as addressed in this study and this is supported by the findings of Davies et al. (2006), who found that land use had weak explanatory power at the scale of bio-geographic regions, but had a stronger role at the global scale.

More importantly, land use and geo-climatic variables exhibited strong shared effects, significantly higher than the pure land use effects. These shared effects imply a strong collinearity of both descriptor groups, which translates to highly concordant patterns of land use, geo-topographical and climatic conditions. It suggests that land use is not independent of geo-climate at the geographical scale covered by our data. This does not mean that land use effects on biodiversity are subordinate to geo-climatic drivers, but they simply cannot be fully disentangled and thus should be considered in tandem. In a similar study, Brucet et al. (2013) regressed fish diversity metrics in 1,632 European lakes against a selection of anthropogenic stressor variables and natural (geographic) descriptors. They reported that ‘geographical factors dominate over anthropogenic pressures’, which is largely supported by our data, but also requires qualification in that geo-climatic factors not only dominate but act in concert with land use. This is important to distinguish and raises the issue of interaction between both descriptor groups (see next paragraph). As a consequence, studies that consider only one descriptor group run the risk of overlooking the strong shared explanatory power of land use and geo-climatic factors.

Interactions of land use with geo-climatic factors

The high proportion of shared variation revealed by the BRT analyses suggests an interaction of variables in both descriptor groups. This was further investigated and quantified by 33 GLM models, a third of which included significant interaction terms providing evidence for the combined effect of both descriptor groups. In particular latitude, longitude and annual precipitation most often interact with land use, reflecting a geographical and (historic) climatic pattern in the distribution of urban and agricultural areas in Europe. Since most interactions account for less than five percent of the model deviance and since significant interactions are not found in two thirds of models, we conclude that the additive shared effects obtained from BRTs cannot be translated to the multiplicative interactions identified by GLM. We are unable to explain further the nature of this linkage or interpret with any confidence the interaction of geo-climatic and anthropogenic gradients. Further investigation using the spatial distribution of biodiversity (i.e. the potential spatial pattern) in Geographic Weighted Regression (GWR) may help to locate regions where the shared effect of land use and geo-climatic factors is particularly strong (Gouveia et al., 2013).

The role of geo-climatic descriptors in smaller data subsets

The dominant role of geo-climatic descriptors (altitude, latitude and longitude) over human impact at ecoregional or continental scales may be explained by the relatively short human impact gradients at both scales in comparison to climatic patterns (Davies et al., 2006). We, therefore, hypothesised that data subsetting along the major geo-climatic descriptor gradients (i.e. cutting the gradient) would enhance the land use effects on biodiversity. Our results partly confirm the hypothesis, but generally reveal inconsistent patterns, without a general increase (or decrease) of the role of human impact in the data subsets. The comparison between GLM models using the full data and the data subsets, however, reveal climatic gradients (temperature, precipitation) influence freshwater biodiversity to a greater extent than geographical gradients (latitude, longitude). Climatic and geographical gradients, although strongly linked at the continental scale, are not necessarily congruent. They reveal different patterns: while latitude and longitude represent continuous gradients from the north to the south and from the east to the west, climatic gradients are changing with altitude and other factors and hence are rather discontinuous at the European scale. The outcome of this study reveals that the role of land use increased only if the subsets were split along climatic gradients. This supports a rather discontinuous pattern of temperature and precipitation across ecoregions as compared to the geographical gradients. If we assume similar discontinuous patterns are inherent in our freshwater biodiversity data, this may explain the greater role of climatic descriptors in the full dataset too.

In summary, the data subsetting exercise highlights land use plays a stronger role in driving freshwater biodiversity in geo-climatically more homogeneous data subsets. Yet, this does not necessarily mean the subsets cover a reduced geographical extent, e.g. comparable alpine climates are found in mountainous central Europe as well as parts of flatter northern Europe. As this study is the first to address these patterns at the broad scale and across numerous freshwater ecosystem types and organism groups, future studies are required to investigate the role of spatial patterns in human land uses in respect of freshwater biodiversity responses. A key focus should be the identification of the spatial scale best suited to detect land use and other human impacts.

The general response of freshwater biodiversity to land use

There is considerable evidence that urban (reviewed by Paul & Meyer, 2001) and agricultural (reviewed by Allan, 2004, see also Feld et al., 2013) land uses adversely affect the biodiversity and integrity of lotic ecosystems. Likewise, pond macrophyte and invertebrate richness are impacted by agriculture (Declerck et al., 2006; Della Bella & Laura, 2009) and pond amphibian and macrophyte richness by urbanisation (Akasaka et al., 2010; Hartel et al., 2010). Similar adverse effects of human land use on freshwater biodiversity are reported for lakes (Brucet at al., 2013) and obligate groundwater fauna (Malard et al., 1996). For lakes, land-use change is considered the most severe driver of biodiversity change (Sala et al., 2000), so that adverse effects on plankton diversity through mechanisms of nutrient loading (e.g. Nielsen et al., 2012) and water quality deterioration (e.g. Jeppesen et al., 2000) were highly anticipated also in this study.

This general decline of biodiversity in response to agricultural and urban land uses is not fully supported by our findings. Besides the generally weak pure effect of land use, we found both positive and negative relationships between biodiversity indices and both land use groups in equal parts. This has rarely been reported from other ecosystems. Davies et al. (2007) found human population density to be positively correlated with bird richness and concluded, in agreemeent with Balmford et al. (2001), "the tendency for higher levels of human density and species richness to be favoured by similar kinds of environments […] overwhelms any negative effect of those densities on avian richness." The authors also found a positive response to high levels of agricultural land use, although whether this applies to aquatic ecosystems remains speculative.

It is uncertain whether whole-community based biodiversity metrics are suitable measures to indicate adverse land use effects. Freshwater communities are often species-rich and may dramatically change along anthropogenic impact gradients, while both species richness and evenness may remain relatively stable along the same gradient and even at its end points (Feld et al., 2013). Consequently, many whole community measures of biodiversity fail to detect species turnover, which renders them poor indicators of ecosystem degradation, in particular with species-rich assemblages such as benthic macroinvertebrates. This turnover might be detected by measures of beta diversity, which was not considered here. Future studies could usefully focus on changes in species composition along environmental impact gradients using measures that quantify the spatial turnover and nestedness components of beta diversity (Baselga, 2012).

With the comparison of measures of alpha diversity, we also need to take the potential methodological constraints into consideration that may hamper a comparative analysis of biodiversity patterns at the broad scale. Monitoring sampling methodology, for instance, usually aims at obtaining data for a site's quality assessment, but does not allow for sampling the whole biodiversity of a given site, in particular not if only one season is being addressed. This in particular applies to lake phytoplankton biodiversity, which is notoriously difficult to estimate (Carstensen et al., 2005; Uuistalo et al., 2013) due to a large number of species, many of which are usually present in very low abundance. Further, phytoplankton species (or taxon) richness is strongly linked to the sampling and counting methodology (Carstensen et al., 2005) and often restricted by the use of light microscopy of preserved samples in routine monitoring schemes (Ojaveer et al., 2010). Hence, there is potential for methodological inconsistency in our data, which, in part, may have caused the weak response patterns observed for lake phytoplankton, but nevertheless which resulted in the consistently weak pure effects of land use on biodiversity across organism groups and ecosystems.

Implications for monitoring freshwater biodiversity

This study posits three major conclusions, with strong implications for future research on freshwater biodiversity and its response to le anthropogenic stressors at large spatial scales:

1. The combined analysis of both geo-climatic and anthropogenic impact gradients is a prerequisite for the detection and quantification of human threats to biodiversity. Natural geo-climatic and anthropogenic factors may be collinear, jointly explain a considerable amount of (shared) variation in the response variable and interact with each other, all of which complicate the detection of biodiversity response to anthropogenic impact. As this interaction can be assumed to be inherent to any large-scale (e.g. ecoregional or continental) dataset, separating analysis of geo-climatic and anthropogenic gradients cannot account for the shared effects and interactions as this would result in erroneous interpretation of biodiversity response patterns to environmental gradients.
2. Geo-climatic descriptors form strong gradients in large-scale datasets. These gradients may mask anthropogenic gradients and thus complicate or even hinder the detection of the latter. More homogeneous datasets (with reduced gradients of natural explanatory variables) can help overcome the dominance of natural gradients and may also provide stronger models explaining more variance in the biological response variable.
3. Whole community-based biodiversity metrics, such as species richness, Shannon-Wiener Diversity, Piélou‘s evenenness or taxonomic distinctness show responses to anthropogenic stressor gradients, but there is sufficient evidence of contrasting response directions, with increasing as well as decreasing biodiversity values along various stressor gradients. Further, as whole-community biodiversity metrics may fail to detect the turnover in species composition, other metrics capable of accounting for species identity and turnover should be tested in addition when the biodiversity response to land use and other anthropogenic stressors in freshwater ecosystems is under consideration.

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References

Akasaka M., Takamura N., Mitsuhashi H. & Kadono Y. (2010) Effects of land use on aquatic macrophyte diversity and water quality of ponds. Freshwater Biology, 55, 909–922.

Allan J.D. (2004). Landscapes and Riverscapes: The Influence of Land Use on Stream Ecosystems. Annual Review of Ecology, Evolution, and Systematics, 35, 257–284.

Araújo M.B., Nogués-Bravo D., Diniz-Filho J.A.F., Haywood A.M., Valdes P.J. & Rahbek C. (2008) Quaternary climate changes explain diversity among reptiles and amphibians. Ecography 31, 8–15.

Balmford A., Moore J.L., Brooks T., Burgess N., Hansen L.A., Williams P. & Rahbek C. (2001) Conservation Conflicts Across Africa. Science, 291, 2616–2619.

Baselga A., Gomez-Rodrıguez C., Lobo J.M. (2012) Historical legacies in world amphibian diversity revealed by the turnover and nestedness components of beta diversity. PLoS ONE 7, 323–341.

Birk S., Bonne W., Borja A., Brucet S., Courrat A., Pokane S., Solimini A., van de Bund W., Zampoukas N. & Hering D. (2012) Three hundred ways to assess Europe's surface waters: An almost complete overview of biological methods to implement the Water Framework Directive. Ecological Indicators, 18, 31–41.

Böhmer J. (2012). Amphibienvorkommen und deren säurebedingten Laichschäden im Nordschwarzwald und Odenwald in 2012 im Vergleich mit den Jahren 1987-1990, 1996 und 2002 (p. 51). BioForum GmbH, Kirchheim/Teck.

Brucet S., Pédron S., Mehner T., Lauridsen T.L., Argillier C., Winfield I.J., Volta P., Emmrich M., Hesthagen T., Holmgren K., Benejam L., Kelly F., Krause T., Palm A., Rask M. & Jeppesen E. (2013) Fish diversity in European lakes: geographical factors dominate over anthropogenic pressures. Freshwater Biology, 58, 1779–1793.

Carstensen J., Frohn L.M., Hasager C.B. & Gustafsson B.G. (2005) Summer algal blooms in a coastal ecosystem: the role of atmospheric deposition versus entrainment fluxes. Estuarine, Coastal and Shelf Science, 62, 595–608.

Clapcott J.E., Collier K.J., Death R.G., Goodwin E.O., Harding J.S., Kelly D., Leathwick J.R., Young R.G. (2012) Quantifying relationships between land-use gradients and structural and functional indicators of stream ecological integrity. Freshwater Biology, 57, 74–90.

Clarke K. & Warwick R. (1998) a taxonomic distinctness index and its statistical properties. Journal of Applied Ecology 35, 523–531.

Clarke K. & Warwick R. (1999) The taxonomic distinctness measure of biodiversity: weighting of step lengths between hierarchical levels. Marine Ecology Progress Series 184, 21–29.

Crisp D.T., Laffan S., Linder H.P. & Monro A. (2001) Endemism in the Australian flora. Journal of Biogeography, 28, 183–198.

Cutler D. R., Edwards T.C., Beard K.H., Cutler A., Hess K.T., Gibson J. & Lawler J.J. (2007) Random forests for classification in ecology. Ecology, 88, 2783–2792.

Dahm V., Hering D., Nemitz D., Graf W., Schmidt-Kloiber A., Leitner P., Melcher A., Feld C.K. (2013) Effects of physico-chemistry, land use and hydromorphology on three riverine organism groups: a comparative analysis with monitoring data from Germany and Austria. Hydrobiologia, 704, 389–415.

Davies R.G., Orme C.D.L., Olson V., Thomas G.H., Ross S.G., Ding T.-S., et al. (2006) Human impacts and the global distribution of extinction risk. Proceedings Biological Sciences / The Royal Society, 273, 2127–2133.

Davies R.G., Orme C.D.L., Storch D., Olson V.A., Thomas G.H., Ross S.G., Ding T.S., Rasmussen P.C., Bennett P.M., Owens I.P.F., Blackburn T.M. & Gaston K.J. (2007) Topography, energy and the global distribution of bird species richness. Proceedings of the Royal Society B: Biological Sciences, 274, 1189–1197.

De Meester L., Declerck S., Stoks R., Louette G., Van De Meutter F., De Bie T., Michels E. & Brendonck L. (2005). Ponds and pools as model systems in conservation biology, ecology and evolutionary biology. Aquatic Conservation: Marine and Freshwater Ecosystems, 15, 715–725.

Declerck S., De Bie T., Ercken D., Hampel H., Schrijvers S., Van Wichelen J., Gillard V., Mandiki R., Losson B., Bauwens D., Keijers S., Vyverman W., Goddeeris B., De Meester L., Brendonck L. & Martens K. (2006). Ecological characteristics of small farmland ponds: associations with land use practices at multiple spatial scales. Biological Conservation, 131, 523–532.

Deharveng L., Stoch F., Gibert J., Bedos A., Galassi D., Zagmajster M., Brancelj A., Camacho A., Fiers F., Martin P., Giani N., Magniez G. & Marmonier P. (2009) Groundwater biodiversity in Europe. Freshwater Biology, 54, 709–726.

Della Bella V. & Mancini L. (2009). Freshwater diatom and macroinvertebrate diversity of coastal permanent ponds along a gradient of human impact in a Mediterranean ecoregion. Hydrobiologia, 634, 25–41.

Dudgeon D., Arthington A.H., Gessner M.O., Kawabata Z.-I., Knowler D.J., Lévêque C., Naiman R.J., Prieur-Richard A.-H., Soto D., Stiassny M.L.J. & Sullivan C.A. (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews, 81, 163.

Elith J., Leathwick J. R. & Hastie T. (2008). A working guide to boosted regression trees. Journal of Animal Ecology, 77, 802–813.

Ellenberg H., Weber H. E., Düll R., Wirth V., Werner W. & Paulißen D. (1992). Indicator values of plants in Central Europe (Vol. 18, p. 258). Erich Goltze Verlag, Göttingen.

Evans K.L., Warren P.H. & Gaston K.J. (2005) Species–energy relationships at the macroecological scale: a review of the mechanisms. Biological Reviews 80, 1–25.

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. & Friberg N. (2011) Chapter 3 - 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. & Dolédec S. (2013) Biodiversity of traits and species both show weak responses to hydromorphological alteration in lowland river macroinvertebrates. Freshwater Biology, 59, 233–248.

Field R., Hawkins B. a., Cornell H. V., Currie D.J., Diniz-Filho J.A.F., Guégan J.-F., et al. (2009) Spatial species-richness gradients across scales: a meta-analysis. Journal of Biogeography 36, 132–147.

Gallardo B., Gascón S., Quintana X., Comín F.A. (2011) How to choose a biodiversity indicator - Redundancy and complementarity of biodiversity metrics in a freshwater ecosystem. Ecological Indicators, 11, 1177–1184.

Gouveia S.F., Hortal J., Cassemiro F. a. S., Rangel T.F. & Diniz-Filho J.A.F. (2013) Nonstationary effects of productivity, seasonality, and historical climate changes on global amphibian diversity. Ecography 36, 104–113.

Guégan J.-F., Lek S. & Oberdorff T. (1998) Energy availability and habitat heterogeneity predict global riverine fish diversity. Nature, 391, 382–384.

Harding J.S., Benfield E.F., Bolstad P.V., Helfman G.S. & Jones E.B.D. III. (1998) Stream biodiversity: The ghost of land use past. Proceedings of the National Academy of Science USA, 95, 14843–14847.

Hartel T., Schweiger O., Öllerer K., Cogălniceanu D. & Arntzen J. W. (2010). Amphibian distribution in a traditionally managed rural landscape of Eastern Europe: Probing the effect of landscape composition. Biological Conservation, 143, 1118–1124.

Hawkins B.A., Field R., Cornell H. V., Currie D.J., Guégan J.-F., Kaufman D.M., Kerr J.T., Mittelbach G.G., Oberdorff T., O'Brien E.M., Porter E.E. & Turner J.R.G (2003) Energy, water, and broad-scale geographic patterns of species richness. Ecology, 84, 3105–3117.

Hijmans R.J., Cameron S.E., Parra J.L., Jones P.G. & Jarvis A. (2005). Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology, 25, 1965–1978.

Hijmans R.J., Phillips S., Leathwick J. & Elith J. (2013) dismo: Species Distribution Modeling. R Package Version 0.8-11. Available at: http://CRAN.R-project.org/package=dismo.

Homes V., Hering D. & Reich M. (1999). The distribution and macrofauna of ponds in stretches of an alpine floodplain differently impacted by hydrological engineering. Regulated Rivers: Research & Management, 417, 405–417.

Hortal J., Diniz-Filho J.A.F., Bini L.M., Rodríguez M.Á., Baselga A., Nogués-Bravo D., et al. (2011) Ice age climate, evolutionary constraints and diversity patterns of European dung beetles. Ecology Letters, 14, 741–748.

Illies J. (1978) Limnofauna Europaea. 2. Auflage. Gustav Fischer Verlag, New York, Stuttgart. 532 pp.

Jeppesen E., Meerhoff M., Holmgren K., Gonzalez-Bergonzoni I., Teixeira-de Mello F., Declerck A.A.J. et al. (2010) Impacts of climate warming on lake fish community structure and potential effects on ecosystem function. Hydrobiologia, 646, 73–90.

Jeppesen E., Mehner T., Winfield I.J., Kangur K., Sarvala J., Gerdeaux D., et al. (2012) Impacts of climate warming on the long-term dynamics of key fish species in 24 Euro- pean lakes. Hydrobiologia 694, 1–3.

Jeppesen E., Peder Jensen J., Sondergaard M., Lauridsen T. & Landkildehus F. (2000). Trophic structure, species richness and biodiversity in Danish lakes: changes along a phosphorus gradient. Freshwater Biology, 45, 201–218.

Knight L. (2012) Hypogean Crustacea Recording Scheme. Data available at: http://hcrs.freshwaterlife.org.

Legendre P. & Legendre L. (1998) Numerical Ecology, 2nd edition. Elsevier, Amsterdam.

Leprieur F., Tedesco P., Hugueny B., Beauchard O., Dürr H.H., Brosse S., et al. (2011) Partitioning global patterns of freshwater fish beta diversity reveals contrasting signatures of past climate changes. Ecology Letters, 14, 325–334.

Linder H.P. (2001) Plant diversity and endemism in sub-Saharan tropical Africa. Journal of Biogeography, 28, 169–182.

Loh J. & Wackernagel M. (ed.) (2004) Living Planet Report 2004. World-Wide Fund for Nature International (WWF), Global Footprint Network, UNEP World Conservation Monitoring Centre, Gland, Switzerland.

MacArthur R.H. & Wilson E.O (1967) The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.

Malard F., Mathieu j., Reygrobellet J.-L. & Lafont M. (1996) Biomonitoring groundwater contamination: application to a karst area in Southern France. Aquatic Sciences, 58, 158–187.

MEA (Millennium Ecosystem Assessment) (2005). Ecosystems and Human Well-being: Synthesis. Island Press, Washington, DC.

Mittelbach G.G., Schemske D.W., Cornell H.V, Allen A.P., Brown J.M., Bush M.B., et al. (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. Ecology Letters, 10, 315–331.

Moe S.J., Schmidt-Kloiber A., Dudley B.J. & Hering D. (2013). The WISER way of organising ecological data from European rivers, lakes, transitional and coastal waters. Hydrobiologia, 704, 11–28.

Myers N., Mittermeier R.A., Mittermeier C.G., da Fonseca G.A.B. & Kent J. (2007) Biodiversity hotspots for conservation priorities. Nature, 403, 853–858.

Nagorskaya L., Moroz M., Laeno T., Veznovetz V., Moller Pillot H., Dijkstra K.D.B. & Reemer M. (2002). Macrofauna in floodplain pools and dead branches of the Pripyat river, Minsk. Institute of Zoology, National Academy of Science Belarus, p. 158.

Nielsen A., Trolle D., Søndergaard M., Lauridsen T.L., Bjerring R., Olesen J.E., Jeppesen E. (2012) Watershed land use effects on lake water quality in Denmark. Ecological Applications, 22, 1187–1200.

Oberdorff T., Tedesco P., Hugueny B., Leprieur F., Beauchard O., Brosse S., et al. (2011) Global and Regional Patterns in Riverine Fish Species Richness: A Review. International Journal of Ecology, 2011, 1–12.

Oertli B., Auderset Joye D., Castella E., Juge R., Lehmann A. & Lachavanne J.-B. (2005) PLOCH: a standardized method for sampling and assessing the biodiversity in ponds. Aquatic Conservation: Marine and Freshwater Ecosystems, 15, 665–679.

Ojaveer H., Jaanus A., MacKenzie B.R., Martin G., Olenin S., Radziejewska T., Telesh I., Zettler M.L. & Zaiko A. (2010) Status of Biodiversity in the Baltic Sea. PLoS ONE, 5, e12467.

Paul M.J. & Meyer J.L. (2001) Streams in the urban landscape. Annual Review of Ecology and Systematics, 32, 333–365.

Phillips G., Lyche-Solheim, A., Skjelbred B., Mischke U., Drakare S., Free G., Järvinen M., de Hoyos C., Morabito G., Poikane S. & Carvalho L. (2012) A phytoplankton trophic index to assess the status of lakes for the Water Framework Directive. Hydrobiologia, 704, 75–95.

R Development Core Team (2013) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.R-project.org. (Version: 2.15.3)

Reyjol Y., Hugueny B., Pont D., Bianco P.G., Beier U., Caiola N., Casals F. Cowx I.G., Economou A., Ferreira M. T., Haidvogl G., Noble R., de Sostoa A., Vigneron T. & Virbickas T. (2007). Patterns in species richness and endemism of European freshwater fish. Global Ecology and Biogeography, 16, 65–75.

Ridgeway G. (2013) gbm: Generalized Boosted Regression Models R Package Version 2.0-8. Available at: http://CRAN.Rproject. org/package=gbm.

Ruffo S. & Stoch F. (2006) Checklist and distribution of the Italian fauna. 10,000 terrestrial and inland waters species. Memorie del Museo Civico di Storia Naturale di Verona, 2. serie. Sezione Scienze della Vita, 17, 1–307. (data on CD-ROM)

Sala O.E., Chapin F.S. III, Armesto J.J., Berlow E., Bloomfield J., Dirzo R., Huber-Sanwald E., Huenneke L.F., Jackson R.B., Kinzig A., Leemans R., Lodge D.M., Mooney H.A., Oesterheld M., Poff N.L., Sykes M.T., Walker B.H., Walker M. & Wall D.H. (2000) Global Biodiversity Scenarios for the Year 2100. Science, 287, 1770–1774.

Sastre P., Roca P., Lobo J.M. & EDIT co-workers (2009) A Geoplatform for the accessibility to environmental cartography. Journal of Biogeography, 36, 568.

Sayer C.D., Davidson T. & Jones J. I. (2010). Seasonal dynamics of macrophytes and phytoplankton in shallow lakes: a eutrophication-driven pathway from plants to plankton? Freshwater Biology, 55, 500–513.

Scheuerell M.D. & Schindler D.E. (2004) Changes in the spatial distribution of fishes in lakes along a residential development gradient. Ecosystems, 7, 98 –106.

Schindler D.W. (2006) Recent advances in the understanding and management of eutrophication. Limnology and Oceanography, 51, 356 –363.

Sobkowiak S. (2003) Vergleichende Untersuchungen zur Makroinvertebratenfauna von Auengewässern – unter besonderer Berücksichtigung der Kinzig-Aue (Hessen). Diploma thesis, University of Duisburg-Essen, Germany.

Stendera S., Adrian R., Bonada N., Cañedo-Argüelles M., Hugueny B., Januschke K., Pletterbauer F., & Hering D. (2012) Drivers and stressors of freshwater biodiversity patterns across different ecosystems and scales: a review. Hydrobiologia, 696, 1–28.

Tisseuil C., Cornu J.-F., Beauchard O., Brosse S., Darwall W., Holland R., Hugueny B., Tedesco P.A. & Oberdorff T. (2013) Global diversity patterns and cross-taxa convergence in freshwater systems. Journal of Animal Ecology, 82, 365–376.

Uusitalo L., Fleming-Lehtinen V., Hällfors H., Jaanus A., Hällfors S. & London L. (2013) A novel approach for estimating phytoplankton biodiversity. ICES Journal of Marine Science. doi:10.1093/icesjms/fss198

Venables W.N. & Ripley B.D. (2002) Modern Applied Statistics with S (MASS). 4th Ed. Springer, New York. Available: http://cran.r-project.org/web/packages/MASS/index.html. (Accessed on 1 April 2014).

Vörösmarty C.J., McIntyre P.B., Gessner M.O., Dudgeon D., Prusevich A., Green P., Glidden S., Bunn S.E., Sullivan C.A., Reidy Liermann C. & Davies P.M. (2010) Global threats to human water security and river biodiversity. Nature, 467, 555–561.

Warton D.I. & Hui F.K.C. (2011) The arcsine is asinine: the analysis of proportions in ecology. Ecology 92, 3–10.

Wetzel R. (2001) Limnology—Lake and River Ecosystems. Academic Press, New York.

Wright D.H. (1983). Species-energy theory: an extension of species-area theory. Oikos, 41, 496–506.

Zomer R.J, Trabucco A,, Bossio D.A., van Straaten, O. & Verchot L.V. (2008) Climate Change Mitigation: A Spatial Analysis of Global Land Suitability for Clean Development Mechanism Afforestation and Reforestation. Agriculture, Ecosystems and Environment, 126, 67–80.

Zuur A.F., Ieno E.N. & Smith G.M. (2007) Analysing ecological data. Springer, New York, 672 pp.

Tables

Table 1: Spatial scale considered and data sources used to generate arable and urban land use data.

	Land use data source	Area [km²]	Shape of area	Comment
Rivers	CORINE 2006	variable	irregular	entire catchment upstream of a site
Floodplains	CORINE 2006	78.5 km²	circle around site (radius = 5 km)	
Ponds	CORINE 2006	4.9 km²	circle around pond (radius = 125 m)	
Lakes	CORINE 2006	10,000 km²	100 x 100 km grid	
Groundwater	GlobCover	10,000 km²	100 x 100 km grid	

Table 2: Matrix of strength and direction of biodiversity metrics in response to urban and agricultural land use across all ecosystem types and organism groups. Response strengths and direction ('+': positive, '–': negative relationship) are according to the highest deviance explained by land use (without interaction terms) in the GLM models using the complete datasets: >|10%| = +++/– – – ; >|5%| = ++/– –; >|3%| = +/–; ≤|3%| = O.

		Richness		Rareness/endemicity		Taxonomic distinctness	
Ecosystem	Organism group	Urban	Arable	Urban	Arable	Urban	Arable
Rivers	Fishes	O	+	O	++	O	O
Rivers	Invertebrates	O	–	O	O	++	+++
Rivers	Macrophytes	– –	O	O	– –	O	O
Lakes	Phytoplankton	O	O	O	O	O	O

		Richness		Rareness/endemicity		Taxonomic distinctness	
Ecosystem	Organism group	Urban	Arable	Urban	Arable	Urban	Arable
Ponds	Amphibia	O	+	O	O	+++	– –
Ponds	Coleoptera/Odonata/Gastropoda	O	+++	++	O	O	O
Ponds	Macrophytes	O	++	O	++	–	O
Floodplains	Carabidae	– – –	– –	++	–	O	O
Floodplains	Mollusca	O	+	O	O	O	– –
Floodplains	Macrophytes	– –	O	O	O	O	O
Groundwater	Crustacea	+	O	O	O	O	– –

Table 3: Percent deviance explained by significant interaction terms including land use in the GLM models based on the complete datasets. If more than one interaction was significant, the total deviance explained by all interactions is provided. Geo-climatic descriptor(s) interacting with land use are listed in brackets; area = catchment size; lat = latitude; lon = longitude; ppt = annual precipitation; temp= mean annual air temperature; pet = potential evapo-transpiration; hab = habitat diversity.

		Richness		Rareness/endemicity		Taxonomic distinctness	
Ecosystem	Organism group	Urban	Arable	Urban	Arable	Urban	Arable
Rivers	Fishes		1.4 (area)				
Rivers	Invertebrates						
Rivers	Macrophytes				1.5 (lat)		
Lakes	Phytoplankton						

		Richness		Rareness/endemicity		Taxonomic distinctness	
Ecosystem	Organism group	Urban	Arable	Urban	Arable	Urban	Arable
Ponds	Amphibia	14.4 (lon)			3.1 (lon)	11.3 (lon)	
Ponds	Coleoptera/Odonata/Gastropoda			5.1 (lat, ppt, temp)	6.6 (lat)	2.7 (ppt)	
Ponds	Macrophytes	1.8 (ppt)	2.3 (lat, ppt)	3.7 (pet)			1.2 (lat)
Floodplains	Carabidae		11.1 (ppt)	9.5 (ppt)			
Floodplains	Mollusca	4.1 (lon)		17 (ppt)			
Floodplains	Macrophytes				3.7 (temp)		1.9 (lon)
Groundwater	Crustacea	1 (hab)					

Table 4: Split points used to generate two data subsets for each combination of ecosystem type, organism group and biodiversity metric. Split points were identified using the partial dependence plots provided by the Boosted Regression Tree models, but were modified in order to achieve a more

balanced sample size in both subsets. For clarity, subset 1 always encompasses the samples ≤ split point and subset 2 the samples > the split point. See text for details.

Ecosystem	Metric	Strongest geo-climatic descriptor variable	Split point	Sample size subset 1	Sample size subset 2
Rivers	Fish richness	Catchment size	500 km^2	516	74
Rivers	Fish rareness	Catchment size	500 km^2	516	74
Rivers	Fish taxonomic distinctness	Catchment size	500 km^2	516	74
Rivers	Invertebrate richness	Latitude	51° N	639	582
Rivers	Invertebrate rareness	Latitude	51° N	639	582
Rivers	Invertebrate taxonomic distinctness	Latitude	51° N	639	582
Rivers	Macrophyte richness	Longitude	6° E	96	555
Rivers	Macrophyte rareness	Latitude	51° N	292	359
Rivers	Macrophyte taxonomic distinctness	Latitude	51° N	191	303
Lakes	Phytoplankton richness	Mean annual air temperature	6 °C	192	644
Lakes	Phytoplankton rareness	Mean annual air temperature	7.7 °C	315	521

Ecosystem	Metric	Strongest geo-climatic descriptor variable	Split point	Sample size subset 1	Sample size subset 2
Lakes	Phytoplankton taxonomic distinctness	Mean annual air temperature	9.3 °C	655	181
Ponds	Amphibia richness	Mean annual air temperature	8.8 °C	110	38
Ponds	Amphibia rareness	Ecoregion	4 (yes/no)	alpine: 84	non-alpine: 64
Ponds	Amphibia taxonomic distinctness	Mean annual air temperature	8.9 °C	89	35
Ponds	Coleoptera/Odonata/Gastropoda richness	Annual precipitation	992 mm	119	58
Ponds	Coleoptera/Odonata/Gastropoda rareness	Latitude	48 °N	109	62
Ponds	Coleoptera/Odonata/Gastropoda taxonomic distinctness	Mean annual air temperature	8.8 °C	53	124
Ponds	Macrophyte richness	Latitude	49 °N	338	263
Ponds	Macrophyte rareness	Latitude	49 °N	338	263
Ponds	Macrophyte taxonomic distinctness	Annual precipitation	839 mm	238	327

Ecosystem	Metric	Strongest geo-climatic descriptor variable	Split point	Sample size subset 1	Sample size subset 2
Floodplains	Carabidae richness	Annual mean air temperature	9.9 °C	62	70
Floodplains	Carabidae rareness	Altitude	37 m a.s.l.	62	70
Floodplains	Carabidae taxonomic distinctness	Altitude	55 m a.s.l.	76	55
Floodplains	Mollusca richness	Annual precipitation	630 mm	51	30
Floodplains	Mollusca rareness	Longitude	16.5 °E	32	47
Floodplains	Mollusca taxonomic distinctness	Longitude	12.3 °E	32	47
Floodplains	Macrophyte richness	Annual mean air temperature	9.9 °C	170	182
Floodplains	Macrophyte rareness	Altitude	49 m a.s.l.	150	202
Floodplains	Macrophyte taxonomic distinctness	Altitude	19 m a.s.l.	124	198
Groundwater	Crustacea richness	Evapotranspiration (AET)	600 mm	406	120
Groundwater	Crustacea endemicity	Mean annual air temperature	10.9 °C	134	256

Ecosystem	Metric	Strongest geo-climatic descriptor variable	Split point	Sample size subset 1	Sample size subset 2
Groundwater	Crustacea taxonomic distinctness	Altitude	462 m a.s.l.	217	121

Figure captions

Figure 1: Variation partitioning scheme using four biodiversity metrics and eleven organism groups sampled in five ecosystem types. Each plot displays the pure and shared proportions of variance explained by land use and geo-climatic variables in the Boosted Regression Tree analyses (see text for details). NA = Shannon's diversity cannot be computed with presence/absence data.

Figure 2: Proportion of deviance explained by land use and interactions with land use in the GLM models using three biodiversity metrics calculated for eleven organism groups. Each model run was repeated using the full dataset (filled symbol) and two data subsets (empty symbols). Data subsets were generated separately for each biodiversity metric and based on the split points identified by Boosted Regression Tree analysis for the strongest geo-climatic environmental descriptor variable in each model (see text for details).

Figure 3: Changes in the proportion of deviance explained by land use (GLM models, absolute values) against percent range of latitude and longitude covered by data subsets 1 and 2 in comparison to the range of the full dataset. High percent values on the x-axis indicate a higher resemblance of latitude and longitude gradients to those of the full dataset. For the definition of subsets 1 and 2, see Table 4.

Figures

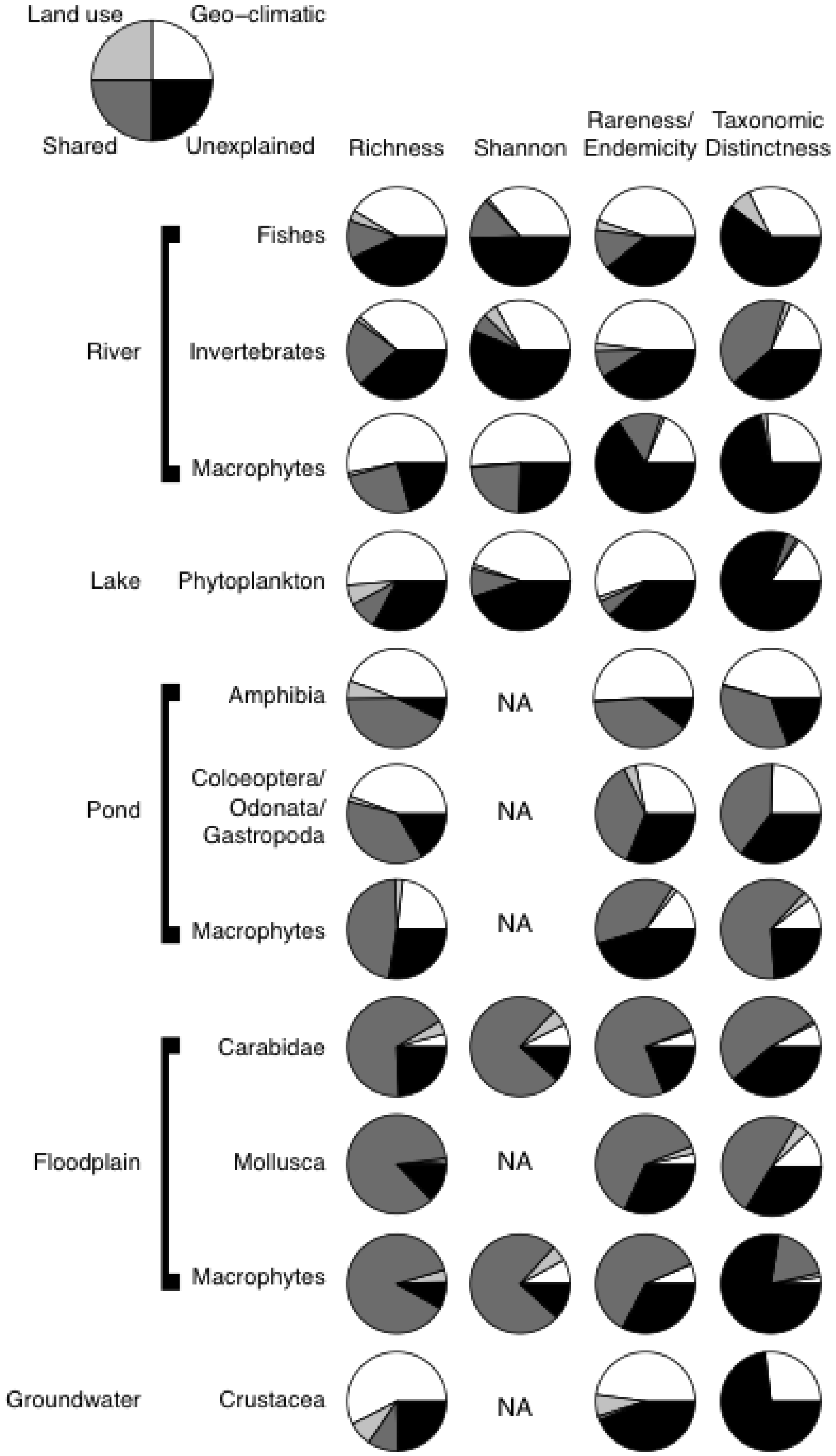


Figure 1

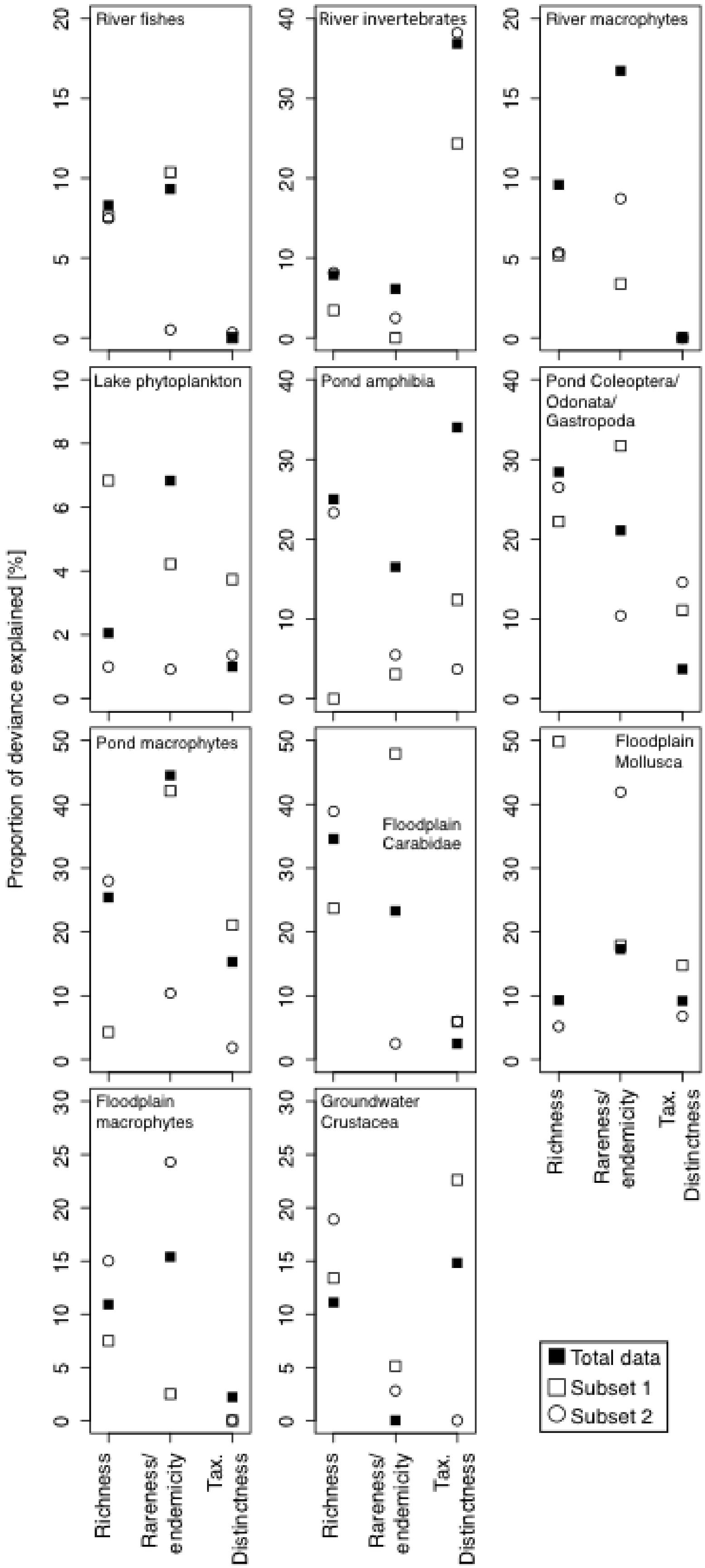

River fishes
River invertebrates
River macrophytes
Lake phytoplankton
Pond amphibia
Pond Coleoptera/ Odonata/ Gastropoda
Pond macrophytes
Floodplain Carabidae
Floodplain Mollusca
Floodplain macrophytes
Groundwater Crustacea
Proportion of deviance explained [%]
Richness
Rareness/ endemicity
Tax. Distinctness
■ Total data
□ Subset 1
○ Subset 2
0
5
10
15
20
25
30
40
50
2
4
6
8

Figure 2

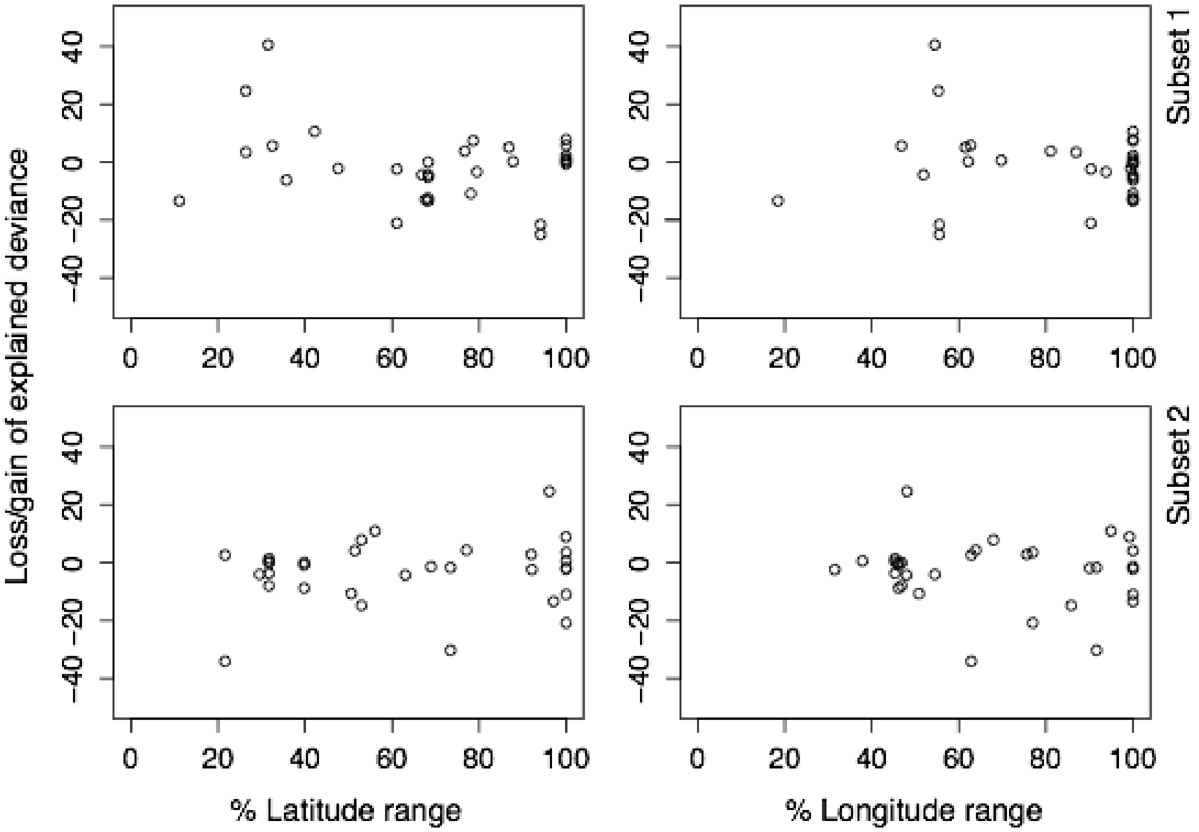

Loss/gain of explained deviance
Subset 1
Subset 2
40
20
0
−20
−40
0
20
40
60
80
100
% Latitude range
% Longitude range

Figure 3

Supplementary material

Table S1: Non-collinear geo-climatic variables used as descriptors in the Boosted Regression Trees and Generalised Linear Modelling.

Descriptors	Lakes	Rivers	Ponds	Wetlands/ floodplains	Groundwater
Longitude (°E)	x	x	x	x	x
Latitude (°N)		x			
Altitude (m a.s.l.)	x		x	x	x
Mean annual temperature (°C)	x	x	x	x	x
Annual precipitation (mm)	x	x	x	x	x
Catchment size (km^2)		x			
Actual evapo-transpiration (mm)					x
Potential evapo-transpiration (mm)			x		
Surface area (km^2)	x				

Chapter 2

Comparison of the effects of multiple stressors on freshwater biodiversity patterns

Abstract

1. One of the most pressing tasks of freshwater ecology and conservation biology is to unravel the effects of multiple stressors on species as well as on entire communities, and to estimate the implications for ecosystem processes and functions. Multiple stressors impose a serious threat on freshwater biodiversity. For the conservation and management of biodiversity, the knowledge of multiple stressor effects on biodiversity is a prerequisite.
2. Multiple stressors, such as the organic pollution, eutrophication, habitat degradation and fragmentation of rivers and their floodplains, may simply add individually to the multi-stressor ‘cocktail’, but more likely, stressors may interact synergistically or antagonistically. In addition, natural drivers of biodiversity such as temperature, radiation or slope determine biodiversity patterns in many freshwater ecosystems. These natural effects on biodiversity may mask or even counteract with multiple stressor effects, which renders the study of biodiversity response to multiple stressors challenging.
3. Here, we used a biodiversity dataset of three different ecosystems (rivers, floodplains, ponds) and three organism groups each per ecosystem to analyse the effects of land use, human modification and pollution on four biodiversity metrics: taxon richness, taxon rareness, Shannon-Wiener diversity and taxonomic distinctness. The diversity metrics were analysed against four groups of descriptor variables: land use, human modification, physico-chemical deterioration (not for ponds) and natural geo-climatic variables.
4. A variation partitioning scheme using redundancy analysis (RDA) was applied to identify the unique and shared proportions of variation in the diversity metrics explained by the descriptor groups. Overall, we found geo-climatic variables to explain more variation than any other descriptor group in most cases. The total variation explained by the analyses showed large differences between ecosystems, with highest values in ponds and lowest values in rivers. Generalised linear modelling (GLM) was applied to identify the most important significant descriptors contributing to the biodiversity observed. GLM largely supported the dominant role of geo-climatic variables, but also revealed strong influences of catchment land use on river diversity or of nutrient enrichment on river and pond diversity. Notably, the sign of the relationships was not consistent, but revealed positive and negative response of diversity to increasing stress.
5. Our results demonstrate a reasonably good response of richness (all ecosystems and taxonomic groups) and taxonomic distinctness and rareness (rivers, floodplains) to land use and nutrient enhancement, while the stressor effects are strongly linked to geo-climatic effects. The findings imply a strong interaction or overlap of natural and anthropogenic descriptors and require a careful interpretation in order to avoid the misinterpretation of the observed biodiversity patterns.

Introduction

Freshwater ecosystems are exposed to a variety of different environmental and anthropogenic stressors, with multiplicative, synergistic or antagonistic effects that can severely reduce biodiversity and change ecosystem processes (Townsend et al., 2008; Ormerod et al., 2010). Still, land use changes, habitat loss and fragmentation constitute major direct threats for freshwater biodiversity (MEA 2005). But the potential amplification by new stress agents is alarming; species invasions, extensive nitrogen and pollutant depositions and currently also climate change and hydrological regime shifts emerged during the last decades and are likely to continue to decline biodiversity in the future. While the understanding of the biodiversity effects of single stressors increased in course of numerous research studies addressing terrestrial and aquatic ecosystems, we are still far from reliably predicting the impacts of several environmental and anthropogenic stressors acting simultaneously, i.e. the effects of multiple stressors. Therefore, one of the most pressing tasks of ecology and conservation biology is to unravel the effects of multiple stressors on species and communities, and to estimate their implications for ecosystem processes and functions (Crain et al., 2008; Townsend et al., 2008).

Although the relationship between environmental impacts and biodiversity of is one of the oldest topics in ecology, there is still no consistent usage of the term “stressor”. Environmental stressors are frequently defined as ‘abiotic or biotic variables that exceed their natural range of variation due to human influence’ (Sanderson et al., 2002; Halpern et al., 2007). But there are also definitions referring to the often negative impacts of stressors on biodiversity, such as the one by Folt et al. (1999), who considered stressors as ‘any environmental factor that reduces population growth via a reduction in survivorship or reproduction relative to optimum conditions’. Tockner et al. (2010) gave another definition and stated that ‘stress can be considered as a sublethal effect on the physiology of plants and animals, leading to a decline in feeding and fecundity, or to a biochemical change’. Although such definitions are useful in a specific context, they may turn difficult in the realm of broad-scale biodiversity studies that apply landscape proxies of environmental stressors rather than environmental features directly affecting species physiology or populations reproduction. Agriculture, for example, is frequently considered a composite stressors (e.g. Allan, 2004; Feld, 2011) combining numerous more direct stressors such as nutrient enrichment, toxification through pesticides and fine sediment pollution. Thus, the definition of a stressor is, among other features, dependent on the spatial scaling considered. More importantly, the spatial scaling of a biodiversity study is linked to the gradient(s) in the natural drivers of biodiversity covered. Temperature and precipitation gradients, for example, constrain the distribution of species at broad (e.g. regional or continental) scales as a result of long-term evolutionary processes. Likewise, natural drivers of diversity can be classified direct drivers (e.g. temperature directly influences an animals physiology) or rather indirect drivers (e.g. altitude determined temperature, but depending on the latitude).

The different temporal scaling of environmental drivers and stressors of biodiversity adds another component of variability to broad-scale biodiversity studies. While natural drivers affect species and populations at evolutionary time scales, anthropogenic stressors of biodiversity act i) at much shorter time scales and ii) through novel (combinations of) ecological processes (Tockner et al., 2010). For example, the distribution and the functional adaptations of species inhabiting highly dynamic floodplain ecosystems is a consequence of long-term periodic fluctuations of inundation and dry cycles. The increasing frequency and magnitude of extreme weather events caused by climate change, in combination with human modifications of major floodplains, however, can impact floodplain biota in the short term, for the tolerance levels of many species to hydrological stress are repeatedly exceeded (Ilg et al. 2008; Gerisch et al., 2012).

Within a multi-stressor environment, the quantification of biodiversity response becomes even more complex; several single stressors can interact synergistically or antagonistically (Wagenhoff et al., 2011), with often unclear implications on biodiversity. Recent studies support the general assumption of many ecologists that the effects of multiple stressors are not simply the sum of single variable effects and that their combined effect cannot be predicted based on evidence from single-stressor studies (Breitburg et al., 1999; Folt et al., 1999; Vinebrooke et al., 2004). This is strongly supported by a review study by Crain et al. (2008), who found combined effects of single stressors in marine and coastal ecosystems were more often than not larger or smaller than the single stressor effects. However, the authors also noted many of the studies included in the review were based on lab experiments, hence impeding the transfer of results to more natural (in situ) conditions.

Despite the growing insight into the response of biodiversity to environmental drivers and stressors, broad-scale empirical studies on multiple stressors are rare and the development of theoretical frameworks of multiple stressor – biodiversity relationships is still in its infancy (but see Vinebrooke et al. 2004). Moreover, much of the past work addressed single ecosystems or single taxonomic groups, which renders further differentiation and generalization among ecosystems and organism groups difficult.

In this study, we compared the effects of multiple stressors on biodiversity patterns of individual taxonomic groups and within different freshwater ecosystems. Using a comparative cross-taxa-cross-ecosystem approach, we aimed at synthesizing the existing knowledge on i) the stressor types (and related spatial scales) that primarily affect freshwater biodiversity and ii) the taxonomic group(s) that respond most sensitive to the stressors. Therefore, we first used empirical data from three freshwater ecosystems (rivers, floodplains, ponds) to test the response patterns as reported in the literature. The outcome allowed us to estimate the biodiversity response patterns to several stressors at different spatial scales and to disentangle the relative importance of natural drivers *vs.* anthropogenic stressors. We hypothesized that no simple diversity-stressor relationships exist for each of the ecosystems and taxonomic groups studied, and that there are pronounced differences depending on the ecological requirements of the species. However, our main assumption was that stressors related to habitat loss and chemical/nutrient load will have strongest effects on freshwater biodiversity. Second, we <analysed the peer-reviewed body of literature on the response of biodiversity to anthropogenic stressors in various freshwater ecosystems. The review aimed to generate further insight into the hierarchy of stressors that impact biodiversity and the response pattern of biodiversity to the stressors. The identification of such response patterns focussed on the aspect of biodiversity considered in the reviewed studies (e.g. structural or functional diversity).

Methods

Explanatory data and diversity metrics

This study investigates the response of four different diversity metrics of nine taxonomic groups in three different freshwater ecosystems to multiple environmental and anthropogenic stressors. With response pattern, we refer to i) the sign (negative, positive, no sign), strength (e.g. expressed as explained deviance or variance), and significance of the relationship between diversity metrics and different stressor variables.

In total, 15 stressor variables were available for this study, while seven stressor variables (five land uses and two broad-scale proxies of human impact) were consistently available for all ecosystems and were used as explanatory data in a comparative analysis (Table 1). One important task was to estimate the explanatory power of different sets of variables and also to consider the role of spatial scale. For this, we grouped the explanatory data into four groups: (I) natural variables, (II) land cover (reflecting small scale land use), (III) human modification (reflecting larger scale land use), and (IV) physico-chemistry (Table 1). The first three groups were available for all ecosystems, while group IV was available only for ponds and rivers. With the groups I–III, we addressed landscape properties around each sampling site while group IV addressed the environmental conditions at a specific site.

The natural variables (I) covered latitude, longitude, altitude and catchment size derived from digital maps using ArcGIS 10. Mean annual air temperature and annual precipitation were abstracted from the WorldClim database version 1.4 (Hijmans et al., 2005). WorldClim summarises measured data at weather stations between 1950 and 2000 as monthly mean values, interpolated by a thin-plate smoothing spline algorithm to fit a raster grid (grid size: 30 arc seconds, approximately 1 km at the equator). Mean annual air temperature was averaged from long-term yearly means, whereas a yearly mean was averaged from monthly means throughout a year. Annual precipitation was based on the sum of long-term monthly mean precipitation values. Potential evapo-transpiration (PET) was derived from the CGIAR-CSI Global-PET database (for details, see Zomer et al., 2008; http://www.cgiar-csi.org). These natural variables were generally used in order to account for natural drivers of biodiversity patterns that might interfere or overlap with the gradients of human impact.

Buffer-scale (all ecosystems) and catchment (rivers only) land cover (II) were derived from CORINE land cover maps (European Environmental Agency; http://www.eea.europa.eu/publications/COR0-landcover) at the scale of different buffer areas around a sampling site or upstream (rivers only) (Table 1). For floodplains, CORINE variables were estimated using both a 5 and a 10 km buffer radius around each sampling site in order to reflect the land use on different spatial scales. Both buffer sizes were also used for river ecosystems. Because rivers are linear systems, CORINE variables were additionally estimated by creating a polygonal shape representing the catchment delineation of each river site. Hence, proportional land use was available for two different areas around the floodplain sites, and for three areas around or upstream of the river sites (Table 1). Due to their small size, land use data were derived within a 1 km buffer radius for ponds.

Human modification (III) was estimated using data on annual emission values of nitrogen oxides (NOx) (Theloke et al., 2011) and the Human Influence Index (HII) (Sanderson et al., 2002) as additional proxies of the influence of human activities (among others also land use). NOx emissions are quantified as proportional release from diffuse sources (transport, non-industrial combustion, industrial production). The HII combines human population pressure (population density), human land use and infrastructure (built-up areas, night-time lights, land use/land cover) and human access (coastlines, roads, railroads, navigable rivers). The index ranges from 0 to 72, with higher scores indicating greater human influence. Both parameters are related to CORINE land use (II), but add complementary aspects of anthropogenic stress regarding nutrient emissions (NOx) and general human-induced impact (HII).

Physico-chemical variables (IV) were available for rivers and ponds and were recorded during biological sampling using standard field measurement devices for physical variables and lab analytical procedures for chemical variables. All stressor variables were transformed (logit for percent values, log x + 1 for all others except for pH) to approximate normal distribution.

The response of the different taxonomic groups to the environmental and anthropogenic stressors was measured using four different components of diversity: the number of species within a community (referred to as species richness in the following), the community’s dominance structure or equity (Shannon diversity; not applicable to the pond dataset), the frequency of species occurrence in the entire dataset (rareness, according to the calculation of endemicity in Crisp et al. (2001) and Linder (2001)) and the phylogenetic diversity of a community (taxonomic distinctness, Clarke & Warwick, 1998; 1999).

Table 1: Stressor groups and mean values and range (in brackets) of the stressor variables used in this study.

Ecosystem type	Stressor group	Variable	Abbreviation	Mean/*median (Range)	Unit
Rivers	Natural (I)	Latitude	LAT	50.56 (42.81–54.80)	°N
		Longitude	LON	9.222 (-3.894–15.810)	°E
		Altitude	ALT	214.11 (2–811)	m a.s.l.
		Annual precipitation	ANP	750.8 (480–1,323)	mm
		Annual mean air temperature	AMT	9.5 (6.4–14.6)	°C
		Catchment area	CAR	349.2 (11–7,863.2)	km^2
	Buffer land use (II)	Forest	FRT5	28.9 (0–91.4)	%
		Pasture	PST5	10.3 (0–68.9)	%
		Non-irrigated arable land	CRP5	38.2 (0–95.3)	%
		Continuous and discontinuous urban fabric	URB5	9.3 (0–56.2)	%
	Catchment land use and human modification (III)	Forest	FRT	35.1 (0–100)	%
		Pasture	PST	11.8 (0–100)	%
		Non-irrigated arable land	CRP	45.4 (0–100)	%
		Continuous and discontinuous urban fabric	URB	6.4 (0–68)	%
		Human Influence Index	HII	29.2 (12–53)	
		Emission values of nitrogen oxides	NOx	113 (12.4–558.4)	t a^{-1}
	Physico-chemistry (IV)	Chloride	CHL	45.2 (0–2,063)	mg l^{-1}
		Ammonia	AMO	0.2 (0–9.8)	mg l^{-1}
		Nitrite	NIT	0.1 (0–3.5)	mg l^{-1}
		Nitrate	NAT	15.5 (0–101.4)	mg l^{-1}
		Ortho-phosphate	OPO	194.1 (0–3,527.1)	µg l^{-1}
		Total phosphorus	TPO	428.8 (0–14,108.5)	µg l^{-1}

Ecosystem type	Stressor group	Variable	Abbreviation	Mean/*median (Range)	Unit
		Oxygen	OXY	8.9 (0–15.6)	mg l^{-1}
Floodplains	Natural (I)	Latitude	LAT	49.0 (38.5-65.2)	°N
		Longitude	LON	11.5 (-8.7 – 25.8)	°E
		Altitude	ALT	93.7 (1.0 – 1094.0)	m a.s.l.
		Annual precipitation	ANP	720.8 (493.0-1336.0)	mm
		Annual mean air temperature	AMT	10.4 (1.0-17.7)	°C
	Land use (II)	Forest	FRT	36.6 (0-99.3)	%
		Pasture	PST	20.6 (0-83.3)	%
		Non-irrigated arable land	CRP	30.0 (0-100)	%
		Continuous and discontinuous urban fabric	URB	12.8 (0-100)	%
	Human modification (III)	Human Influence Index	HII	31.5 (9.3-56.0)	
		Emission values of nitrogen oxides	NOx	111.5 (1.2-517.6)	t a^{-1}
Ponds	Natural (I)	Latitude	LAT	47.62 (45.98 - 51.33)	°N
		Longitude	LON	7.16 (3.43 - 10.40)	°E
		Potential evapo-transpiration	PET	692 (318 - 870)	mm a^{-1}
		Altitude	ALT	566* (2 – 2,752)	m a.s.l.
	Land use (II)	Forests	FRT	24.2 (0 - 100)	%
		Pastures	PST	0* (0 - 75)	%
		Non-irrigated arable land	CRP	9.5* (0-100)	%
		Continuous and discontinuous urban fabric	URB	1.6* (0 - 55.2)	%
		Complex cultivation patterns	CCP	0* (0 - 46.5)	%
	Human modification (III)	Human Influence Index	HII	29.7 (15.7 - 47.6)	
		Emission values of nitrogen oxides	NOx	130.7 (1.9 - 484.7)	t a^{-1}
	Physico-chemistry (IV)	Total phosphorus	TP	39* (1 - 632)	µg l^{-1}

Ecosystem type	Stressor group	Variable	Abbreviation	Mean/*median (Range)	Unit
		Conductivity	CON	336 (6 – 1,124)	µS cm^{-1}

General analytical approach

We followed a four-step-analysis in order to identify, quantify and verify the biodiversity metrics' response patterns. First, we checked all environmental anthropogenic stressor variables (referred to as 'descriptors' in the following) for collinearity, first for each stressor group separately (within group collinearity) and then using all remaining variables together (between-group collinearity). This was done based on a triangular correlation matrix (Spearman's) of each variable against all others and on each descriptor's variance inflation factor (VIF). Following Zuur, Ieno & Smith (2007), all variables with a VIF >8 and a correlation coefficient >0.7 were excluded. The final set of descriptors was then used in a univariate variation partition analysis of each response metric to quantify the share of the deviance (i.e. the variation) in the respective metric explained by all descriptors together, by each pair of descriptor groups and by each descriptor group individually. Variation partitioning is based on a series of Redundancy Analyses (RDA) using the different groups of descriptor variables individually and all possible combinations thereof to additively quantify the variation of each descriptor group or combination, respectively (Borcard & Legendre 1992). With three descriptor groups in the analyses, this resulted in eight fractions of variation for each biodiversity metric (three single groups, three pairs of groups, all descriptors together and the residual deviance not explained). The arithmetic variation partitioning process has been widely applied in similar studies (e.g. Marzin et al., 2013; Peres-Neto et al., 2006; Pavlin et al., 2011) and is well-described by Borcard et al. (2011).

In a third step we applied boosted regression trees (BRT) in order to estimate the explanatory power of the individual variables for each diversity metric, and to identify possible interactions between explanatory variables and exponential terms. BRTs constitute a relatively novel machine-learning technique and allow of the identification and quantification of the influence that numerous descriptors have on a single response variable. They provide both a statistic with the contribution of each descriptor to the deviance explained by a model and a function to identify interactions between pairs of descriptors. Further, they allow the identification of quadratic (i.e. curvilinear) relationships between each predictor and the response variable in its partial dependence plots, which are part of the standard output of each analysis (Elith et al., 2008). BRT were run for each diversity metric, including all non-collinear explanatory variables.

In the final step, we used generalised linear regression modelling (GLM) to quantify the role of each descriptor individually for the observed response patterns. First, the full model was calculated using all non-collinear variables together. Second, stepwise backward regression was run to identify the final (optimal) model, i.e. the model with only significant descriptors remaining in the model and with the highest possible fraction of deviance explained. In addition, we checked for quadratic relationships and interactions between pairs of descriptors and included both quadratic and interaction terms in the null models. We used the Poisson distribution function for richness (count measure) and the Gaussian function for Shannon diversity, rareness and taxonomic distinctness. In case of overdispersion, i.e. when the metric's variability was higher than the variability of a corresponding theoretical poisson distribution, we used a negative binomial distribution function for richness. Because of their proportional character, rareness and taxonomic distinctness were logit-transformed.

All analyses were done using R (R Development Core Team 2013). Diversity metrics were calculated using the 'vegan' library (Oksanen et al., 2013). See Crisp et al. (2001) and Feld (2013) for details on the calculation of rareness and taxonomic distinctness, respectively. Variation partitioning was calculated using the function 'varpart' (included in vegan). Negative binomial GLM models were fitted using 'MASS' (Venables & Ripley, 2002) and BRT were calculated using the library 'gbm' (Ridgeway, 2013) and the 'dismo' package (Hijmans et al., 2013).

Study sites

Rivers

Site-specific river data were derived from the WISER river database (Moe et al., 2013), encompassing taxa lists of fish 523 sites), macroinvertebrates (1,221 sites) and macrophytes (247 sites) across Central Europe (Central/Western Mountains and Central/Western Plains ecoregions of France, Germany and Austria; Illies, 1978). The taxa lists originate from national monitoring surveys and followed the national monitoring standards defined for field sampling methodology and sample processing (see Dahm et al., 2012 and Feld, 2013 for details).

Prior to the calculation of biodiversity metrics, the raw taxa lists obtained from the WISER river database were manually adjusted to eliminate the researcher-dependent bias, for example, caused by different targeted determination levels for macroinvertebrates (e.g. Oligochaeta, Diptera). Species-level was achieved for fish and macrophytes, while genus level was targeted for macroinvertebrates, as it is the standard determination level in France.

Floodplains

The floodplain database is based on publications of European datasets on plants, ground beetles, and molluscs in riverine wetland ecosystems referred to as floodplains in this study. A search of the peer-reviewed literature was conducted in the Web of Science, targeting publications between 1990 and 2012. Altogether, 78 publications were reviewed in detail to generate three taxa lists (total number of sample sites: 360): 214 sites for floodplain vegetation, 83 sites for ground beetles and 35 sites for molluscs. Samples from distinct and separated habitat types within the same floodplain were interpreted as different sites. The sites are located in 17 countries and on 33 river floodplains across Europe, with the majority of sites located in Central Europe: Poland: 92 sites, Germany: 62, France: 43, and Belgium: 26 sites. 46 sites were located in UK, and 46 sites in Greece.

Standardisation of species abundances among studies was impossible due to the lack of information on sampling effort in most studies. The bias in sampling effort was minimised by omitting studies with an extremely short or long field sampling period and those with strongly skewed or otherwise inconsistent data.

Ponds

Amphibian species were recorded once at 72 Swiss ponds (Oertli et al., 2000). Macrophyte species records covered 143 samples at 134 ponds in Belgium (Flanders) (Stiers et al., 2011) and Switzerland (Oertli et al., 2000) (genus level targeted for *Chara* sp. and *Callitriche* sp.; only hygrophytes, helophytes and hydrophytes with Ellenberg's moisture values ≥ 7 and stoneworts considered; Ellenberg et al., 1992). Macroinvertebrate taxa lists were collated from samples at 68 Swiss ponds (species level) (Oertli et al., 2000).

Review study

In order to place and discuss the response patterns empirically derived from our field data in light of the existing evidence of biodiversity response to anthropogenic stressors in the literature, we conducted a comprehensive review study. The review focussed on the three ecosystems addressed here and started with a search in the Web of Science and Scopus. The following search terms were used in common: biodiversity OR diversity AND freshwater AND [ecosystem type] AND [organism groups] AND land use OR modification OR impact. The search was further refined in order to increase the focus on studies that addressed the qualitative or quantitative analysis of biodiversity response to environmental stressors. To enable a qualitative analysis of the review outcome, a set of criteria was derived from each reference and transferred to an Excel sheet (see Supplementary Table 1 for the set of criteria reviewed). Each reported relationship between a biodiversity measure and a stressor variable or multiple stressor variables was interpreted as a separate item, which allowed of multiple entries for a single study.

Overall, the reviewed criteria encompassed i) the origin and set up of the studies including the number of sites and samples, the type of stressor variable(s) addressed, the type of biodiversity metric addressed, the sign and strength of the response (e.g. positive/negative, explained deviance, R^2) and a narrative judgement of the quality of the study (high, intermediate, low). The latter was based on the sample size and the analytical design of the study and, although being a rather subjective statement, allowed to distinguish broad-scale, extensive and comprehensive surveys from those based on a few samples within a rather local context.

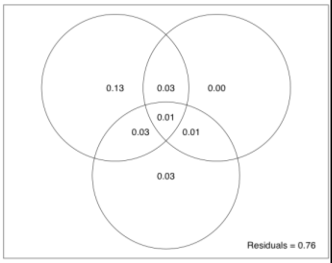
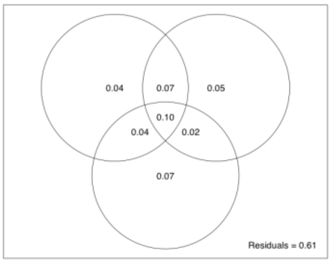
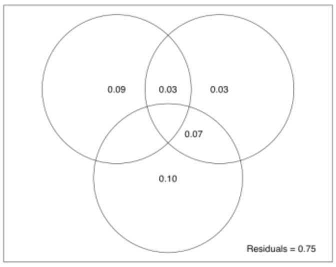
Results

We applied variation partitioning to estimate the importance of different environmental stressor groups and their shared effects on biodiversity. In total, 45 variation partitioning schemes were calculated for nine taxonomic groups and four diversity metrics in three ecosystems. A total of 29 GLMs were calculated in order to quantify the relationships between single and multiple stressors and diversity metrics in the different ecosystems. In the following, the results are presented for each ecosystem separately, providing a comparison between the ecosystems thereafter.

Rivers

Variation partitioning

Geoclimatic variables, land-use, and physico-chemistry explained on average 25.3% of the variation in the diversity metrics across all taxonomic groups studied in rivers. The results only slightly differed between buffer land use (LUB) and catchment land use (LUC) in the analysis, with catchment land use explaining slightly more variance in several biodiversity metrics. Taxonomic distinctness of invertebrates was best explained by all stressor groups combined (42%), followed by invertebrate richness (37.6%) and macrophyte rareness (36.5%). Benthic invertebrate diversity revealed the strongest relationship to the stressors considered, with 32.3% explained variation on average, followed by macrophytes (22.5%) and fishes (21%). Pure effects were most prominent and comparatively strong for catchment land use (max: 15% for invertebrate taxonomic distinctness) and geo-climatic variables (max: 13% for fish richness) (Figure 1 and 2). Shared effects were higher in benthic invertebrates and macrophytes than in fish, with maximum values >20% for fish and invertebrate taxonomic distinctness (Figure 1 and 2).

	Fishes	Benthic invertebrates	Macrophytes
Richness			

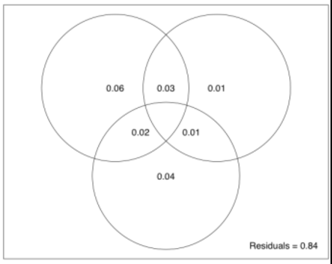
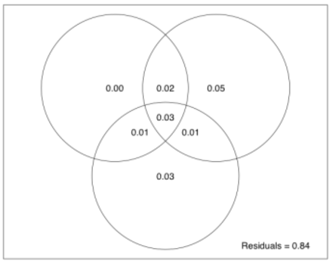
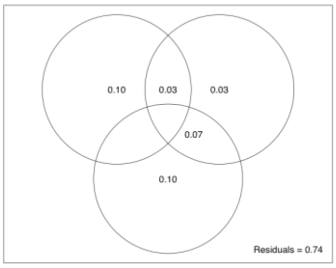
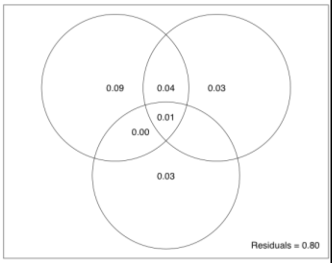
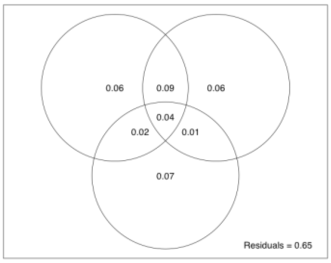
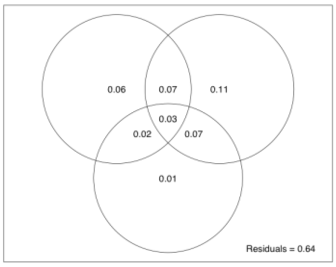
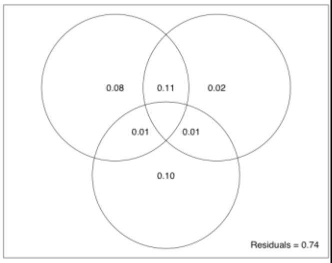
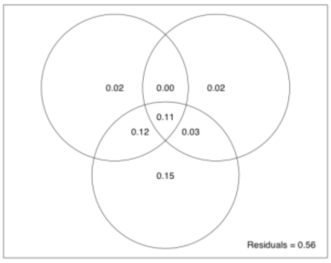
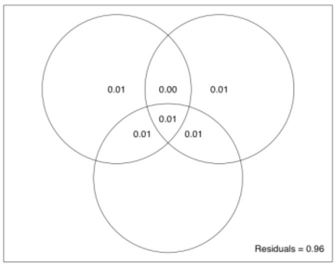
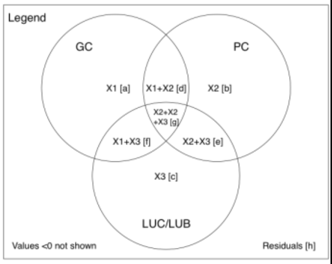
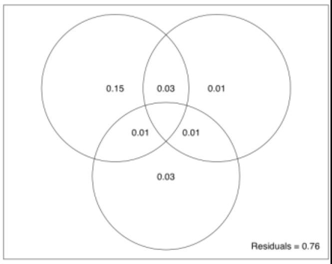
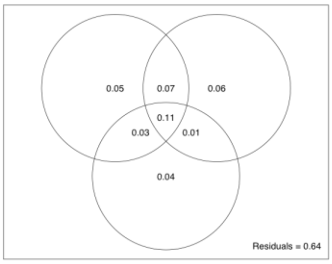
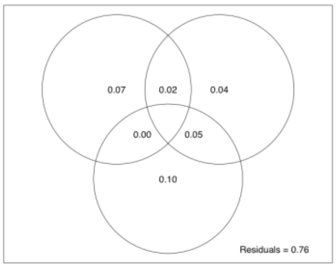
Shannon			
Rareness			
Tax. Distinctness			
			

Figure 1: Variation partitioning of diversity metrics by geo-climatic (GC), physico-chemical (PC) and catchment land use variables (LUC).

	Fishes	Benthic invertebrates	Macrophytes
Richness			

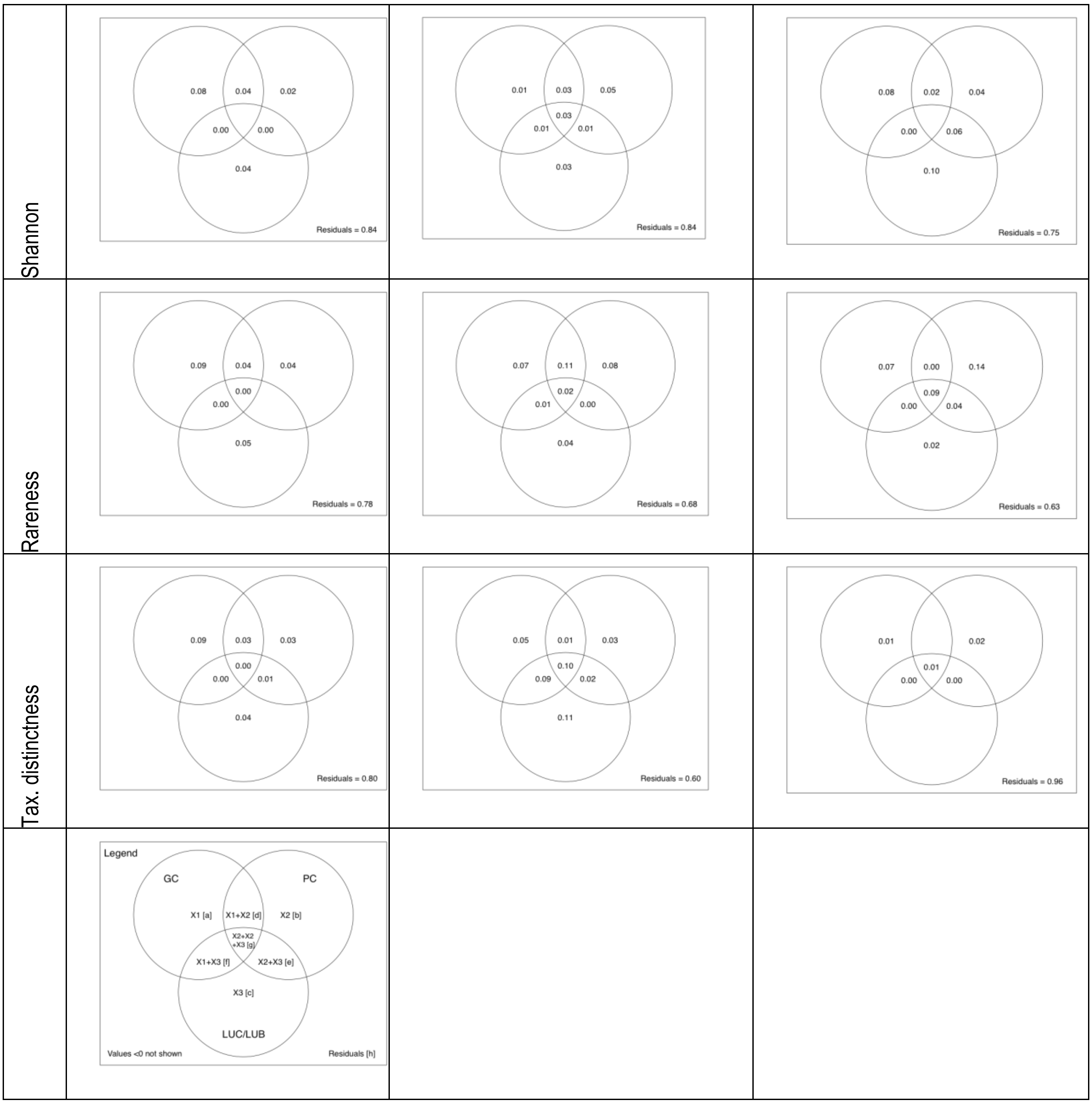


Figure 2: Variation partitioning of diversity metrics by geo-climatic (GC), physico-chemical (PC) and buffer land use variables (LUB).

Among all diversity metrics and across all taxonomic groups, species rareness was best explained by the three stressor groups (mean variation explained: 30.3%), followed by species richness (29.3%), taxonomic distinctness (24.6%), and Shannon diversity (19.4%, Table 2; all results for LUC). This explanatory power did not change with spatial scale of land-use (LUC *vs.* LUB), as similar patterns were detected for land use within the 5 km buffer around the sites, and land-use within the river catchment, respectively (see Table 2 and Methods for details). The standard deviation, however, reveal that the results were most variable for taxonomic distinctness, and least variable for Shannon diversity and richness.

There were notable differences between the stressor groups with regard to the variation they explained in the different diversity metrics. While geo-climatic variables explained species richness best, (8.7%, Table 2), physico-chemistry, on average, explained 6.7% in the variation of species rareness. Taxonomic distinctness was best explained by land-use on smaller spatial scales (LUB: 8.3%), while catchment land-use and human modification (LUC) explained richness and Shannon diversity best (both: 5.7%). Across all metrics considered, fish diversity was best explained by geo-climatic variables, and both invertebrate and macrophyte diversity were best explained by land-use variables (Table 4). The explanatory power was, however, relatively small with the highest values ranging between 4.5% and 12.9%.

Table 2: Mean (±SD) deviance of diversity metrics across organism groups explained by all variables in the variation partitioning (VarPart) and by the final GLM model, respectively.

	Richness	**Shannon**	**Rareness**	**Tax. distinctness**
Rivers				
VarPart LUC	29.3 (8.9)	19.3 (5.6)	30.3 (8.8)	24.6 (20.1)
VarPart LUB	27.9 (6.7)	18.8 (5.5)	30.6 (8.0)	21.3 (18.1)
GLM	30.3 (7.9)	21.1 (6.5)	31.9 (10.9)	26.9 (17.3)
Floodplains				
VarPart	75,4 (5.0)	19 (20.0)	33.3 (30.5)	29.7 (28.0)
GLM	65.8 (15.4)	44 (29.4)	44.5 (12.7)	21.1 (21.1)
Ponds				
VarPart	34.3 (15.9)	NA	36.7 (30.4)	33.0 (26.0)
GLM	47.6 (13.7)	NA	46.4 (21.1)	41.5 (28.3)
Total mean	**44.4**	**24.4**	**36.3**	**28.3**

GLM

The patterns determined by variation partitioning largely support the GLM results, which performed best in explaining rareness, followed by species richness, taxonomic distinctness, and Shannon diversity (Table 2). The models explained most of the deviance in taxonomic distinctness of invertebrates (45%, Table 2), followed by macrophyte rareness (39.9%), and invertebrate richness (39.2%). Both geo-climatic and physico-chemistry explained most of the deviance in the rareness and richness across all taxonomic groups, which is well in line with the variation partitioning. GLMs also proved that geoclimatic variables explained most of the fish diversity, while land-use variables explained most of the invertebrate diversity (Table 4).

Fish richness, rareness, and Shannon diversity increased with catchment area and also with the amount of forests (richness, rareness), and pastures (Shannon) (Table 5). There was a negative impact of decreasing oxygen levels on Shannon diversity and rareness of fish. On the contrary, invertebrates and macrophyte diversity decreased notably with altitude. Invertebrate richness, Shannon diversity, and rareness decreased strongly with ammonium concentration and human modification, while macrophyte diversity decreased strongly with increasing nitrogen oxide depositions and percent urban area.

Ponds

Variation partitioning

Geo-climatic variables, land-use, and physico-chemistry explained on average 34.7 % of the variation in the diversity metrics across all taxonomic groups studied in ponds. Diversity of amphibians was best explained by all stressor groups combined, with taxonomic distinctness being the highest (63%, Figure 3), followed by rareness (59%), and richness (52%). There were pronounced shared effects present between geo-climatic variables and land use in benthic invertebrate richness and between all descriptor variables in plant rareness and in taxonomic distinctness of amphibians.

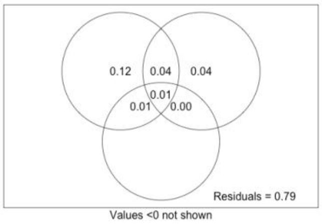
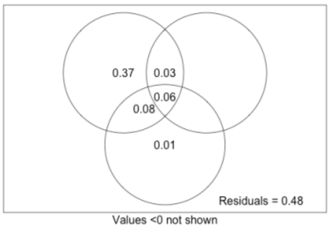
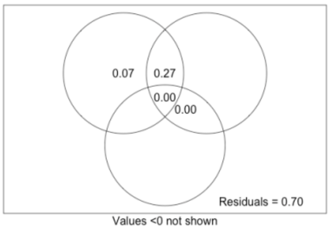
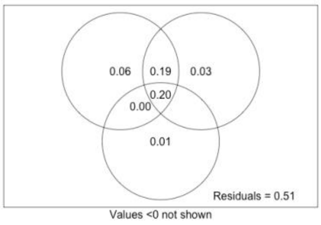
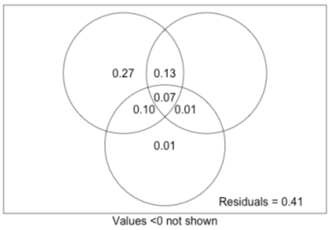
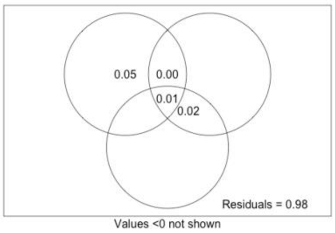
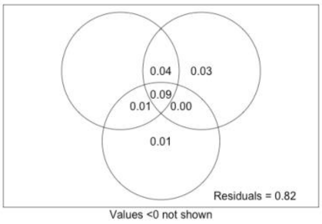
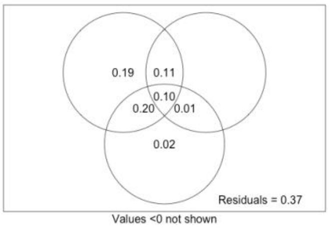
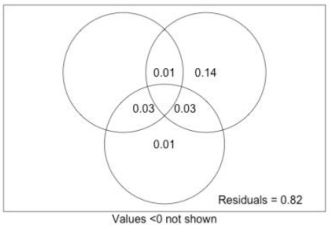
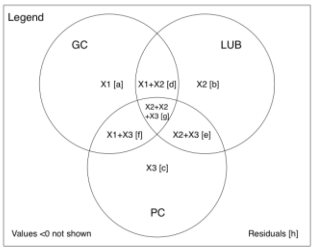
	Macrophytes	Amphibians	Benthic invertebrates
Richness			
Rareness			
Tax. Distinctness			
			

Figure 3: Variation partitioning of diversity metrics by geo-climatic (GC), buffer land use (LUB) and physico-chemistry (PC) in pond ecosystems.

There were only slight differences in the explanatory power by the three stressor groups across all taxonomic groups investigated in ponds. Highest variation explained was detected for species rareness (mean variation explained: 36.7%, Table 2), followed by species richness (34.3%), and taxonomic distinctness (33.0%). Shannon diversity could not be calculated for ponds.

Most of the variation in richness, rareness, and taxonomic distinctness of pond biodiversity was explained by geo-climatic variables (Table 3). Land-use and physico-chemistry explained only very small proportions of the diversity metrics calculated across all taxonomic groups. This was comparable both for variation partitioning and GLMs. Again, amphibian diversity was best explained by geo-climatic variables also in GLM (62.2%), which explained also notable degrees of variation in the diversity of macrophytes (26.9%) and pond insects (17.8%).

Table 3: Variation in diversity metrics explained by natural (GC) and anthropogenic stressor groups (PC, LUC, LUB). LUC=Land use in river catchments, LUB=Land use in 5 km buffer (rivers, floodplains) or 1 km (ponds) around the sites. For each diversity metric, data are expressed as the mean deviance (±SD) across all studied taxonomic groups, explained by the descriptor groups in the variation partitioning analyses (VarPart) and the members of the descriptor groups in the final GLM-model, respectively (highest values in bold). NA = not applicable.

Ecosystem x diversity metric	**GC**		**PC**		**LUC**		**LUB**	
	VarPart	GLM	VarPart	GLM	VarPart	GLM	VarPart	GLM
Rivers								
Richness	**8.7** (4.5)	8.6 (7.5)	2.7 (2.5)	7.4 (12.8)	6.7 (3.5)	**9.8** (4.5)	**5.7** (3.8)	3.9 (3.4)
Shannon	5.3 (5)	6.1 (2.9)	3.0 (2)	4.4 (4.0)	5.7 (3.8)	7.4 (7.4)	**5.7** (3.8)	1.5 (2.6)
Rareness	7.0 (1.7)	**10.2** (2.4)	**6.7** (4)	**17.4** (11.8)	3.7 (3.1)	2.9 (3.6)	3.7 (1.5)	1.6 (1.5)
Tax. distinctness	3.7 (3.8)	6.2 (5.5)	1.7 (0.6)	1.7 (1.4)	**8.3** (7.6)	7.2 (6.4)	5.0 (5.6)	**8.0** (13.8)
Floodplains								
Richness	**34.33** (21)	**33.1** (NA)	NA	NA	**2.7** (3.8)	10.8 (NA)	**40.3** (14.6)	**43.25** (16.47)
Shannon	9.7 (15.9)	16.2 (24.3)	NA	NA	2.0 (3.5)	**11.15** (2.8)	6.7 (5.8)	8.5 (4.1)
Rareness	20 (21.7)	34.2 (NA)	NA	NA	2.3 (2.1)	1.2 (NA)	6.7 (8.3)	**53.25** (NA)

Tax. distinctness	0.3 (0.6)	2.8 (1.6)	NA	NA	0 (0)	4.5 (NA)	3.3 (3.5)	32.0 (NA)
Ponds								
Richness	**18.9** (16.0)	**42.1** (19.5)	0.3 (0.6)	0.6 (1.1)	NA	NA	1.3 (2.2)	3.5 (3.1)
Rareness	**12.4** (12.5)	**36.9** (27.2)	0.5 (0.5)	1.6 (1.5)	NA	NA	1.1 (1.8)	2.6 (2.2)
Tax. distinctness	**6.4** (11.0)	**27.9** (32.5)	1.6 (0.3)	0.1 (0.2)	NA	NA	5.7 (7.4)	7.9 (10.3)
Total mean	**11.5**	**20.4**	**2.4**	**4.7**	**3.9**	**6.9**	**7.7**	**15.1**

GLM

GLMs revealed that almost all diversity metrics in the taxonomic groups decreased considerably with increasing altitude, except vegetation rareness, which increased significantly with altitude (Table 5). There were different effects of land-use on diversity metrics, with vegetation richness increasing with the amount of pastures, but invertebrate taxonomic distinctness decreasing. The rareness and taxonomic distinctness of amphibians increased with increasing amount of forests, while invertebrate richness decreased. Conductivity decreased amphibian rareness and distinctness, but increased invertebrate rareness.

Table 4: Mean variation across all diversity metrics explained by natural (GC) and anthropogenic stressor groups (PC, LUC, LUB). LUC=Land use in river catchments, LUB=Land use in 5 km buffer (rivers, floodplains) or 1 km (ponds) around the sites. For each taxonomic group, data are expressed as the mean deviance (±SD) across all diversity metrics, explained by respective descriptor groups in the variation partitioning (VarPart) and the variables of the descriptor groups in the final GLM-model, respectively (highest values in bold). NA = not applicable.

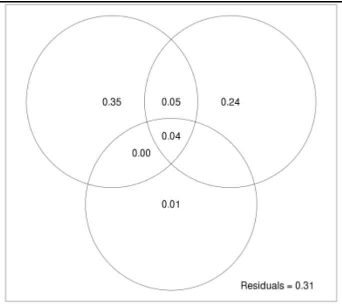
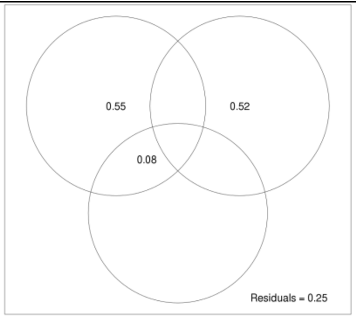
	GC		**PC**		**LUC**		**LUB**	
Rivers	VarPart	GLM	VarPart	GLM	VarPart	GLM	VarPart	GLM
Fish	**9.0** (2.9)	**12.5** (3.4)	1.5 (1.3)	1.9 (2.5)	4.0 (0.8)	2.2 (2.6)	5.0 (3.4)	5.2 (4.1)
Invertebrates	3.0 (2.6)	5.9 (3.7)	**4.5** (1.7)	**12.9** (8.9)	**5.5** (3.7)	**6.1** (11.9)	**8.0** (5)	**7.9** (5.7)
Macrophytes	6.5 (4)	4.9 (2.9)	**4.5** (4.4)	8.4 (13.7)	**5.5** (5.3)	3.0 (3.0)	5.3 (5.5)	7.4 (7.6)
Floodplains								
Grounds	14.3 (20.1)	2.1 (2.1)	NA	NA	**4** (3.2)	**8.8** (6.1)	**18.5** (18.4)	**18.9** (14.9)

Molluscs	13.8 (27.5)	NA	NA	NA	0	NA	13 (26)	NA
Vegetation	**20.3** (14.8)	**11.6** (11.2)	NA	NA	1.3 (1.9)	5.5 (5.1)	11.3 (8.8)	15.0 (13.1)
Ponds								
Amphibians	**27.8** (9.0)	**62.2** (3.4)	1.2 (0.7)	0.7 (1.0)	NA	NA	0.0 (0.0)	0.7 (0.9)
Insects	4.2 (3.8)	**17.8** (19.4)	0.5 (0.9)	1.0 (1.7)	NA	NA	**4.7** (8.1)	8.9 (9.4)
Macrophytes	6.0 (6.1)	**26.9** (17.3)	0.8 (0.7)	0.6 (1.1)	NA	NA	3.4 (0.4)	4.3 (2.0)
Total mean	**11.7**	**18.0**	**2.2**	**4.2**	**3.4**	**5.1**	**7.7**	**8.5**

Floodplains

Variation partitioning

Geo-climatic variables, land-use in 5 km buffers (LUB), and human modification in 10 km buffers explained on average 39.1% of the variation in the diversity metrics across all taxonomic groups studied in floodplain ecosystems. Richness was best explained by all stressor groups combined, with the highest value found for ground beetles (79%, Figure 4), followed by richness of molluscs (75%), and plant richness (69%). Other metrics performed partly well, for example, ground beetle rareness (63%) and mollusc taxonomic distinctness (57%). Less than 5% of the variation was explained for rareness and Shannon diversity of molluscs, as well as for taxonomic distinctness of ground beetles. Pronounced shared effects between stressor groups on floodplain diversity were present only in few cases (e.g. plant taxonomic distinctness, Figure 4).

	Vegetation	Ground beetles	Molluscs
Richness			

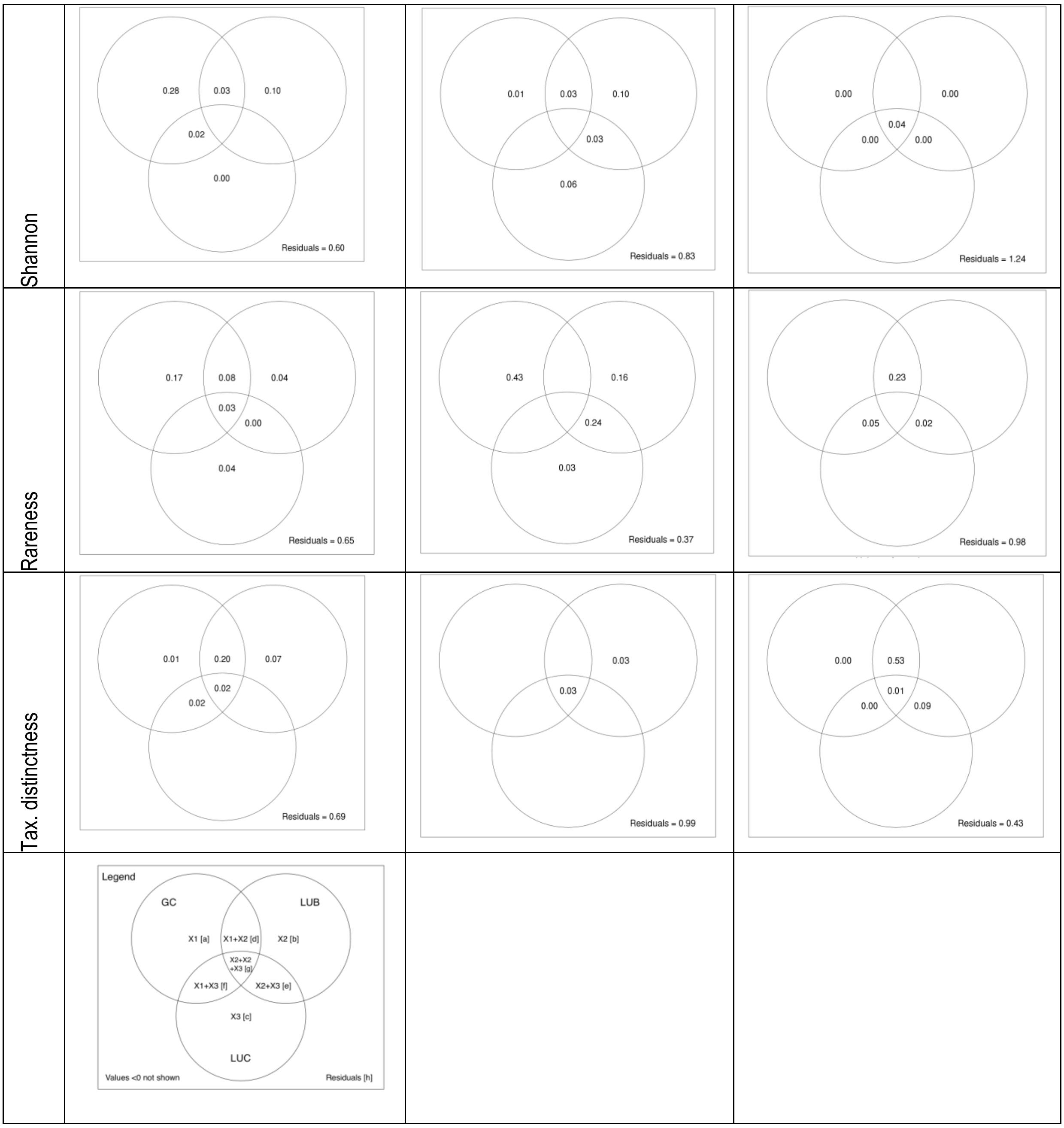


Figure 4: Variation partitioning of diversity metrics by geo-climatic (GC), small-scale land use (LUB), and large-scale land use variables (LUC) in floodplain ecosystems.

GLM

GLMs revealed specific relationships between vegetation and ground beetles, and stressors in floodplains (Table 5). Small-scale land use (LUB) had strong effects on plant diversity, with a pronounced negative effect of the amount of pastures increasing on plant taxonomic distinctness and weak negative effects on plant richness. On the contrary, geo-climatic variables were mostly positively related to plant diversity. Land use at the larger scale had different impacts on vegetation patterns, with plant richness and Shannon diversity increasing with nitrogen and human modification, respectively, and plant rareness decreasing with HII. Annual precipitation was related to ground beetle diversity, with positive effects on Shannon diversity and negative effects on taxonomic distinctness. The amount of arable land was significantly positively related to both ground beetle richness and rareness.

Table 5: Deviance explained by the final GLM models and representation of the best descriptor variable of each descriptor group. Numbers in brackets indicate the slope of the variable (for abbreviations see Table 1).

Ecosystem	**Taxonomic group**	**Diversity metric**	**Total deviance explained (%)**	**Strongest GC variable**	**Strongest PC variable**	**Strongest LU variable**
Rivers	Fish	Richness	27.4	CAR (+13.9)	NA	FRT5 (+5.4)
		Shannon	17.8	CAR (+9.1)	OXY (-2.4)	PST (+3.6)
		Rareness	19.5	CAR (+8.6)	OXY (-4.3)	FRT5 (+3.2)
		Taxonomic Distinctness	25.2	LAT (+6.1)	NA	CRP (-5)
	Invertebrates	Richness	39.2	ANP (+1.1)	AMO (-19.8)	HII (-10.4)
		Shannon	16.9	LAT (-2.6)	AMO (-8.5)	HII (-2.6)
		Rareness	36.2	ALT (-7.1)	AMO (-13.1)	HII (-4.5)
		Taxonomic Distinctness	45	ALT (-5.5)	AMO (+2.4)	FRT5 (-24)
	Macrophytes	Richness	24.2	ALT (-5.5)	NA	NOx (-12.3)
		Shannon	28.6	ALT (-5.9)	NAT (-1.8)	URB (-8.1)
		Rareness	39.9	AMT (5.7)	TPO (-24.5)	URB (-1.9)
		Taxonomic Distinctness	10.6	ALT (-0.8)	CHL (-1.8)	NA
Ponds	Vegetation	Richness	35.6	LAT (-18.2)	TPO (-1.9)	PST (+3.8)
		Rareness	52.7	ALT (+45.7)	NA	CCP (-4.2)
		Taxonomic Distinctness	23.8	ALT (-11.5)	NA	NOx (-2.1)
	Amphibians	Richness	62.6	ALT (-50.1)	NA	NA

		Rareness	63.6	ALT (-55.3)	CON (-1.9)	FRT (+0.3)
		Taxonomic Distinctness	74.1	ALT (-62.3)	CON (-0.3)	FRT (+1.0)
	Invertebrates	Richness	44.6	ALT (-36.8)	NA	FRT (-3.3)
		Rareness	22.8	LAT (-5.4)	CON (+3.0)	URB (-2.7)
		Taxonomic Distinctness	26.5	LAT (+6.8)	NA	PST (-8.2)
Floodplains	Vegetation	Richness	76,6	AMT (1)	PST (-2,4)	NOx (0,6)
		Shannon	64,8	ALT (1,9)	PST (2,2)	HII (1,6)
		Rareness	35,5	AMT (0,1)	NA	HII (-0,1)
		Taxonomic Distinctness	36,0	AMT (-8)	PST (-18,2)	NA
	Ground beetles	Richness	54,9	NA	CRP (1,1)	NA
		Shannon	23,3	ANP (1,8)	FRT (1)	NOx (-0,3)
		Rareness	53,3	NA	CRP (0,189)	NA
		Taxonomic Distinctness	6,2	ANP (-4,8)	NA	NOx (1,4)

Stressors response patterns across freshwater ecosystems

Among all biodiversity metrics, taxonomic groups and ecosystems, species richness showed the highest explained variation (mean: 44.4%, Table 2). Rareness and taxonomic distinctness performed also well, with 36.3% and 28.3% explained variation, respectively. These global results were well in line with the specific results obtained for individual organism groups. This also applies to the overall weak results obtained for Shannon diversity.

Among the different descriptor variable groups, geo-climatic variables explained most of the variation in the diversity metrics (Table 3), which was even stronger pronounced in the GLM models, with 10% more deviance explained if compared to the variation partitioning scheme. Also buffer (or small-scale) land-use explained much variation, and again the results obtained from GLMs explained about 10% more deviance than the variation partitioning. While physico-chemistry explained relatively high proportions of variation in the diversity metrics in rivers, this descriptor group was less relevant in ponds (not analysed in floodplains).

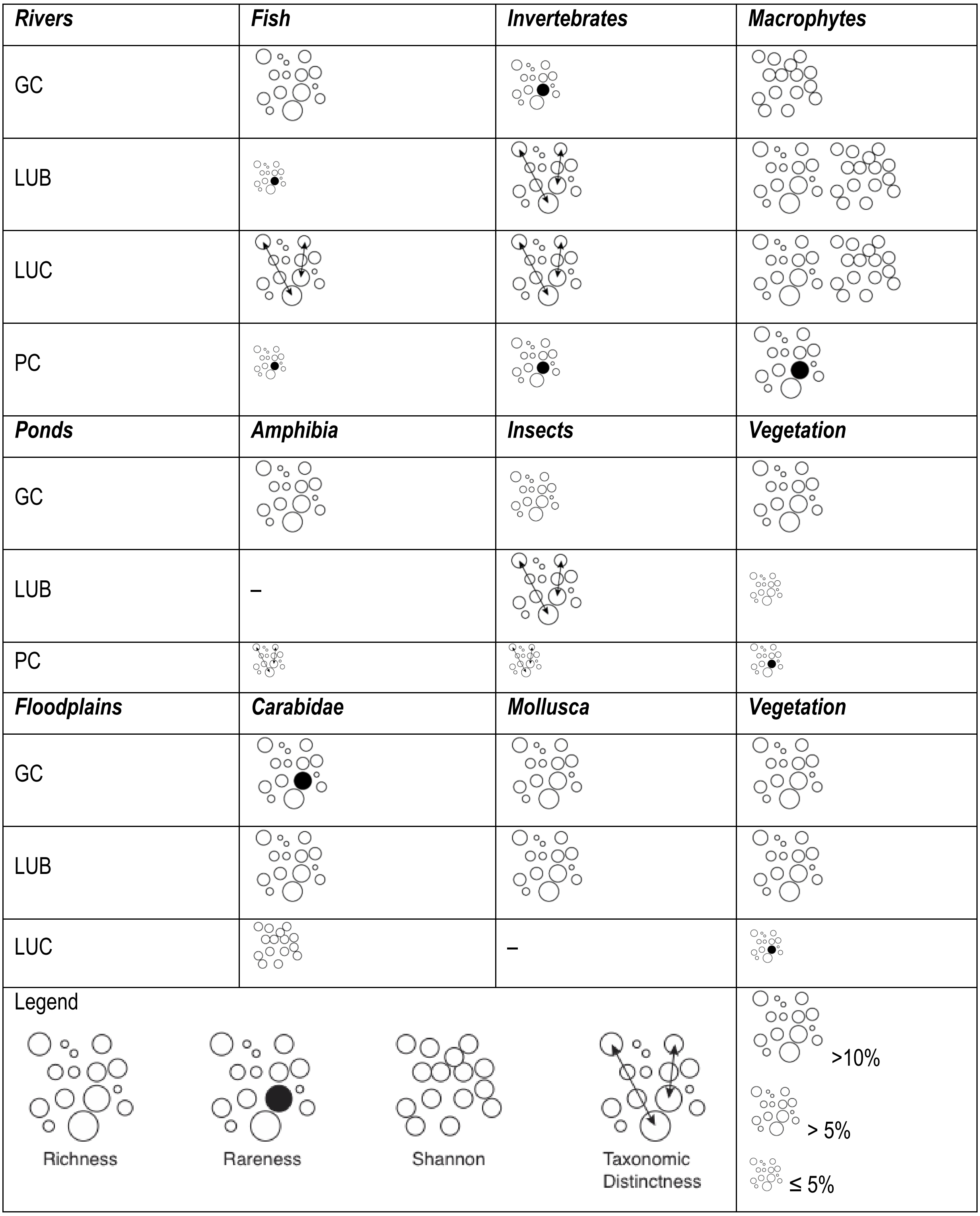


Figure 5: Biodiversity response to natural and anthropogenic descriptor groups in three different ecosystems. Symbols represent the strongest metric relationship, symbol size represent the strength of the relationship. All results derived from the variation partitioning scheme applied in this study.

Similar patterns emerged when comparing the explained variation across all diversity metrics within the taxonomic groups. Geo-climatic variables explained most of the diversity metrics, on average 11.7% (VarPart) and 18.0% (GLM), respectively. Notably, the role of geo-climatic descriptors for pond biodiversity differed strongly between variation partitioning and GLMs. In comparison to these two ecosystems, the highest explained variations were relatively little in rivers. Land-use variables acting on the smaller spatial scale were again better in explaining diversity variations in floodplains. The final matrix of biodiversity response patterns to multiple drivers and stressors of biodiversity is illustrated in Figure 5.

Review study

Our review study resulted in altogether 271 papers (rivers. 112; floodplains: 103; ponds: 56), which fulfilled our search criteria and provided sufficient information extractable from the studies. The studies date back to 1994 and hence cover the biodiversity research within the past two decades (Figure 6). A peak research on stressor-biodiversity relationships is detectable between 2008 and 2012, with a decrease in the number of studies in 2013. Notably, the majority of studies originate from Europe (70%), followed by North and South America (12 and 8%, respectively). Roughly 83% of the studies address local or regional biodiversity patterns, for example at the spatial extent of sites within a small study region or catchment. Thereby, the number of sites was in most cases below 25 (55% of the references), which underpins the rather small-scale spatial extent of the studies.

Four groups of descriptors turn out to be of primary interest for biodiversity research studies: multiple stressors (24% of the references), land use (22%), natural drivers (22%) and eutrophication (15%) (Figure 7). Biotic interactions, represented with 14% of the references, add to the descriptor groups. Multi-stressor studies address between two and five different stressors with various origins: physico-chemical deterioration (pollution), hydrological and morphological impairment, land use and effects of climate change. Most multi-stressor studies (70%) were conducted on floodplain biodiversity.

Among the biodiversity measures (i.e. metrics), species/taxon richness is by far the most frequently used biodiversity measure (Figure 8); almost 90% of the references include species richness. To a lesser degree, Shannon-Wiener diversity, Simpson diversity and Pielous evenness are addressed, all of which represent measures of alpha diversity. Beta diversity (i.e. species or taxa turnover among sites) was addressed by roughly a fifth of the studies, primarily by those addressing the larger (regional) scale. Measures of endemicity (or rareness, respectively) are rarely addressed in the reviewed body of literature.

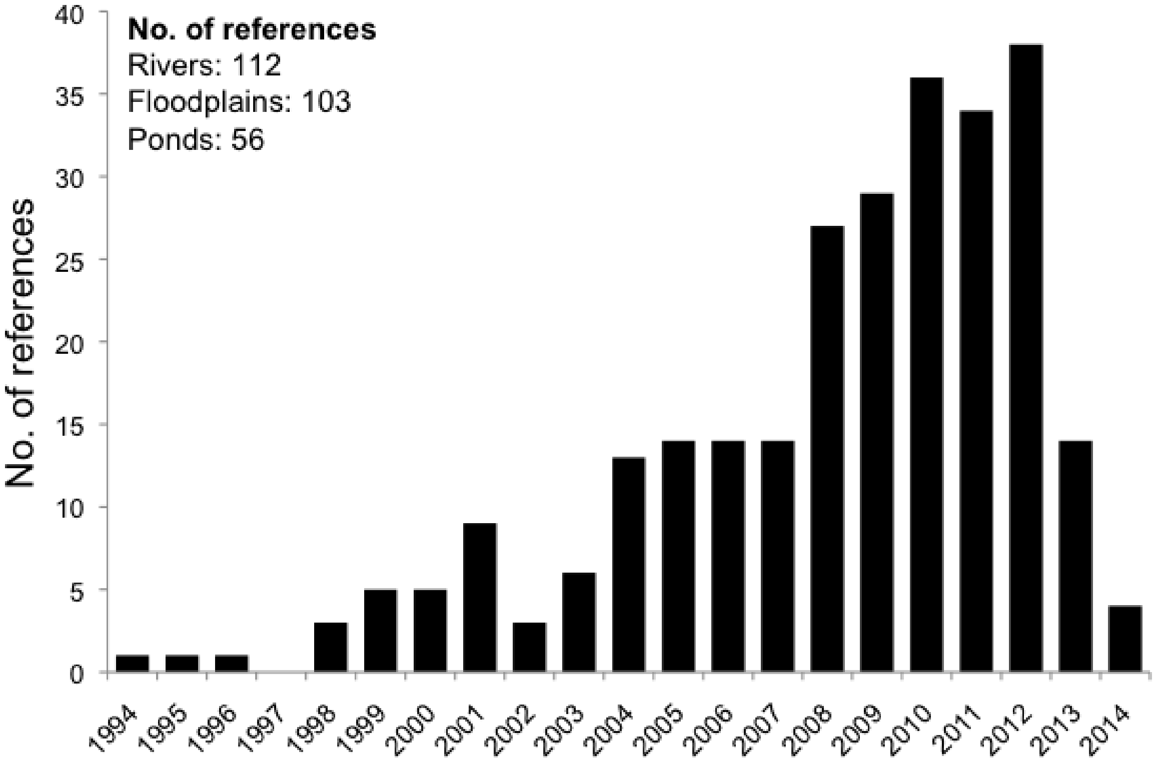


Figure 6: Number of references per publication year found for the period 1994–2014.

Three taxonomic (organism) groups dominate the reviewed biodiversity literature: benthic macroinvertebrates (52% of the references), aquatic vegetation/macrophytes (23%) and fish (13%). In particular, benthic invertebrates (incl. terrestrial and semi-terrestrial insects and molluscs) are frequently used across all ecosystems reviewed, irrespective of the stressor(s) addressed. On the contrary, fish are primarily addressed in river studies. Thereby, most studies address a single taxonomic group, with only 13% of the studies addressing two or more groups.

The reported response of biodiversity to the environmental descriptors is varying. Thirty-nine percent of the studies report both, the increase and decrease of biodiversity measures in course of increasing environmental impact (or stress, respectively).

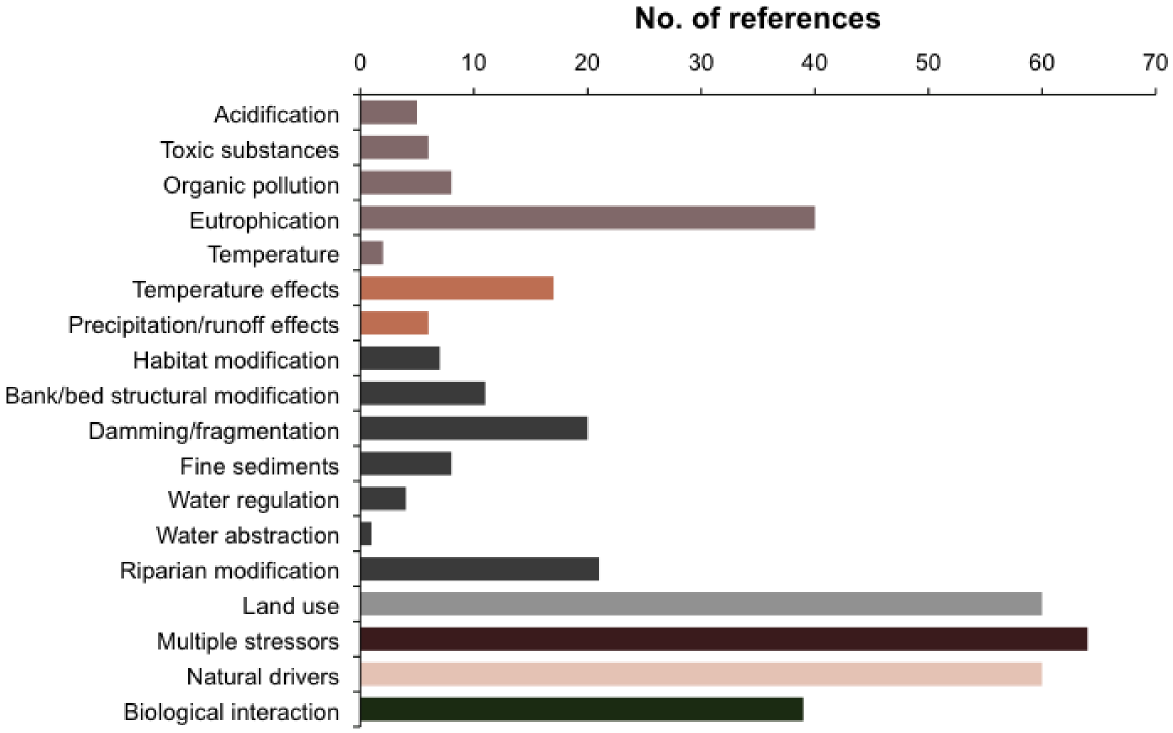


Figure 7: Groups of explanatory variables (stressors, natural drivers of biotic interactions) primarily addressed in the reviewed literature. Colours represent different stressor groups: physico-chemistry, climate change, hydromorphological degradation, land use, multiple stressors, natural drivers and biological interactions (from top to bottom).

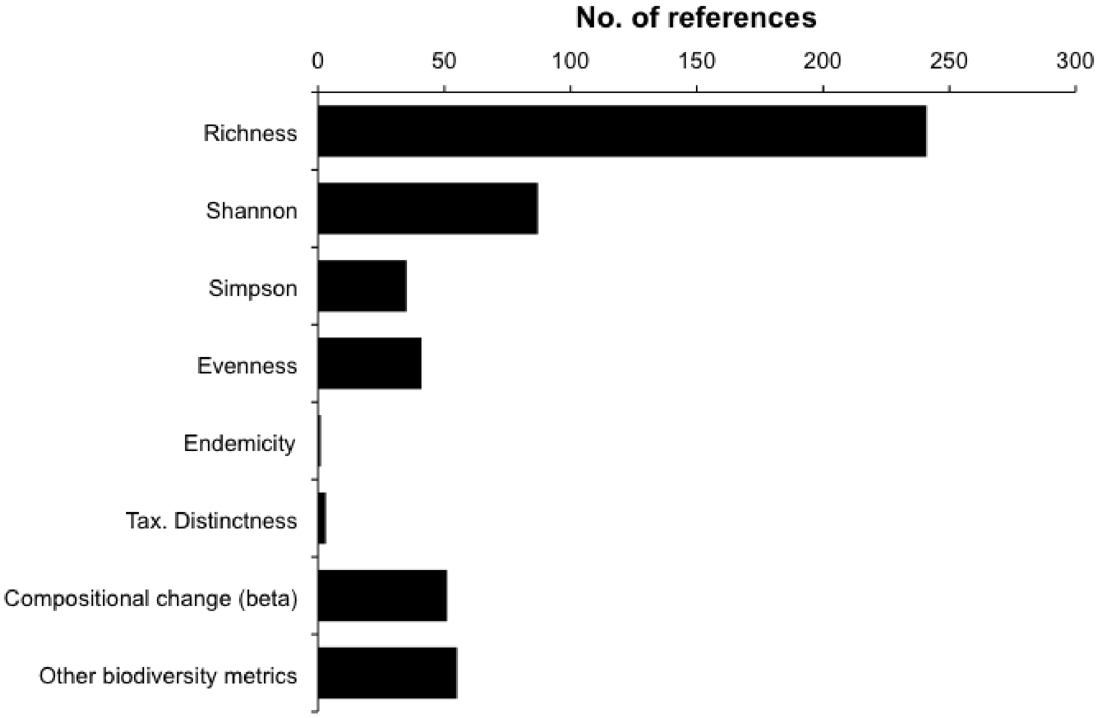


Figure 8: Type of biodiversity metrics addressed in the reviewed literature.

The unambiguous decrease of diversity towards the impact of stressors is reported in 23% of the reviewed studies. Yet, 20 additional studies (7%) also reported significant increases of biodiversity towards stressors (e.g. Gallardo et al., 2009; Januschke et al., 2011). Thirty-four studies addressed the response of benthic invertebrate richness and allowed for a more detailed analysis of response patterns. Among those, 14 studies clearly reported a decrease in richness towards environmental stressors, while almost the same amount of studies reported varying response with both increasing and decreasing richness in the studies. Hence, the lack of clear response patterns in the reviewed body of literature suggests that the often reported bias towards the publication of "positive" findings is not much developed in the context of our review.

Discussion

Rivers

The strongest and most consistent response of lotic biodiversity to natural and anthropogenic environmental descriptors was identifiable for taxon richness and rareness. Taxonomic distinctness performed less consistent, while Shannon-Wiener diversity revealed only a weak response to the descriptors tested in our study. Yet, the variability in the patterns detected for rareness and taxonomic distinctness suggest a notable variation in the response patterns. This is largely supported by the literature review, which revealed both varying lotic biodiversity patterns with regard to the strength of the relationships and the sign of the relationships. Feld et al. (2013) likewise found highly variable response patterns for species richness, but also for functional and phylogenetic diversity, in response to hydromorphological stress. The authors explained their findings with the generally high richness in lotic benthic macroinvertebrates, which allows for a high richness along the entire environmental gradient, including the gradient's end points. Further, such variable responses were reported already by Gerisch et al. (2011) and Gallardo et al. (2011) for floodplain systems. The low variation in the response of richness, combined with a relatively high responsiveness to the environmental descriptors tested here, underpins a general utility of this biodiversity component to detect environmental impact. This also holds true for the other ecosystems addressed in this study (see below). Similarly, species rareness revealed a good combination of high responsiveness and low variation across the three lotic organism groups, so that we may conclude on a utility ranking from richness > rareness > taxonomic distinctness > Shannon-Wiener diversity. The utility of richness in this study is in line with the overwhelming use of taxa richness in related biodiversity studies, as revealed by our review.

Nevertheless, as already pointed out in a previous analysis using similar case study datasets (Feld et al. submitted, see Chapter 1), we cannot address biodiversity patterns in course of human impact isolated from the influence of natural geo-climatic descriptors. Both act in concert so that one descriptor group may mask the effects detected for another. For example, we found fish taxonomic distinctness strongly related to catchment land use, while fish richness showed a strong response to catchment size. The natural longitudinal shift in lotic fish richness from headwaters to large rivers is well reported (e.g. Oberdorff, Guilbert & Lucchetta, 1993) and suggests longitudinal shifts in taxonomic distinctness too, although both biodiversity components in general are not linked to each other (Gallardo et al., 2011; see also Figure S1 in Feld et al., 2013). Hence, such biodiversity response patterns are stream size-dependent and require thorough analysis and interpretation. This in particular applies to taxonomic groups with a limited overall richness (< 250 fish species inhabit Europe's rivers as opposed to > 5,000 benthic macroinvertebrate species), for both richness and taxonomic distinctness of communities are likely to be linked to the general species pool available within a region.

This strong stream size-dependent pattern in biodiversity is probably also valid for aquatic macrophytes (reduced richness in shaded headwater sections), but not for benthic invertebrates, the latter of which occur in diverse communities along the entire continuum. With benthic invertebrates, we found taxonomic distinctness and taxon rareness to show the strongest response, with taxon distinctness responding particularly to buffer land use.

However, as the sign of the relationship was negative for % forest cover in the buffer, we infer that small forested upstream sections inhabited phylogenetically less diverse communities. Obviously, increasing land use does not negatively impact invertebrate phylogenetic diversity in rivers, which is in line with similar findings for hydromorphological impact (Marchant, 2007; Feld et al., 2013). The good mean relationship of taxon rareness, in particular to physico-chemical impact, suggests the utility of this biodiversity component. Indeed, taxon rareness, if translated to the frequency of naturally rare and often 'sensitive' taxa may constitute a suitable indicator component; sensitive indicator taxa are frequently used in European river assessment schemes (e.g. Lorenz et al., 2004). Yet, whether the rareness component addressed in this study sufficiently corresponds with a taxon's sensitivity to anthropogenic stressors requires further investigation. Thereby, it will be important to thoroughly delineate the area considered for the calculation of an individual taxon's rareness.

With regard to individual stressors, we found the human impact index (HII) and several physico-chemical variables (oxygen, ammonia, nitrate) to dominate the biodiversity patterns (based on GLM results). Most relationships were negative, i.e. biodiversity decreased with increasing stressor intensity. Nevertheless, the GLMs largely support the findings based on the variation partitioning schemes with regard to the role of geo-climatic descriptors. Hence, we cannot consider human impact isolated from the influence of, for example, altitude and latitude, or ecologically more relevant, from slope and temperature, respectively. Geo-climatic variables are included in almost all GLM models and, thus constitute important predictors of lotic biodiversity. This holds true irrespective of the organism group and biodiversity metric considered.

Floodplains

In floodplains, species richness was best explained across all taxonomic groups (plants, ground beetles, molluscs), stressor groups (natural, land use, human modification), and model types (VarPart, GLM). This indicates that richness is the diversity metric with both the highest sensitivity but also with the strongest ecological link to the stressors used in this study. Also in wetland ecosystems, species richness has a prominent role as biodiversity surrogate and was often reported to respond strongly to land use changes. For example, Wesche et al. (2012) reported on consistent trends towards much more species-poor communities after fifty years of land-use change in German floodplains, which was attributable mainly to local nutrient input. Similar patterns were found by Hardtle et al. (2006), who noted that plant species richness in floodplains decreases significantly under grazing, with increasing phosphate supply and productivity of stands. Several studies showed that birds are more species rich and abundant in floodplain ecosystem than in adjacent farmland or urban systems (Warkentin & Reed, 1999) and there is a body of literature highlighting that land use in floodplains can strongly control the species richness of invertebrates (Eyre, 2006; Arscott et al., 2005; Dziock et al., 2012). All these studies show that land abandonment and reducing management intensities can promote both the taxonomical and the functional richness and diversity of floodplain communities (Girel & Manneville, 1998). This is mainly because of the dynamic environmental conditions in these coupled systems, offering multiple ecological niches for the species (Robinson et al., 2002).

Next to richness, also rareness was relatively well explained by the stressors. There are only few studies which systematically assessed the role of land-use and species rarity in wetlands, with often inconsistent results. Schaich & Barthelmes (2012) found that rare and conservation-relevant plant species did not significantly differed between the management alternatives. On the contrary, the number of rare habitat specialist carabid species was found to increase at unregulated rivers (Sadler et al., 2004). In our case, most of the variation in rareness was explained by natural variables, indicating the role of altitude and temperature. However, ground beetle rareness increased with the degree of urbanisation, which might be a result of the presence of pioneer sites that exist in these areas (such as open, sun exposed habitats, gravel banks, ruderal habitats etc.), more than in the often agriculturally used vicinity. The low performance of Shannon might be explained by species abundances that are not always based on similar sampling effort and thus add further noise into the index.

We found no general response pattern between taxonomic groups and environmental stress. Indeed, the relationships were very specific for certain organisms and for certain diversity metrics. For example, plant diversity was best explained by natural (geoclimatic) variables, which is in line with many studies highlighting the role of temperature and precipitation for the structuring of plant communities and vegetation patterns (Thuiller et al., 2008; Zavaleta et al., 2003). On the contrary, land use in the 5 km buffer (i.e. on the small spatial scale) was a strong stressor group for ground beetles. This is supported by a variety of studies, highlighting that these organisms strongly depend on the habitat type and management intensity, but also on small-scale environmental variability provided by natural floodplain habitats (Gerisch et al., 2006; Antvogel & Bonn, 2001; Bonn et al., 2002).

For plants, it becomes also clear that the amount of pastures is not always increasing diversity, as we found negative impacts on taxonomic distinctness (i.e., more homogeneous species with increasing amount of pastures) and lower species richness. This is interesting, because many studies highlight the value of grasslands for biodiversity (Hoekstra et al., 2005; Watkinson & Ormerod, 2001). We strongly support this and explain our results with the changing species pool in grasslands compared to urban or more natural areas. In grasslands, there will be mainly herbaceous plants, which are phylogenetically more similar to each other compared to plants in forests or in urban areas, where also shrubs, trees, and other plants than grasses appear.

Ponds

The results obtained for the pond case study underpin the paramount influence of altitude, with a generally negative relationship between altitude and the diversity of pond organisms addressed in this study. Although covering only a small spatial extent, our pond data represent the full altitudinal gradient existing in Europe (altitude range: 2–2,752 m a.s.l.). The ponds are thus located in very diverse climatic settings characterised by distinct atmospheric conditions regarding, for instance, radiation, air temperature and precipitation. This strong altitudinal influence on pond biodiversity allowed Rosset et al. (2010) to model the warming effects expected from climate change. The authors concluded on a likely increase of species richness at higher altitudes with rising air temperature in the next decades, backing up our findings on low species richness at high altitudes under current conditions. Also Oertli et al. (2005) demonstrate the prominent role of altitude on species richness across various biological groups (aquatic plants, benthic invertebrates and amphibians). They also found varying physico-chemical parameters related to the biodiversity of these groups, which is in line with our findings. Overall, the dominance of natural gradients in the explanation of pond diversity may explain the relatively little extra gain in explanatory power using land use variables.

The general negative trend of biodiversity at higher altitudes, however, corresponds with the positive relationship of vegetation rareness to pond altitude. The alpine, mostly oligotrophic ponds feature distinct plant communities composed of oligotaphrent alpine specialist taxa such as *Luzula alpinopilosa* (Chaix) Breistr. or *Eriophorum scheuchzeri* Hoppe. This pattern was found only for pond vegetation; amphibian and invertebrate rareness decreased at higher altitudes (with invertebrate rareness mainly responding to the interaction of altitude and conductivity).

Overall, the weak explanatory power of both anthropogenic stressors in comparison with the geo-climatic gradient in our case study suggests a predominant role of natural environmental drivers in niche formation. To detect significant responses of mayfly diversity to nutrient pollution, for instance, Menetrey et al. (2008) had to restrict the full dataset on Swiss ponds to locations in the colline and montane vegetation zone (200–1,400 m a.s.l.). Oertli et al. (2008) even reported on a reverse stressor–biodiversity relationship at the upper end of the altitudinal gradient: the increase of total nitrogen (to a maximum of 0.5 mg l^{-1}) enhances invertebrate species richness in high alpine, oligotrophic ponds. Other studies covering moderate geo-climatic gradients well demonstrate distinct negative effects of increasing nutrient loads on macrophyte richness (Akasaka et al., 2010), benthic invertebrates in general (Fuentes-Rodriguez et al., 2012) and dragonflies in particular (Carchini et al., 2005).

Synthesis

Our study demonstrates that the response of freshwater biodiversity to human land use and physico-chemical deterioration is not consistent, but largely dependent on the organism group and biodiversity metric considered. Further, natural environmental drivers of biodiversity, if expressed as altitude, latitude or temperature, to a large degree can shape the diversity patterns observed. Therefore, the joint analysis of environmental stressors and natural drivers (such as the geo-climatic variables addressed in this study) is of paramount importance for the detection and monitoring of biodiversity effects in course of human impact on freshwater ecosystems.

In rivers, we found benthic invertebrate richness, rareness and taxonomic distinctness to be strongly related to catchment land use and P and N enhancement. Insect taxonomic distinctness was also responding best to land use within a 1 km buffer around ponds, while pond Amphibia and vegetation was largely driven by altitude and thus did not reveal strong relations to both land use and nutrient enhancement. Eventually, the richness of carabid beetles, molluscs and vegetation was strongly linked to land use within a 5 km buffer around floodplains. Hence, our results suggest a reasonable utility of richness, and in part also of taxonomic distinctness, to detect human impact on freshwater biodiversity. Yet, the close relation of both metrics to natural descriptors requires a careful interpretation of the biodiversity patterns.

Further, we may infer from this that various stressors affect different components of diversity, and that each component adds additional, complementary information to the overall picture of biodiversity-stressor effects. It becomes evident from this work that focusing on the effect of multiple stressors on more than one organism group and in different ecosystems has the potential to broaden our view of how biodiversity is affected by different environmental drivers. On the other hand, the outcome of such cross-ecosystem-cross-taxa studies is far from a standard analytical exercise and requires further effort to highlight the stressor-biodiversity relationships. Therefore, the availability of stressor data, including those variables directly affecting biodiversity at the level of communities, populations, or even single specimens, is a fundamental prerequisite. These data largely lack at the broad scale, which is why many studies, including this study, utilise broad-scale indirect proxies (e.g. land use) of environmental stressors rather than direct stressors such as oxygen depletion, flow velocity, habitat availability or water temperature.

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References

Allan J.D. (2004). Landscapes and Riverscapes: The Influence of Land Use on Stream Ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, **35**, 257–284.

Antvogel H. & Bonn A. (2001) Environmental parameters and microspatial distribution of insects: a case study of carabids in an alluvial forest. *Ecography*, **24**, 470–482.

Akasaka M., Takamura N., Mitsuhashi H. & Kadono, Y. (2010) Effects of land use on aquatic macrophyte diversity and water quality of ponds. *Freshwater Biology*, **55**, 909–922.

Arscott D., Tockner K. & Ward J. (2005). Lateral organization of aquatic invertebrates along the corridor of a braided floodplain river. *Journal of the North American Benthological Society*, **24**, 934–954.

Bonn A., Hagen K. & Wohlgemuth-von Reiche D. (2002) The significance of flood regimes for carabid beetle and spider communities in riparian habitats—A comparison of three major rivers in Germany. *River Research and Applications*, **18**, 43–64.

Borcard D. and Legendre P. (1992). Partialling out the spatial component of ecological variation. *Ecology*, **73**, 1045–1055.

Borcard D., Gillet F. & Legendre P. (2011) *Numerical Ecology with R* (eds R. Gentleman, K. Hornik & G.G. Prmigiani). Springer, New York, Dordrecht, London, Heidelberg, 306 pp.

Breitburg D.L., Sanders J.G., Gilmour C.C., Hatfield C.A., Osman R.W., Riedel G.F., Seitzinger S.B. & Sellner, K.G. (1999) Variability in responses to nutrients and trace elements, and transmission of stressor effects through an estuarine food web. Limnology and Oceanography, **44**, 837–863.

Carchini G., Solimini A.G. & Ruggiero A. (2005) Habitat characteristics and odonate diversity in mountain ponds of central Italy. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **15**, 573–581.

Clarke K. & Warwick R. (1998) a taxonomic distinctness index and its statistical properties. *Journal of Applied Ecology*, **35**, 523–531.

Clarke K. & Warwick R. (1999) The taxonomic distinctness measure of biodiversity: weighting of step lengths between hierarchical levels. *Marine Ecology Progress Series*, **184**, 21–29.

Crain C.M., Kroeker K. & Halpern B.S. (2008) Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters*, **11**, 1304–1315.

Crisp D.T., Laffan S., Linder H.P. & Monro A. (2001) Endemism in the Australian flora. *Journal of Biogeography*, **28**, 183–198.

Dahm V., Hering D., Nemitz D., Graf W., Schmidt-Kloiber A., Leitner P., Melcher A., Feld C.K. (2013) Effects of physico-chemistry, land use and hydromorphology on three riverine organism groups: a comparative analysis with monitoring data from Germany and Austria. *Hydrobiologia*, **704**, 389–415.

Dziock F., Gerisch M., Siegert M., Hering I., Scholz M. & Ernst R. (2011) Reproducing or dispersing? Using trait based habitat templet models to analyse Orthoptera response to flooding and land use. *Agriculture, Ecosystems and the Environment*, **145**, 85–94.

Elith J., Leathwick, J.R. & Hastie, T. (2008). A working guide to boosted regression trees. *The Journal of Animal Ecology*, **77**, 802–813.

Ellenberg H., Weber H.E., Düll R., Wirth V., Werner W. & Paulißen D. (1992). *Indicator values of plants in Central Europe* (Vol. 18, p. 258). Erich Goltze Verlag, Göttingen.

Eyre M.D. (2006) A Strategic Interpretation of Beetle (Coleoptera) Assemblages, Biotopes, Habitats and Distribution, and the Conservation Implications. *Journal of Insect Conservation*, **10**, 151–160.

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., de Bello F. & Dolédec S. (2013) Biodiversity of traits and species both show weak responses to hydromorphological alteration in lowland river macroinvertebrates. *Freshwater Biology*, **59**, 233–248.

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. & Friberg N. (2011) Chapter 3 - From Natural to Degraded Rivers and Back Again: a Test of Restoration Ecology Theory and Practice. *Advances in Ecological Research*, **44**, 119–209.

Folt C.L., Chen C.Y., Moore M.V. & Burnaford J. (1999) Synergism and antagonism among multiple stressors. *Limnology and Oceanography*, **44**, 864–877.

Fuentes-Rodríguez F., Juan M., Gallego I., Lusi M., Fenoy E., León D., Peãlver P., Toja J. & Casas J.J. (2012) Diversity in Mediterranean farm ponds: trade-offs and synergies between irrigation modernisation and biodiversity conservation. *Freshwater Biology*, **58**, 63–78.

Gallardo B., Gascón S., Quintana X., Comín F.A. (2011) How to choose a biodiversity indicator - Redundancy and complementarity of biodiversity metrics in a freshwater ecosystem. *Ecological Indicators*, **11**, 1177–1184.

Gerisch M., Schanowski A., Figura W., Gerken B., Dziock F. & Henle, K. (2006) Carabid beetles (Coleoptera, carabidae) as indicators of hydrological site conditions in floodplain grasslands. *International Review of Hydrobiology*, **91**, 326–340.

Gerisch M., Dziock F., Schanowski A., Ilg C. & Henle K. (2012): Community resilience following extreme disturbances: the response of ground beetles to a severe summer flood in a Central European lowland stream. *River Research and Application*, **28**, 81–92.

Gerisch M., Agostinelli V., Henle K. & Dziock F. (2011) More species, but all do the same: contrasting effects of flood disturbance on ground beetle functional and species diversity. *Oikos*, **121**, 508–515.

Girel J. & Manneville O. (1998) Present species richness of plant communities in alpine stream corridors in relation to historical river management. *Biological Conservation*, **85**, 21–33.

Halpern B.S., Selkoe K.A., Micheli F. & Kappel C.V. (2007) Evaluating and Ranking the Vulnerability of Global Marine Ecosystems to Anthropogenic Threats. *Conservation Biology*, **21**, 1301–1315.

Härdtle W., Redecker B., Aßmann T. & Meyer H. (2006) Vegetation responses to environmental conditions in floodplain grasslands: prerequisites for preserving plant species diversity. *Basic and Applied Ecology*, **7**, 280–288.

Hijmans R.J., Cameron S.E., Parra J.L., Jones P.G. & Jarvis A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Hijmans R.J., Phillips S., Leathwick J. & Elith J. (2013) dismo: Species Distribution Modeling. R Package Version 0.8-11. Available at: http://CRAN.R-project.org/package=dismo.

Hoekstra J.M., Boucher T.M., Ricketts T.H. & Roberts C. (2005) Confronting a biome crisis: global disparities of habitat loss and protection. *Ecology Letters*, **8**, 23–29.

Ilg C., Dziock F., Foeckler F., Follner K., Gerisch M., Gläser J., Rink A., Schanowski, A., Scholz, M., Deichner, O. & Henle, K. (2008) Long-term reactions of plants and macroinvertebrates to extreme floods in floodplain grasslands. *Ecology*, **89**, 2392–2398.

Januschke K., Brunzel S., Haase P. & Hering D. (2011) Effects of stream restorations on riparian mesohabitats, vegetation and carabid beetles. *Biodiversity and Conservation*, **20**, 3147–3164.

Linder H.P. (2001) Plant diversity and endemism in sub-Saharan tropical Africa. *Journal of Biogeography*, **28**, 169–182.

Lorenz A., Hering D., Feld C.K. & 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.

Marchant R. (2007) The use of taxonomic distinctness to assess environmental disturbance of insect communities from running water. *Freshwater Biology*, **52**, 1634–1645.

Marzin A., Verdonschot P.F.M. & Pont D. (2012) The relative influence of catchment, riparian corridor, and reach-scale anthropogenic pressures on fish and macroinvertebrate assemblages in French rivers. *Hydrobiologia*, **704**, 375–388.

MEA (Millennium Ecosystem Assessment) (2005). *Ecosystems and Human Well-being: Synthesis*. Island Press, Washington, DC.

Menetrey N., Oertli B., Sartori M., Wagner A. & Lachavanne J. B. (2008) Eutrophication: are mayflies (Ephemeroptera) good bioindicators for ponds? *Hydrobiologia*, **597**, 125–135.

Moe S.J., Schmidt-Kloiber A., Dudley B.J. & Hering D. (2013). The WISER way of organising ecological data from European rivers, lakes, transitional and coastal waters. *Hydrobiologia*, **704**, 11–28.

Oberdorff T., Guilbert E. & Lucchetta J.-C. (1993) Patterns of fish species richness in the Seine River basin, France. *Hydrobiologia*, **259**, 157–167.

Oertli B., Auderset Joye D., Castella E., Juge R. & Lachavanne J.-B. (2000) Diversité biologique et typologie écologique des étangs et petits lacs de Suisse. Laboratoire d'Ecologie et de Biologie aquatique, Université de Genève, Genève.

Oertli B., Auderset Joye D., Castella E., Juge R., Lehmann A. & Lachavanne J.-B. (2005) PLOCH: a standardized method for sampling and assessing the biodiversity in ponds. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **15**, 665–679.

Oertli B., Indermuehle N., Angélibert S., Hinden H. & Stoll A. (2008) Macroinvertebrate assemblages in 25 high alpine ponds of the Swiss National Park (Cirque of Macun) and relation to environmental variables. *Hydrobiologia*, **597**, 29–41.

Oksanen J., Blanchet F.G., Kindt R., Legendre P., Minchin P.R., O'Hara R.B., Simpson G.L., Solymos P., Stevens M.H.H. & Wagner H. (2013) vegan: Community Ecology Package. R package version 2.0-7. http://CRAN.R-project.org/package=vegan.

Ormerod S.J., Dobson M., Hildrew A.G. & Townsend C.R. (2010) Multiple stressors in freshwater ecosystems. *Freshwater Biology*, **55**, 1–4.

Pavlin M., Birk S., Hering D. & Urbanič G. (2011) The role of land use, nutrients, and other stressors in shaping benthic invertebrate assemblages in Slovenian rivers. *Hydrobiologia*, **678**, 137–153.

Peres-Neto P.R., Legendre P., Dray S. & Borcard D. (2006) Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology*, **87**, 2614–2625.

R Development Core Team (2013) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.R-project.org. (Version: 2.15.3).

Ridgeway G. (2013) gbm: Generalized Boosted Regression Models R Package Version 2.0-8. Available at: http://CRAN.Rproject. org/package=gbm.

Robinson, C.T., TOCKNER K. & WARD J.V. (2002) The fauna of dynamic riverine landscapes. *Freshwater Biology*, **47**, 661–677.

Rosset V., Lehmann A. & Oertli B. (2010) Warmer and richer? Predicting the impact of climate warming on species richness in small temperate waterbodies. *Global Change Biology*, **16**, 2376–2387.

Sadler J.P., Bell D. & Fowles A.P. (2004) The hydroecological controls and conservation value of beetles on exposed riverine sediments in England and Wales. *Biological Conservation*, **118**, 41–56.

Sanderson E.W., Jaiteh M., Levy M.A., Redford K.H., Wannebo A.V. & Woolmer G. (2002) The Human Footprint and the Last of the Wild. *BioScience*, **52**, 891–904.

Schaich H. & Barthelmes B. (2012) Management of grasslands in rewetted floodplains: effects of grazing and cutting on vegetation development. *Tuxenia*, **32**, 207–231.

Stiers I., Crohain N., Josens G. & Triest L. (2011) Impact of three aquatic invasive species on native plants and macroinvertebrates in temperate ponds. *Biological Invasions*, **13**, 2715–2726.

Theloke J., Thiruchittampalam B., Orlikova S., Uzbasich M. & Gauger T. (2011) Methodology development for the spatial distribution of the diffuse emissions in Europe, Report for the European Commission, 070307/2009/548773/SER/C4 http://circa.europa.eu/Public/irc/env/e_prtr/library?l=/diffuse_releases_e-prtr/methodology_2011/_EN_1.0_&a=d.

Thuiller W., Araújo M. B. & Lavorel S. (2004) Do we need land-cover data to model species distributions in Europe? *Journal of Biogeography*, **31**, 353–361.

Tockner K., Pusch M., Borchardt D. & Lorang M.S. (2010). Multiple stressors in coupled river-floodplain ecosystems. *Freshwater Biology*, **55**, 135–151.

Townsend C.R., Uhlmann, S.S. & Matthaei C.D. (2008) Individual and combined responses of stream ecosystems to multiple stressors. *Journal of Applied Ecology*, **45**, 1810–1819.

Venables W.N. & Ripley B.D. (2002) Modern Applied Statistics with S (MASS). 4th Ed. Springer, New York. Available: http://cran.r-project.org/web/packages/MASS/index.html. (Accessed on 1 April 2014).

Vinebrooke R.D., Schindler D.W., Findlay D.L., Turner M.A., Paterson, M. & Mills K.H. (2004) Trophic Dependence of Ecosystem Resistance and Species Compensation in Experimentally Acidified Lake 302S (Canada). *Ecosystems*, **6**, 101–113.

Wagenhoff A., Townsend C.R., Phillips N. & Matthaei C.D. (2011) Subsidy-stress and multiple-stressor effects along gradients of deposited fine sediment and dissolved nutrients in a regional set of streams and rivers. *Freshwater Biology*, **56**, 1916–1936.

Warkentin I.G. & Reed J.M. (1999) Effects of habitat degradation and habitat type on the diversity and abundance of montane riparian birds in the desert Great Basin. *The Great Basin Naturalist*, **59**, 205–212.

Watkinson A.R. & Ormerod S. (2001) Grasslands, grazing and biodiversity: editors' introduction. *Journal of Applied Ecology*, **38**: 233–237.

Wesche K., Krause B., Culmsee H. & Leuschner C. (2012) Fifty years of change in Central European grassland vegetation: large losses in species richness and animal-pollinated plants. *Biological Conservation*, **150**, 76–85.

Zavaleta E.S., Shaw M.R., Chiariello N.R., Thomas B.D., Cleland E.E., Field C.B. & Mooney H.A. (2003) Grassland responses to three years of elevated temperature, CO_2, precipitation, and N deposition. *Ecological Monographs*, **73**, 585–604.

Zomer R.J, Trabucco A,, Bossio D.A., van Straaten, O. & Verchot L.V. (2008) Climate Change Mitigation: A Spatial Analysis of Global Land Suitability for Clean Development Mechanism Afforestation and Reforestation. *Agriculture, Ecosystems and Environment*, **126**, 67–80.

Zuur A.F., Ieno E.N. & Smith G.M. (2007) *Analysing ecological data*. Springer, New York, 672 pp.

Supplementary material

Table S1: Review criteria derived from the peer-reviewed literature on the effects of multiple stressors on freshwater biodiversity. The time-scale for the review was set to 1990 until present, but older references (e.g. major studies, review papers) were considered on a casewise basis, if useful.

Parameter	Explanation
Bibliographic details	
No	consecutive identifier
First Author	only the first author of the study should be indicated here
Year	year of publication
Full reference	full citation, style: JApplEcol
PDF	PDF available? Yes/No
Geographical information	
Country	add country/countries considered
Region/ecoregion	e.g. ecoregion, part of a continent, larger landscape unit
Altitude	indicate altitude or range of altitudes of the study sites
Spatial extent/scale	local, national, regional, continental, global
Spatial resolution/grain	site, lake section/sub-unit of ecosystem type unit, lake/one ecosystem type unit, several ecosystem type units, grid cell
No. of sites/samples	sample coverage of the study
Temporal scale	day, week(s), year, long-term
Temporal resolution of sampling	single day, several single days, monthly, seasonal, long-term
Physico-chemical stressors	indicate X, if applicable
Acidification	
Toxic Substances	
Organic pollution	
Eutrophication	
Temperature	or any modification, i.e. artificial warming and cooling
Climate Change	including modelling studies
Temperature effects	temperature effects due to Climate Change
Precipitation/runoff effects	changes in precipitation/runoff due to Climate Change
Hydromorphological stressors	indicate X, if applicable
Habitat modification	any specific micro- or mesohabitat modification
Bank/bed structural modification	general modifications of bedform and banks
Damming/fragmentation	any transverse structure forming, e.g. a barrier, disruption of longitudinal connectivity
Fine sediments	
Water regulation	artificial impacts on water tables or flow

Parameter	Explanation
Water abstraction	e.g. due to irrigation or hydropower use
Riparian modification	e.g., bank vegetation removal, indicate X, if applicable, disruption of lateral connectivity
Land use	indicate the land use category, if applicable
Biological interaction	e.g. fish stocking, aquaculture, invasive species, indicate X, if applicable, predators (e.g. cormorant, otter)
Multiple stressors	if stressors are not distinguishable, indicate X, if applicable
Natural drivers	are natural drivers considered in the analyses of the study (yes/no)
Biodiversity metrics	indicate X, if applicable
Richness	
Shannon	
Simpson	
Evenness	
Endemicity	
Tax. Distinctness	
Compositional change (beta)	
Other biodiversity metrics	
Organism group(s)	
Metric reaction	positive-increase/negative-decrerase/unimodal/varying/no reaction/not specified
Statistical relationship	indicate values, if available, otherwise indicate X if some information is provided addressing the direction or strength of a relationship
R-square	
N = Number of samples	
Variance/deviance explained	
AIC	
Sign (positive/negative)	
Regression slope	
Mean	Mean of biodiversity metric(s) addressed
Standard deviation or variance	SD or variance of biodiversity metric(s) addressed
Significance	
Suitability	low/medium/high suitability of the study, judged on, e.g., number of sites/samples considered, spatial extent of the study, the statistics applied, the results obtained...
Comments	important additional information useful in further processing