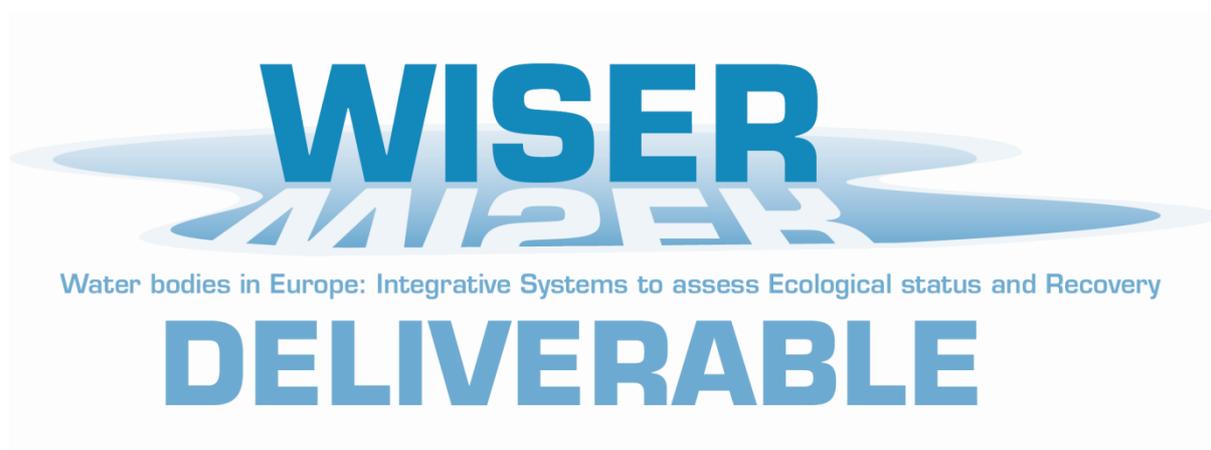Collaborative Project (large-scale integrating project)
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Content

Non-technical summary

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In streams, the structure of fish assemblages showed the strongest response to elevated nutrient concentrations, followed by invertebrates, macrophytes and benthic diatoms. Invertebrate assemblage structure was slightly better correlated with the land use gradient than assemblage structure of macrophytes and fish; benthic diatoms were unrelated to land-use gradient.

For lakes, macrophyte assemblage structure was the best predictor of changes in nutrient concentrations, followed by phytoplankton and fish assemblages. Macrophyte assemblage structure was also better correlated with the landuse gradient compared to phytoplankton and fish assemblages. Fish assemblages in streams and macrophyte assemblages in lakes were correlated with the other taxonomic groups.

Our findings suggest that macrophytes in lakes and fish in streams may be used as surrogates for indicating overall change in diversity to overarching stress types. Our results show that response trajectories differ between taxonomic groups and ecosystem type. These contrasting response signatures show how different taxonomic groups can be used to monitor large-scale, long-term changes to major stress gradients that were apparent, despite using disparate stream and lake types in the analyses.

Cross-taxon responses to stress gradients in streams and lakes [§]

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Abstract

Few studies have compared the response of bioindicators (i.e. different taxonomic groups) to different types of environmental stress across aquatic ecosystems. We regressed assemblage structure of fish, invertebrates, macrophytes, phytoplankton and benthic diatoms to multivariate gradients in nutrient enrichment and land use using data from 67 streams and 59 lakes covering a wide variety of stream and lake types. In streams, the structure of fish assemblages, measured by nonmetric multidimensional scaling, showed the strongest response to elevated nutrient concentrations ($R^2 = 0.47$), followed by invertebrates (0.41), macrophytes (0.23) and benthic diatoms (0.11). Invertebrate assemblage structure was slightly better correlated with the land use gradient (0.2) than assemblage structure of macrophytes (0.17) and fish (0.17); benthic diatoms were unrelated to land-use gradient. For lakes, macrophyte assemblage structure was the best predictor of changes in nutrient concentrations ($R^2 = 0.46$), followed by phytoplankton (0.33) and fish assemblages (0.20). Macrophyte assemblage structure was also better correlated with the landuse gradient (0.56) compared to phytoplankton (0.41) and fish assemblages (0.35). Fish assemblages in streams and macrophyte assemblages in lakes were correlated with the other taxonomic groups. This suggests that these taxonomic groups may be used as surrogates for indicating overall change in diversity to overarching stress types. Our findings show that response trajectories differ between taxonomic groups and ecosystem type. These contrasting response signatures show how different taxonomic groups can be used to monitor large-scale, long-term changes to major stress gradients that were apparent despite using disparate stream and lake types in the analyses.

Key words: biomonitoring, impairment, multiple taxonomic groups, regression

Introduction

Anthropogenic activity increasingly alters the factors that affect biodiversity at local, regional and global scales, ultimately influencing the structure and function of aquatic ecosystems. The main drivers affecting freshwater ecosystems include changes in climate and land use, removal of riparian vegetation, alterations in connectivity patterns, species invasions and contamination. As a result, streams and lakes are among the ecosystems where the footprints of human activity are most evident (Giller & Malmqvist, 1998; Allan, 2004; Strayer & Dudgeon, 2010).

Human-induced alteration of habitat structure and natural disturbance regimes often increase community similarity between habitats, and lead to homogenisation processes (e.g. Johnson et al., 1993; Palmer et al., 1997), which potentially jeopardises the provision of ecosystem goods and services (Hooper et al., 2005). Thus, different approaches have been developed to assess the ecological effects of human stressors on ecosystems (e.g., Rosenberg & Resh, 1993; Dale & Beyeler, 2001). However, surprisingly few studies have compared the discriminatory power of different approaches to detect change (e.g., Fore et al., 1996; Furse et al., 2006; Herbst & Silldorf, 2006), and fewer still have compared the precision and sensitivity of different taxonomic groups commonly used in bioassessment (e.g., Hirst et al., 2002; Johnson et al., 2006; Lewis et al., 2007) and between different ecosystem types (Johnson & Hering, 2009).

Freshwater habitats provide excellent model systems for analyzing the response of biotic assemblages to anthropogenic stress for several reasons. First, use of indicator assemblages and variables are commonly used in biomonitoring of streams (e.g., Resh, 2008) and lakes (Beck & Hutch, 2009). Secondly, there are a number of studies of the response of individual taxonomic groups, covering broad levels of taxonomy and spatial scales, to human-generated stress (e.g., Johnson et al., 2007). Finally, environmental gradients are complex and

multidimensional but measurable (e.g., Vaughan & Ormerod, 2005). However, we currently lack comparative studies of multiple taxonomic groups using standardized data that assess the response trajectories and uncertainties associated with the use of different taxonomic groups to detect anthropogenic change in different aquatic ecosystem types (i.e., streams vs. lakes).

Selection of taxonomic groups to infer the ecological status of an ecosystem is challenging, and multiple indicators may be needed to distinguishing the effects of multiple, anthropogenic stressors (e.g., Dale & Beyeler, 2001; Heino et al., 2005). Responses in one group are often considered to indicate the biological condition of other taxonomic groups, but community responses to environmental change, particularly at broader spatial scales can be context specific (Angeler, 2007), requiring multiple taxonomic groups to strengthen inference and ultimately reduce assessment error (e.g., Stevenson et al*.,* 2004). Multiple indicators provide complementary information about stress responses and help to distinguish the effects of multiple forms of stress. This latter conjecture implies that different taxonomic groups may respond similarly to some stressors (high redundancy, strengthening inference of change) but differently to other stressors (low redundancy, indicators can be used to elucidate the effects of different stressors). To design and implement cost-effective management programmes and to strengthen the use of a multitaxon approach in monitoring and assessment, more knowledge is needed regarding the response trajectories and uncertainty associated with the use of different taxonomic groups to detect ecological change in different aquatic habitats. Ideally, the selection of a response indicator(s) should be a knowledge-based decision using stress–response information to select the 'best' indicator; that is, the indicator with the highest precision (e.g., Johnson, 1998; Pocock & Jennings, 2008).

The precision of indicators based on different taxonomic groups is particularly important when ecological status of water bodies is assessed according to the Water Framework Directive (WFD; European Commission 2000). The so-called "one-out-all-out"

(OOAO) rule states that when ecological status class assessment for individual BQEs (biological quality elements, or major taxonomic groups) are integrated into one joint assessment, the lowest class among all of the BQEs should apply for the whole water body. The reasoning behind this principle is to protect the most vulnerable biological group in the ecosystem. However, this rule has an inherent weakness: the larger the uncertainty (or lower precision) for individual BQEs, the larger is the risk that the integrated assessment will result in a lower status class than the "true" class (see e.g. Hering et al., 2010). Therefore an amendment to the OOAO rule is allowed by the WFD: if there is particularly high uncertainty associated with one BQE, then this BQE can be excluded from the classification before the OOAO rule is applied. Better knowledge on the precision of different indicators is therefore highly relevant for how ecological assessment of water bodies is carried out in practice.

The decision on indicator selection is also depending on the aim, as well as the spatial and temporal scales of the monitoring programme. For European freshwater ecosystems, there are many assessment methods that have been tailored for specific regions and for which indicator responses to stress gradients are well documented (overview in Birk et al., 2011). There are, however, only few methods that can be applied in large geographic areas and across a variety of stream and lake types.

Stream and lake systems are particularly well suited for this type of study as several taxonomic groups, such as fish, invertebrates, macrophytes and algae, are routinely used in bioassessment. Here we evaluate the precision and sensitivity of multiple taxonomic groups, using proxies of multivariate community structure, to detect putative human-induced change in streams and lakes. Environmental gradients are often related to nutrient enrichment from agricultural land use. It can therefore be hypothesized that primary producers (benthic diatoms, phytoplankton and macrophytes), due to their first principle relation with nutrients, would respond strongly to low to moderate changes in nutrients at low levels. This conjecture

is based on the assumption that at high concentrations, nutrients are no longer limiting growth and production. Both primary (many of the invertebrate taxa) and secondary (many of the fish taxa) consumers were expected to respond to nutrient enrichment, albeit less strongly than the primary producers (i.e. response of benthic diatom and phytoplankton ≈ macrophyte > invertebrate > fish). Because streams are physically more disturbed, their biota are more strongly exposed to hydrological disturbance compared to lakes. We therefore expect that taxon responses in streams to nutrient enrichment are weaker compared to lakes.

Specifically, we test the following three main hypotheses. (i) The main taxonomic groups differ in their response to environmental stressors; (ii) Response signatures differ between lakes and streams (iii); Response signatures can be used to select complementary indicators. In addition, we also assessed the spatial coherence (i.e., the strength of correlation of change between communities over the studied spatial scales) of assemblage response to stress to determine if the taxonomic groups studied here could be used as surrogates for the overall biodiversity of streams and lakes.

We used a spatially diverse dataset of Central European streams covering a wide range of environmental conditions and a Central to Northern European dataset of lakes ranging from Ireland to Finland, restricted to waterbodies where different taxonomic groups have been sampled. To test our hypotheses, we regressed structural proxies of biological communities against complex environmental gradients, with particular focus on response variables that are applicable across a variety of natural environmental conditions.

Material and Methods

Study area

Lake and stream data used in this study come from data bases of previous EU projects and more regional data bases which have been standardised and collated in the WISER Central

database (Moe et al., this issue; submitted). To allow for a cross-taxon and between-habitat comparison, the data were stratified to ecosystems where multiple taxonomic groups have been measured. We obtained 67 stream sites in Germany where water quality, hydromorphology, phytobenthos, macrophytes, benthic invertebrates and fish have been measured (Fig. 1). The data originate from monitoring programs of the German federal states Thuringia, Schleswig-Holstein and Northrhine-Westphalia. For the lakes, we obtained 59 sites extending over a broader spatial gradient from the UK to the Baltic countries where water quality, phytoplankton, macrophytes and fish have been measured (Fig. 1). Despite these spatial differences, all stream and lake sites were distributed across disturbance gradients, allowing us to compare biological pressure responses to nutrient enrichment, land use (lakes and streams), and hydrogeomorphological alteration (streams).

The 67 streams cover a wide range of natural environmental conditions. They include six lowland streams in ecoregions 13 (Western Lowlands) and 14 (Central Lowlands), with catchment areas ranging from 69 to 1781 km^2 and located at altitudes from 1.5 to 57 m above sea level. The other 61 streams are classified as mountain streams according to the German national river typology, though not all of them are located in the ecoregion 9 (Central Montains) but partly in ecoregions 13 and 14. The latter, however, have mainly a mountainous catchment and are thus characterized by features typical for mountain streams, such as coarse substrate and high current velocity. The mountain streams are located at altitudes ranging from 119 to 761 m above sea level with catchment areas from 10 to 4174 km^2 (mean: 361 km^2).

The 59 lakes varied in size (0.1 -65 km^2) and catchment area (2-526 km^2), and cover a range of natural environmental conditions and ecoregions, as was the case for the streams. To account for this heterogeneity, the data set could be divided into 5 mountain lakes that were located at > 200 m above sea level, 10 small lowland lakes (surface area: < 9 km^2),

and 44 large lowland lakes (surface area: > 10 km^2) situated at < 160 m above sea level.

The environmental data used in this study are partly taken from the original data sources, i.e. national monitoring data. For streams this relates to hydromorphological data, which were recorded with the standard river habitat survey method in Germany (Länderarbeitsgemeinschaft Wasser, briefly described in Kail & Hering, 2005) and physico-chemical variables. Data on catchment and riparian (buffer strips) land use were recorded for all sampling sites from Corine land cover (http://sia.eionet.europa.eu/CLC2000).

In addition to the strong natural gradients characterizing the stream dataset (lowland vs. mountain streams; catchment areas ranging from 10 to > 4 000 km^2) gradients in pressures are apparent, although near natural streams were not included. For the lowland streams, between 29 and 82% of the catchments are classified as having agricultural land use, with 2-11% classified as forest. For the mountain streams, 0-94% of the catchments are classified as arable land and between 0 and 94% are classified as forest.

The biological data for the streams were recorded in the framework of national monitoring programmes and followed the standards for the Water Framework Directive established in Germany. Phytobenthos and diatoms were sampled according to the Phylib method (Schaumburg et al., 2006). Diatoms were sampled in summer at times of low flow conditions by removing 10 stones from the stream bottom, avoiding zones of exceptionally high and low current velocities. In lowland streams, the upper layer of the bottom substrate was removed. Samples were fixed in the field with 1-4% formalin; in the lab, they were boiled in H$_2$SO$_4$ and mounted on permanent microscope slides. Identification was to species level with 400 valves being determined.

Macrophytes were surveyed between June and September in a 100 m stretch by wading upstream or (in case of large rivers) from a boat or from the shoreline removing submerged macrophytes with a rake. All Characeae, mosses and higher plants growing at

least partly submerged were recorded and determined in the field; in questionable cases specimens were transported to the lab. Abundance was estimated according to Kohler (1978).

Macroinvertebrates were collected with a multi-habitat sampling approach described by Meier et al. (2006) and Haase et al. (2004). Twenty sampling units each covering an area of 25 x 25 cm were sampled with a hand-net (mesh size: 500 μm); sampling units were distributed according to the estimated habitat coverage, with each habitat type accounting for at least 5% of the stream bottom being represented by at least one sampling unit. Specimens were sorted in the lab; at least 1/6 of the sample accounting for a minimum of 350 individuals were sorted and identified to species level with the exception of Oligochaeta and Diptera, which were identified to genus to family level.

Fish were recorded following Dussling et al. (2004), a method compatible to CEN 14011 (CEN 2003), usually within a stop-netted stream section; the recommended sampling area was 10 x the stream width, with a recommended minimum of a 100 m stream length sampled. The fish were held in plastic tubs until the end of the sampling run after which they were identified to species and returned to the stream.

The biological data for lakes were compiled from many different sources including national monitoring programs and previous research projects, from altogether nine countries. Detailed description is available in the WISER metadatabase (http://www.wiser.eu/results/meta-database; Schmidt-Kloiber et al., 2012).

Phytoplantkon data were taken from the former EU-project REBECCA for lakes in Finland, Norway and Sweden (period 1988-2003) (Moe et al., 2008). More recent national monitoring data from these countries (2001-2009) as well as from Ireland (2007) and UK (2008) were provided by the Northern GIG (Geographical Intercalibration Group), and from Estonia (2003-2005), Germany (1995-2008), Ireland (2007), Latvia (1998-2008) and Lithuania (2005-2009) by the Central-Baltic GIG.

Macrophyte data from all countries (1990-2003) were taken from the REBECCA lakes macrophytes database (described by Moe et al., 2008). Much of the data in this database was sourced from the CB GIG intercalibration exercise in a pre-processed form. All fish data (1950-2009) were taken from the Intercalibration fish database (Caussé et al., 2012).

Statistical analyses

Biological response variables - Nonmetric multidimensional scaling (NMDS) was carried out in Primer v.6 (Primer-E Ltd, Plymouth, UK) to determine the biological turnover, or gradient length, of the species data sets as well as to condense the species by site matrix into three indices of community composition; namely NMDS scores of the first, second and third ordination axes. As a nonlinear technique, NMDS ranks points in ordination space in a way that the distance between sampling points reflects community (dis)similarity (ter Braak, 1995). The correspondence of the ordination diagram to the distances is described by a stress value where 0 is a perfect fit. The ordinations are based on Bray–Curtis dissimilarity matrices derived from square-root transformed sample by species matrices of all taxonomic groups. NMDS were calculated separately for each taxonomic group in the streams and lakes. The final solution is based on 500 permutations. Analyses of similarity (ANOSIM) were carried out in Primer to determine if community similarity between types of streams (lowland streams, mountain streams in small and large catchments) and lakes (mountain lakes, large and small lowland lakes) used for analysis differ.

Environmental gradients - Principal Component Analysis (PCA) on centred and standardized variables was carried out in Canoco 4.5 (ter Braak & Smilauer, 2002) to assess correlatively the structure of the environmental data and to reduce the structure to a lower number of environmental gradients as linear combinations of the environmental variables (Johnson &

Wichern, 1988). All variables were log10 - or arcsin- (proportional data) transformed (except pH) to more closely approximate the linear relationships assumed in PCA. The number of meaningful PCs was determined by examining the eigenvalues of the first few axes. PCAs were carried out separately on the lake and stream data sets.

Regression analysis - The multivariate variables of community composition were related to environmental gradients by regression. Model parameters for linear and parabola (second-order polynomial) regressions were estimated using the least-squares principle. Linear and curve (e.g. concave) fits were compared by looking if the parabola fit gave a smaller residual sum of squares than the straight line. This was formally tested by determining if b2 coefficient was equal to 0 using a t-test (Jongman et al., 1995). If the b2 coefficient did not improve the fit, then we concluded that a straight line was sufficient to describe the relation between the response (biological variables) and predictor (environmental gradients) variable. If adding a quadratic term improved the fit (i.e., b2 coefficient was not equal to 0), then we used the parameters of the parabola model in among-taxonomic group comparisons. If the linear fit was significant, this model was selected and used in the comparison of taxonomic groups; if the linear model was not significant but the quadratic model was significant, then the quadratic model was used in among-group comparisons.

Three metrics were used to compare the response of the taxonomic groups to stress. Precision was calculated as the squared correlation (coefficient of determination, adjusted R^2) between the observed and fitted values as a measure of variance accounted for by the model. Sensitivity of a taxonomic assemblage to stress was estimated as the magnitude of change (slope) of a predicted stress–response relationship. If quadratic models were used, the slope was calculated as the absolute value of the sum of the slope (β) coefficients. The error of the predictive model expressed as the root mean square error was used to compare the

robustness of the response relationships (Johnson & Hering, 2009). Across taxonomic-group comparisons were done only if the fitted model was significant ($P < 0.05$).

Spatial congruency - Patterns of within-stream and within-lake group, between-taxonomic group congruency were analysed with a non-parametric Mantel permutation test. Mantel tests for differences between Bray–Curtis dissimilarity of the organism groups were measured using 999 permutations. All Mantel tests were done using the Primer software.

Results

Biological gradients

NMDS analyses revealed different patterns of community dissimilarity among all taxonomic groups in streams (Fig. 2) and lakes (Fig. 3). All taxonomic groups in streams showed a relatively homogenous distribution of sampling sites in ordination space without aggregations into site clusters. However, ANOSIM revealed that for macrophytes and invertebrates there were significant differences between assemblages inhabiting lowland streams, small mountain streams (catchment size < 100 km^2) and large lowland streams (catchment size > 100 km^2), while in the case of phytobenthos only lowland streams and small mountain streams differed at P < 0.01 and differences in fish assemblages were only marginally significant (P < 0.1) for lowland / small mountain streams and for the two mountain stream type groups.

The clustering of sampling sites for lake biota was comparatively more heterogeneous, particularly for fish were sampling sites split into two groups in ordination space. ANOSIM analyses revealed that phytoplankton assemblages did not differ between mountain lakes, and small and large lowland lakes (P > 0.05). In the case of macrophytes, community structure only differed between large and small lakes in lowlands (P = 0.002), while assemblages in mountain lakes were similar to those in both lowland lake types (P >

0.05). Lake-type differences were more obvious for fish, where again community structure differed between large and small lowland lakes (P = 0.033). In addition, fish assemblages in mountain lakes differed from those in large (P = 0.03) but not small lowland lakes (P > 0.05).

Taken together, these results indicate that the dataset is structured by typological variables such as ecosystem size (streams and lakes) and ecoregion (streams) in addition to possible gradients in degradation. All ordinations of stream and lake taxonomic groups had a stress value < 0.2, indicating that NMDS was a useful ordination method for extracting structure from the data (Clarke, 1993).

Environmental gradients

Many of the environmental variables were correlated, and hence, PCA was able to reduce substantially the dimensionality of the environmental variables. For example, the first four PC axes captured from 69% (streams) and 73.3% (lakes) of the variation explained by the environmental variables. The percentage variance decreased between the first and second PC axes (30 to 17% for streams, 28 to 21% for lakes, respectively), indicating the predominance of the first PC axis.

Regarding the streams, correlation scores showed that the first PC axis (PCA 1) was related to variables indicative of nutrient enrichment and land use. For instance, conductivity and nutrient (nitrite, total P) concentrations and percentage arable land cover at the catchment scale correlated negatively, while percentage forest cover at the buffer and catchment scale correlated positively with the first PC axis (Fig. 4). The second PC axis (PCA 2) of streams was explained only through percentage cover of pastures at the buffer scale (Fig. 4).

Regarding the lakes, similar gradients were found as in the streams. The first PC axis (PCA 1) showed a similar relationship with variables indicative of nutrient enrichment

and land use. That is, nutrients (total P concentrations) and percentage cover of pastures in the catchment correlated positively, while percentage forest cover correlated negatively with the first PC axis (Fig. 4). The second PC axis (PCA 2) of lakes was explained only through percentage cover of wetlands (positive correlation) and percentage cover of arable land, urbanised and industrial/commercial areas, artificial vegetation and permanent crops (negative correlations) (Fig. 4).

The first two PC axes of the stream and lake ordinations are used here to represent the two main environmental gradients describing the physicochemical and land-use variability within the ecosystems. The primary gradient (PCA 1) can be considered a nutrient gradient that is associated with percentage land use in the catchments, and the secondary gradient (PCA 2) is referred to as a land-use gradient. As these gradients were derived using PCA, they are orthogonal (i.e. uncorrelated), and hence, represent complex gradients summarizing information on land use and within-habitat characteristics.

Regressions of community composition to environmental gradients

Taxonomic group response to the two environmental gradients differed both among groups and between habitat types (streams *vs* lakes) (Table 1). In streams, invertebrates (0.407) and fish (0.47) had the highest precision (adj. R^2 values) for the nutrient gradient, followed by macrophytes (0.233) and phytobenthos (0.110). By comparison, relationships with the secondary gradient were less robust, with highest precision found for invertebrates (0.200), followed by macrophytes (0.17) and fish (0.168); phytobenthos was not significantly related to the secondary gradient (Table 1). For lakes, macrophytes were more precisely related to the nutrient gradient (max. adj. R^2 value = 0.47) than phytoplankton (max. 0.334) and fish (max 0.189). Contrary to streams, precision was higher for the secondary gradient compared to the nutrient gradient; precision for macrophytes was 0.561, and amounted to 0.411 and 0.353 for

phytoplankton and fish, respectively.

Changes in assemblage structure (NMDS scores) showed strong responses, indicated by slope values, to both environmental gradients (PCA1 and PCA2) in streams and lakes (Figs. 5 and 6). For streams, the strongest relationship (i.e., highest sensitivity) between the primary gradient (PC1) and assemblage structure was found for fish (NMDS 1, slope = 0.500), followed by invertebrates (NMDS 1, slope = 0.414), macrophytes (NMDS 1, slope = -0.345) and phytobenthos (NMDS 2, slope = -0.195) (Fig. 5). Changes in the composition of fish assemblages, as described by NMDS 2, was also significantly related to the primary gradient, but with lower precision and sensitivity (adj. R^2 = 0.08, slope = -0.129). None of the other NMDS dimensions of the other taxonomic groups were significantly related to PC 1 (P > 0.05). When assemblages were regressed only against total P, the responses were generally stronger compared with the PC 1 gradient (Fig. 5). Changes in assemblage composition for fish (NMDS 1), invertebrates (NMDS 2), and macrophytes (NMDS 1) were also related to the secondary gradient (PC 2); however, this relationship was weak and linear for macrophytes (slope = 0.052) but stronger and non-linear for invertebrates (absolute value of sum of slope coefficient = 0.463) and fish (absolute value of sum of slope coefficient = 0.609) (Fig. 5). Regarding measures of robustness of the regression relationships, expressed as RMSE, the stream assemblages usually showed values >0.7 when related to the primary and secondary environmental gradient (Tab. 1).

For lakes, the strongest response was noted for changes in macrophyte assemblages related to the nutrient gradient PCA 1 (NMDS 1, slope = –0. 487), followed by phytoplankton (NMDS 2, slope 0.294), and fish (NMDS 2, absolute value of sum of slope coefficient = 0.288). Similar to streams, changes in assemblage composition were generally higher when assemblage variables were regressed against total P (Fig. 6) than to PCA 1. Contrary to the streams, responses were stronger for the secondary gradient PCA 2 than for

PCA 1; NMDS 1 for phytoplankton had a slope of -0.491, followed by macrophytes (slope = -0.428) and fish (slope = -0.149). For lakes, the measures of robustness (RMSE) were stronger than in the streams, and <0.527 and <0.688 for most assemblages when regressed against PC1 and PC2, respectively (Tab. 1).

Spatial congruency among the organism groups

Mantel tests showed significant between-taxonomic group patterns in congruency for both streams and lakes, although the number of significant relationships was higher for the lakes. For streams, the highest congruency was between fish and macrophytes ($r = 0.329$, $P < 0.001$), followed by invertebrates and fish ($r = 0.193$, $P < 0.001$) and invertebrates and macrophytes ($r = 0.187$, $P < 0.001$). Spatial congruency between phytobenthos and the other taxonomic groups was not significant ($P > 0.05$). For lakes, fish and macrophyte assemblages showed the highest congruency ($r = 0.375$, $P < 0.001$), followed by macrophyte and phytoplankton assemblages ($r = 0.241$, $P = 0.002$) and phytoplankton and fish assemblages ($r = 0.126$, $P = 0.027$).

Discussion

Assemblages inhabiting rivers and lakes are affected by both natural and anthropogenic factors. While natural factors, such as water body size, altitude, ecoregion or catchment geology, determine stream types or lakes types, anthropogenic factors like eutrophication, catchment land use or hydromorphological degradation may cause deterioration of the biota, which may or may not act in a similar way across different water body types or even categories (rivers vs. lakes). Our results support the importance of elevated nutrient levels and alterations in land use as the two main environmental gradients explaining variability in stream and lake condition on a large scale; the first PC axis, interpreted as representing

elevated nutrient concentrations, explained from 30% (streams) to 28% (lakes) of the variation, while the second PC axis, corresponding to land use characteristics, explained another 17% and 21% of the variability among streams and lakes, respectively. It must be noted that the river and lakes included in the analysis covered a wide range of natural types; despite this strong natural variability, nutrient stress and catchment land use act as explanatory variables for the overall assemblage composition.

While all taxonomic groups in both ecosystem types were responding to these two main environmental gradients, trajectories of change varied considerably among the groups, supporting our first hypothesis that taxonomic groups vary in their response to environmental stressors. Also our second hypothesis is supported because the same taxonomic groups showed different responses to environmental gradients in streams and lakes, respectively. However, it must be acknowledged that the stress gradients differed between lakes and streams, and that the observed differences may therefore not be surprising. Based on previous findings (Johnson & Hering 2009, 2010), several of the response signatures were expected to reflect simple first and second principle relations between the organisms and their resources, such as the early response of a primary producer (e.g. algae) to a single growth-limiting element (e.g. phosphorus) and the lagged-response of a secondary producer (consumer of benthic diatoms or invertebrates) to elevated nutrient levels. We expected that benthic diatoms, phytoplankton and macrophytes would show the strongest response to elevated nutrient concentrations, in particular at low nutrient concentrations where phosphorus might limit growth and production. Our findings from lakes support this conjecture when NMDS scores were regressed against total phosphorus (Fig. 6), but using the more complex and multivariate PCA gradients these differences were less obvious because the responses (in terms of slopes) to nutrient enrichment were similar between phytoplankton, macrophytes and fish. Similar results were found for the streams where consumers (invertebrates and fish)

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showed even stronger response than the primary producers to both the PCA gradient and total phosphorus alone. We need to consider, however, that the underlying data source included a high amount or natural variability, i.e. stream types, which are particularly relevant for macrophytes, as different species occur in lowland and mountain streams.

In the case of phytobenthos, the relatively poor response to nutrient concentrations might be due to the restricted gradient mainly including moderately polluted streams. In datasets including low nutrient reference streams there is a strong response of phytobenthos to nutrients, in particular in the transition of low to medium concentrations (Hering et al., 2006; Johnson & Hering, 2009). Despite the limited spatial extension of our stream study, we acknowledge that multiple forms of anthropogenic stress similarly influence many other areas in Europe; we therefore expect that similar relationships may be found elsewhere. In such heavily modified landscapes, it is therefore reasonable to assume that our PCA gradients cover a range of nutrient conditions in which primary producer responses are weakened as nutrients are no longer limiting growth.

The different taxonomic groups also showed varied response to the two environmental gradients. For example, macrophytes showed linear responses to both stressor gradients in lakes and streams. Fish showed a linear response to the nutrient gradient and a non-linear relationship with the secondary gradient in streams, while the opposite relationships were found in lakes. A similar non-linear relationship was found for invertebrates to the secondary gradients in streams. These findings illustrate how selection of taxonomic group can be crucial for detecting change, and support earlier work focussed on single taxonomic groups like fish (Fausch et al., 1990; Poff et al., 2001), macrophytes (e.g. Whitton, 1979), invertebrates (Rosenberg & Resh, 1993), and benthic diatoms (e.g. Stevenson & Pan, 2003). The asymmetric response clearly shows how selection of different taxonomic groups can be used to strengthen inference in a multiple lines of evidence approach and to

select complementary indicators.

We selected response variables that represented important attributes of community diversity and composition. We have chosen multivariate metrics, expressed as NMDS scores, which have been shown to be better predictors of community responses to environmental change than univariate metrics (Johnson & Hering, 2009; Angeler & Goedkoop, 2010) and are particularly appropriate in case of data covering a variety of stream / lake types. However, more important than significance of the regression slopes, is the explanatory power of the response variables. Indeed, previous studies have suggested that only strong correlations (e.g. $R^2 > 0.50$) should be used in the context of selecting robust indicators of change and/or as biodiversity surrogates (e.g. Flather et al., 1997; Heino et al., 2005). Using an R^2 value of 0.5, only one group qualifies as strong indicator of change, namely macrophytes assemblages of lakes in response to the secondary gradient (Table 1). Stream fish ($R^2 = 0.47$) and lake macrophyte communities ($R^2 = 0.46$) are borderline in this regard when it comes to indicate nutrient enrichment. Using an R^2 value of 0.5, our study of spatial congruency between lake and stream taxonomic groups suggests that the communities undergo changes that are largely uncoupled from each other, indicative of strong idiosyncratic behaviour. From the ecological side this is hardly a surprise because all taxa differ fundamentally in their life history traits and other ecological characteristics that mediate responses to environmental conditions (e.g., Heino et al., 2005). Further, we need to consider the high natural variability inherent to the dataset which mixes up the response to stress gradients; within individual lakes types or stream types a much stronger response of the biota to stress gradients has been observed, even to hydromorphological gradients (e.g., Lorenz et al., 2004).

Monitoring changes in biodiversity is costly and therefore much focus has been on finding surrogates for biodiversity (e.g., Williams & Gaston, 1994; McGeoch, 1998). Our study showed that many of the taxonomic groups were significantly correlated with one

another in both ecosystem types, although the strength of correlation coefficients varied markedly between the pairs of taxonomic assemblages. These findings imply that several of the taxonomic groups may be used as surrogates or as proxies of wholesale aquatic biodiversity; that is, indicating change in diversity for other groups, and resulting in considerable economic savings. However, caution is advised since our study included many sites strongly affected by stress, which likely caused homogenization or increased similarity of communities with stress, especially in the stream analyses. Simply put, our findings of among-taxon congruence may be an artefact of response along the gradient of impairment and not a measure of taxonomic coherence. For instance, Johnson & Hering (2009), found significant correlations between macrophyte diversity and invertebrate and diatom diversity in least-impacted lowland streams, and fish diversity and macrophyte and invertebrate diversity in near-pristine mountain streams, suggesting that these two groups (i.e., macrophytes in lowland and fish in mountain streams) may function as surrogate indicators for the diversity of other taxonomic groups. Studying responses along gradients of nutrient enrichment, Johnson & Hering (2009) found macrophyte assemblages in lowland streams and invertebrate assemblages in mountain streams may be more appropriate as biodiversity surrogates for other taxonomic groups. Judged from the strength of correlation between taxonomic groups in this study, we conclude that fish and macrophytes are the best candidates of biodiversity surrogates in streams and lakes for which this study is representative, respectively, i.e. for large-scale gradients including different stream and lakes types. In particular in case of stressed water bodies (e.g. heavily modified water bodies) macrophytes and fish might be suited to assess ecosystem response to stress, even across a gradient of stream or lakes types.

Acknowledgements

References

Allan, J.D., 2004. Landscapes and riverscapes: the influence of land use on stream ecosystems. Annual Review of Ecology and Systematics 35: 257–284.

Angeler, D.G., 2007. Resurrection ecology and global climate change research in freshwater ecosystems. Journal of the North American Benthological Society 26:12-22.

Angeler, D.G. & W. Goedkoop, 2010. Biological responses to liming in boreal lakes: an assessment using plankton, macroinvertebrate and fish communities. Journal of Applied Ecology 47: 478–486.

Beck, M.W. & L.K. Hatch, 2009. A review of research on the development of lake indices of biotic integrity. Environmental Reviews 17: 21-44.

Birk, S., W. Bonne, A. Borja, S. Brucet, A. Courrat, S. Poikane, A. Solimini, W. van de Bund, N. Zampoukas & D. Hering, 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.

CEN 14011 2003. Water Quality – Sampling of Fish with Electricity. EN 14011. European

Committee for Standardization, Brussels.

Caussé S., M. Gevrey, S. Pédron, S. Brucet, K. Holmgren, M. Emmrich, J. De Bortoli, & C. Argillier, 2012. Fish indicators for ecological status assessment of lakes affected by eutrophication and hydromorphological pressures. WISER deliverable 3.4-4 (available at: http://www.wiser.eu/download/D3.4-4.pdf).

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18: 117-143.

Dale, V.H. & S.C. Beyeler, 2001. Challenges in the development and use of ecological indicators. Ecological Indicators 1: 3–10.

Dussling, U., R. Berg, H. Klinger & C. Wolter. 2004, VIII-7.4 Assessing the ecological status of river systems using fish assemblages. Pages 84pp *in* C. Steinberg, W. Calmano, H. Klapper, and R. D. Wilken, editors. Handbuch Angewandte Limnologie. ecomed, Landsberg am Lech.

European Commission, 2000. Directive 2000/60/EC of the European Parliament and of the Council – Establishing a Framework for Community Action in the Field of Water Policy. Brussels, Belgium, 23 October 2000.

Fausch, K.D., J. Lyons, J.R. Karr & P.L. Angermeier, 1990. Fish communities as indicators of environmental degradation. American Fisheries Society Symposium 8: 123–144.

Flather, C.H., K.R. Wilson, D.J. Dean & W.C. McComb, 1997. Identifying gaps in conservation networks: of indicators and uncertainty in geographicbased analyses. Ecological Applications 7: 531–542.

Fore, L.S., J.R. Karr & R.W. Wisseman, 1996. Assessing invertebrate responses to human activities: evaluating alternative approaches. Journal of the North American Benthological Society 15: 212–231.

Furse, M.T., D. Hering, O. Moog, P.F.M. Verdonschot, L. Sandin, K. Brabec, K. Gritzalis, A.

Buffagni, P. Pinto, N. Friberg, J. Murray-Bligh, J. Kokes, R. Alber, P. Usseglio-Polatera, P. Haase, R. Sweeting, B. Bis, K. Szoszkiewicz, H. Soszka, G. Springe, F. Sporka & I. Krno, 2006. The STAR project: context, objectives and approaches. Hydrobiologia 566: 3–29.

Giller, P.S. & B. Malmqvist, 1998. The Biology of Streams and Rivers. Oxford University Press, Oxford, UK.

Haase, P., S. Lohse, S. Pauls, K. Schindehütte, A. Sundermann, P. Rolauffs & D. Hering, 2004. Assessing streams in Germany with benthic invertebrates: development of a practical standardized protocol for macroinvertebrate sampling and sorting. Limnologica 34:349-365.

Heino, J., R. Paavola, R. Virtanene, & T. Muotka, 2005. Searching for biodiversity indicators in running waters: do bryophytes, macroinvertebrates, and fish show congruent diversity patterns? Biodiversity and Conservation 14: 415–428.

Herbst, D.B. & E.L. Silldorff, 2006. Comparison of the performance of difference bioassessment methods: similar evaluations of biotic integrity from separate programs and procedures. Journal of the North American Benthological Society 25: 513–530.

Hering, D., A. Borja, J. Carstensen, L. Carvalho, M. Elliott, C. K. Feld, A.S. Heiskanen, R.K. Johnson, J. Moe, D. Pont, A.L. Solheim & W de Bund, 2010. The European Water Framework Directive at the age of 10: a critical review of the achievements with recommendations for the future. Science of the Total Environment 408: 4007-4019.

Hirst, H., I. Jüttner & S.J. Ormerod, 2002. Comparing the responses of diatoms and macroinvertebrates to metals in upland streams of Wales and Cornwall. Freshwater Biology 47: 1752–1765.

Hooper, D. U., F. S. Chapin, III, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton,

D. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setälä, A. J. Symstad, J. Vandermeer & D. A. Wardle, 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75: 3-35.

Jongman, R.H.G., C.J.F. ter Braak & O.F.R. van Tongeren, 1995. Data analysis in Community and Landscape Ecology. Cambridge University, Cambridge, UK.

ter Braak, C.J.F., 1995. Ordination. In Jongman R., ter Braak & O.F.R. van Tongeren (eds), Analysis in community and landscape ecology. Cambridge University Press, Cambridge: 91–173.

ter Braak, C.J.F. & P. Smilauer, 2002. (eds) Biometrics. Plant Research International, Wageningen, The Netherlands.

Johnson, R.A. & D.W. Wichern, 1988. Applied Multivariate Statistical Analysis. Prentice-Hall Inc., Upper Saddle River, NJ, USA.

Johnson, R.K., 1998. Spatio-temporal variability of temperate lake macroinvertebrate communities: detection of impact. Ecological Applications 8: 61–70.

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

Johnson, R.K. & D. Hering, 2009. Response of taxonomic groups in streams to gradients in resource and habitat characteristics. Journal of Applied Ecology 46: 175-186.

Johnson, R.K. & D. Hering, 2010. Spatial congruency of benthic diatom, invertebrate, macrophyte and fish assemblages in minimally disturbed European streams. Ecological Applications 20: 978¬992.

Johnson, R.K., D. Hering, M.T. Furse & R.T. Clarke, 2006. Detection of ecological change using multiple organism groups: metrics and uncertainty. Hydrobiologia 566: 115–137.

Johnson, R.K., T. Wiederholm & D.M. Rosenberg, 1993. Freshwater biomonitoring using individual organisms, populations and species assemblages of benthic macroinvertebrates. In D.M. Rosenberg & V.H. Resh (eds), Freshwater Biomonitoring and Benthic Macroinvertebrates. Chapman and Hall, New York: 40–158.

Kail, J. & D. Hering, 2005. Using large wood to restore streams in Central Europe: Potential use and likely effects. Landscape Ecology 20: 755-772.

Kohler, A. 1978. Methoden der Kartierung der Flora und Vegetation von Süßwasserbiotopen. Landschaft + Stadt 10: 23-85.

Lewis, B.R., I. Jüttner, B. Reynolds & S.J. Ormerod, 2007. Comparative assessment of stream acidity using diatoms and macroinvertebrates: implications for river management and conservation. Aquatic Conservation: Marine and Freshwater Ecosystems 17: 502–519.

McGeoch, M.A., 1998. The selection, testing and application of terrestrial insects as bioindicators. Biological Reviews 73: 181–201.

Moe, S.J., R. Brænden, B. Dudley, A. Schmidt-Kloiber & J. Strackbein. The WISER way of organising ecological data from European rivers, lakes and coastal waters. Hydrobiologia (submitted to this special issue).

Palmer, M.A., A.P. Covich, B. Finlay, J. Gibert, K.D. Hyde, R.K. Johnson, T. Kairesalo, P.S. Lake, C.R. Lovell, R.J. Naiman, C. Ricci, F.F. Sabater & D.L. Strayer, 1997. Biodiversity and ecosystem function in freshwater sediments. Ambio 26: 571–577.

Pocock, M.J.O. & N. Jennings, 2008.Testing biotic indicator taxa: the sensitivity of insectivorous mammals and their prey to the intensification of lowland agriculture. Journal of Applied Ecology 45: 151–160.

Poff, N.L., P.L. Angermeier, S.D. Cooper, P.S. Lake, K.D. Fausch, K.O. Winemiller, L.A.K.

Mertes, M.W. Oswood, J. Reynolds & F.J. Rahel, 2001. Fish diversity in streams and rivers. In F.S. Chapin, O.E. Sala & R. Huber-Sannwald (eds), Scenarios of Future Biodiversity Springer-Verlag, New York: 315–349.

Resh, V.H., 2008. Which group is best? Attributes of different biological assemblages used in freshwater biomonitoring programs. Environmental Monitoring and Assessment 138: 131–138.

Rosenberg, D.M. & V.H. Resh, 1993. Introduction to freshwater biomonitoring and benthic macroinvertebrates. In D.M. Rosenberg & V.H. Resh (eds), Freshwater Biomonitoring and Benthic Macroinvertebrates. Chapman and Hall, New York: 1–9.

Schaumburg, J., C. Schranz, D. Stelzer, G. Hoffmann, A. Gutowski & J. Foerster, 2006. Handlunngsanweisung für die ökologische Bewertung von Fließgewässern zur Umsetzung der EU-Wasserrahmenrichtlinie: Makrophyten und Phytobenthos. Bayerisches Landesamt für Umwelt.

Stevenson, R.J. & Y. Pan, 2003. Assessing environmental conditions in rivers and streams with diatoms. In J.P. Smol (ed.), The Diatoms: Applications for the Environmental and Earth Sciences. Cambridge University Press, Cambridge, UK: 11–40.

Stevenson, R.J., R.C. Bailey, M.C., Harrass, C.P. Hawkins, J. Alba-Tercedor, C. Couch, S. Dyer, F.A. Fulk, J.M. Harrington, C.T. Hunsaker & R.K. Johnson, 2004. Designing data collection for ecological assessments. In M.T. Barbour, S.B. Norton, H.R. Preston & K.W. Thornton (eds.), Making Ecological Assessment of Aquatic Resources: Linking Science to Decision. SETAC, Pensacola, FL, USA: 55–84.

Strayer, D.L. & D. Dudgeon,. 2010. Freshwater biodiversity conservation: recent progress and future challenges. Journal of the North American Benthological Society 29: 344-358.

Vaughan, I.P. & S.J. Ormerod, 2005. Increasing the value of principal components analysis

for simplifying ecological data: a case study with rivers and river birds. Journal of Applied Ecology 42: 487–497.

Whitton, B.A., 1979. Plants as indicators of river water quality. In A. James & L. Evison (eds.), Biological Indicators of Water Quality. Wiley, Chichester, UK*:* 5.1–5.34.

Williams, P.H. & K.J. Gaston, 1994. Measuring more of biodiversity: Can higher-taxon richness predict wholesale species richness? Biological Conservation 67: 211–217.

Table 1: Summary statistics of regression analysis of three variables of community structure (NMDS axes scores) of taxonomic groups in streams (n=67) and lakes (n=59) against two environmental gradients extracted using principal component analysis (PCA). The primary axis of both streams and lakes was interpreted as showing a gradient in nutrient enrichment and land use and the second PCA axis showing variability in land use alone. Adj. R^2, coefficient of determination; RMSE, root mean square error of the prediction. Only minima and maxima of absolute slopes, adj. R^2 and RMSE from significant regressions are shown; n indicates the number of significant regressions of each taxonomic group variable (i.e., NMDS dimensions 1 – 3) with PCA1/PCA2.

	PCA 1				PCA 2			
	Adj. R^2	Slope	RMSE	n	Adj. R^2	Slope	RMSE	n
Streams								
Phytobenthos	0.110	0.195	0.727	1	---	---	---	0
Macrophytes	0.233	0.345	0.727	1	0.17	0.052	0.802	1
Invertebrates	0.407	0.414	0.706	1	0.200	0.463	0.746	1
Fish	Min: 0.08	0.129	0.409	2	0.168	0.609	0.863	1
	Max: 0.47	0.500	0.718					
Lakes								
Phytoplankton	Min: 0.079	0.736	0.404	3	0.411	0.856	0.587	1
	Max: 0.334	1.173	0.412					
Macrophytes	0.460	0.963	0.527	1	0.561	1.325	0.381	1
Fish	Min: 0.118	0.430	0.804	3	0.083	0.763	0.397	2
	Max: 0.189	1.361	0.300		0.353	0.702	0.688	

Figures

Figure 1: Map of Europe showing the location of the 67 stream (triangles) and 59 lake (dots) sites.

Figure 2: Three-dimensional nonmetric multidimensional scaling ordinations showing gradients in biological community structure of stream assemblages; grey circles: lowland streams; black circles: mountain streams (<100 km^2 catchment area); white circles: mountain streams (>100 km^2 catchment area).

Figure 3: Three-dimensional nonmetric multidimensional scaling ordinations showing gradients in biological community structure of lake assemblages; grey circles: mountain lakes; black circles: small lowland lakes (<10 km^2 surface area); white circles: large lowland lakes (>10 km^2 surface area).

Figure 4: Principal component analysis ordination plots of environmental variables for 67 streams and 59 lakes. For both habitat types the first PC axis can be interpreted as nutrient enrichment gradient and the second PC axis is interpreted as a landuse gradient. Stream symbols: Grey circles: lowland streams; black circles: mountain streams (<100 km^2 catchment area); white circles: mountain streams (>100 km^2 catchment area); lake symbols: grey circles: mountain lakes; black circles: small lowland lakes (<10 km^2 surface area); white circles: large lowland lakes (>10 km^2 surface area).

Figure 5: Regression plots of assemblage composition of stream assemblages against PC 1, PC 2, and log total P. Shown are plots from regressions of NMDS dimensions with the

highest model fit. Trend lines and equation details are also shown (n= 67). Note that regressions are based on unrotated NMDS solutions, and that therefore the absolute values of the slopes, rather than their direction, should be used for inference. Grey circles: lowland streams; black circles: mountain streams (<100 km^2 catchment area); white circles: mountain streams (>100 km^2 catchment area).

Figure 6: Regression plots of assemblage composition of lake assemblages against PC 1, PC 2, and log total P. Shown are plots from regressions of NMDS dimensions with the highest model fit. Trend lines and equation details are also shown (n= 59). Note that regressions are based on unrotated NMDS solutions, and that therefore the absolute values of the slopes, rather than their direction, should be used for inference Grey circles: mountain lakes; black circles: small lowland lakes (<10 km^2 surface area); white circles: large lowland lakes (>10 km^2 surface area).
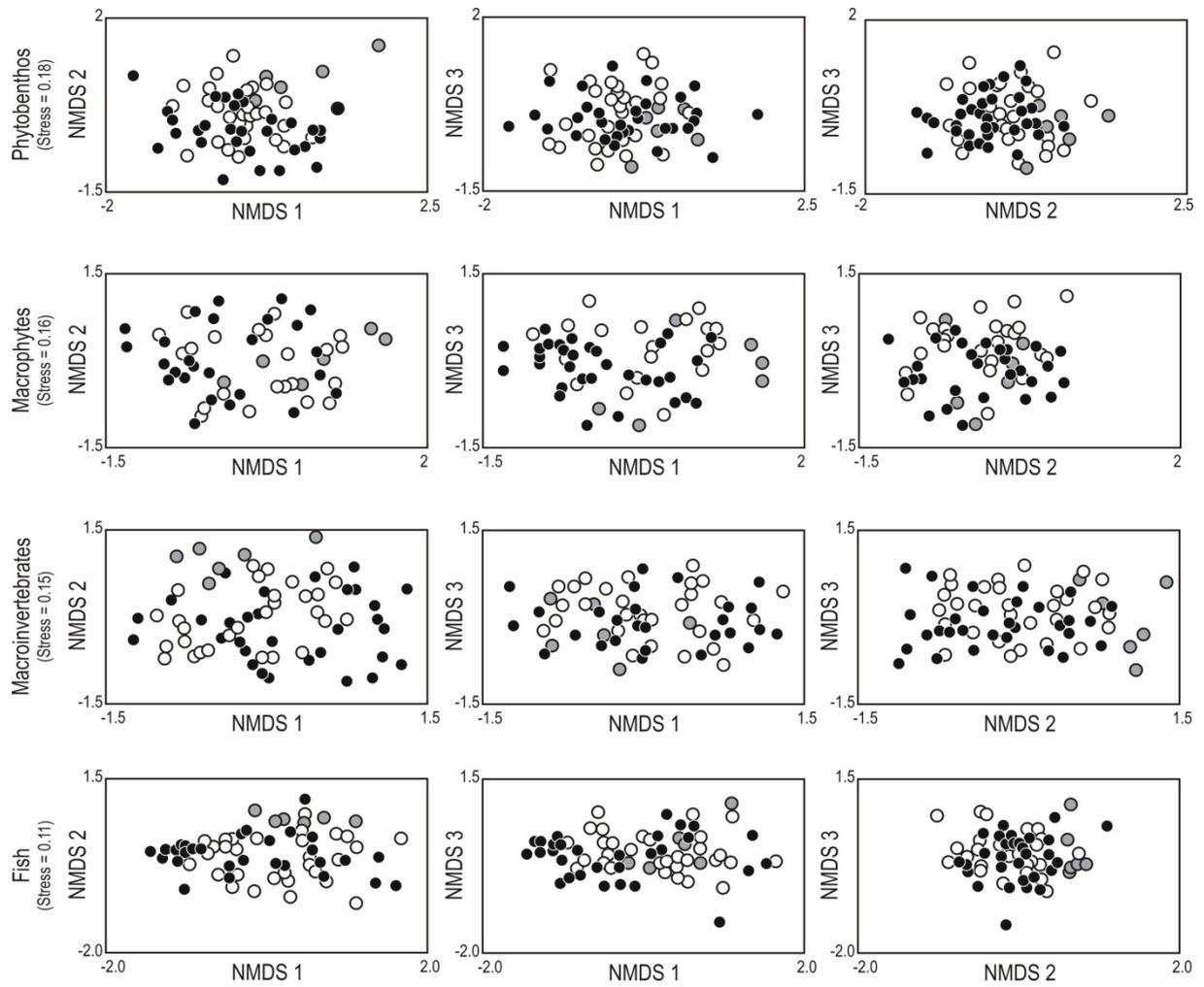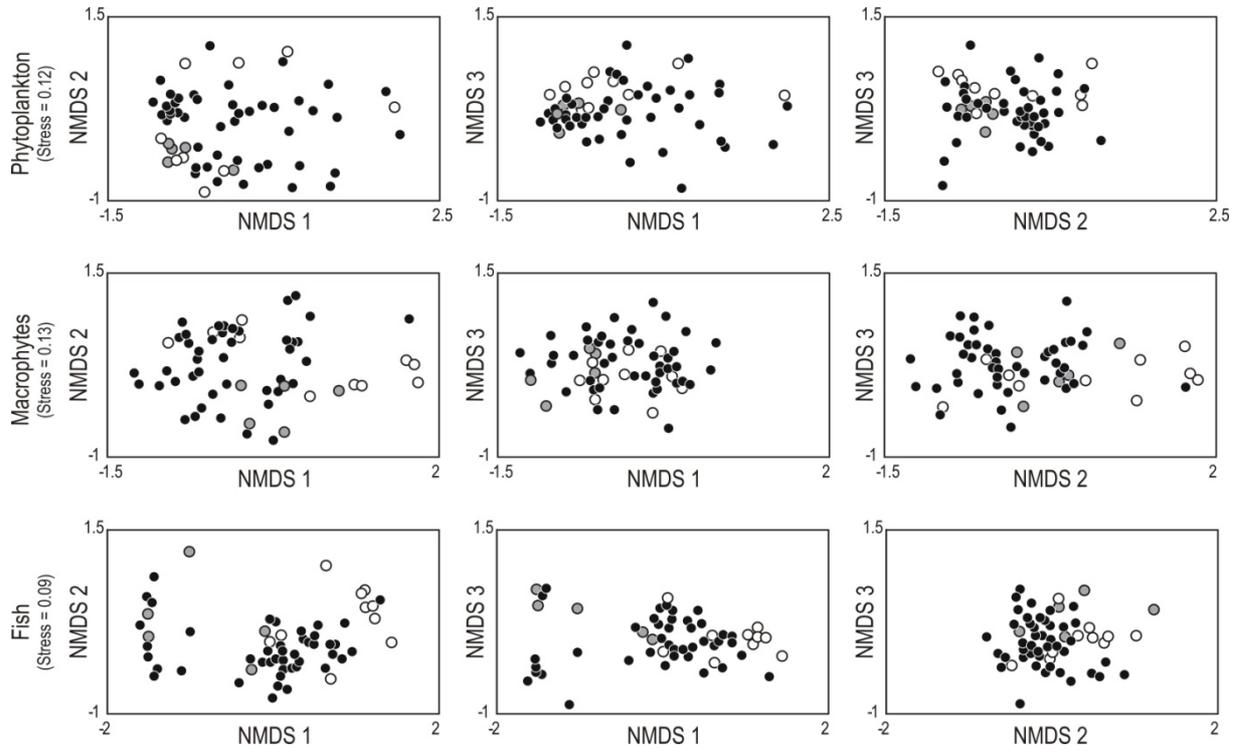
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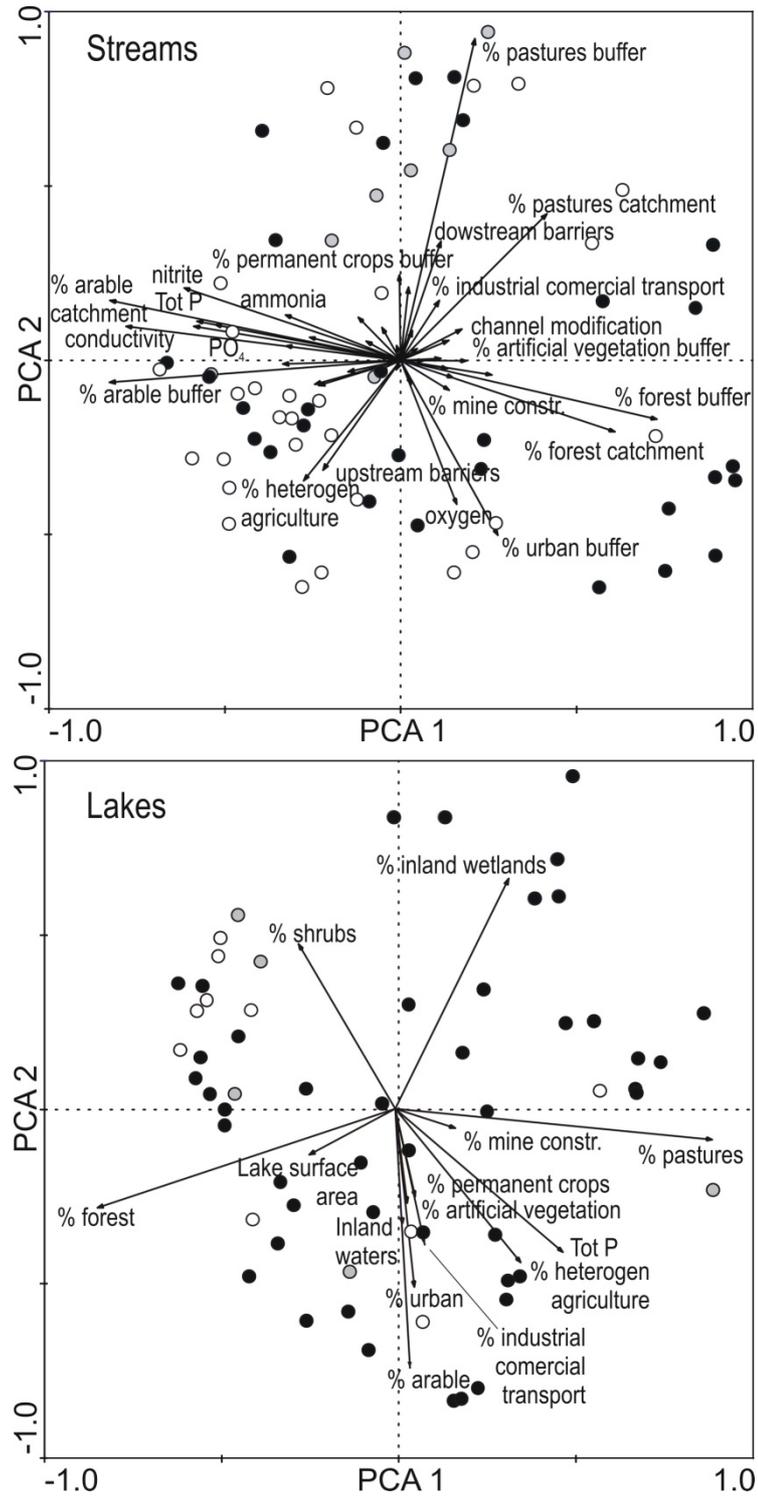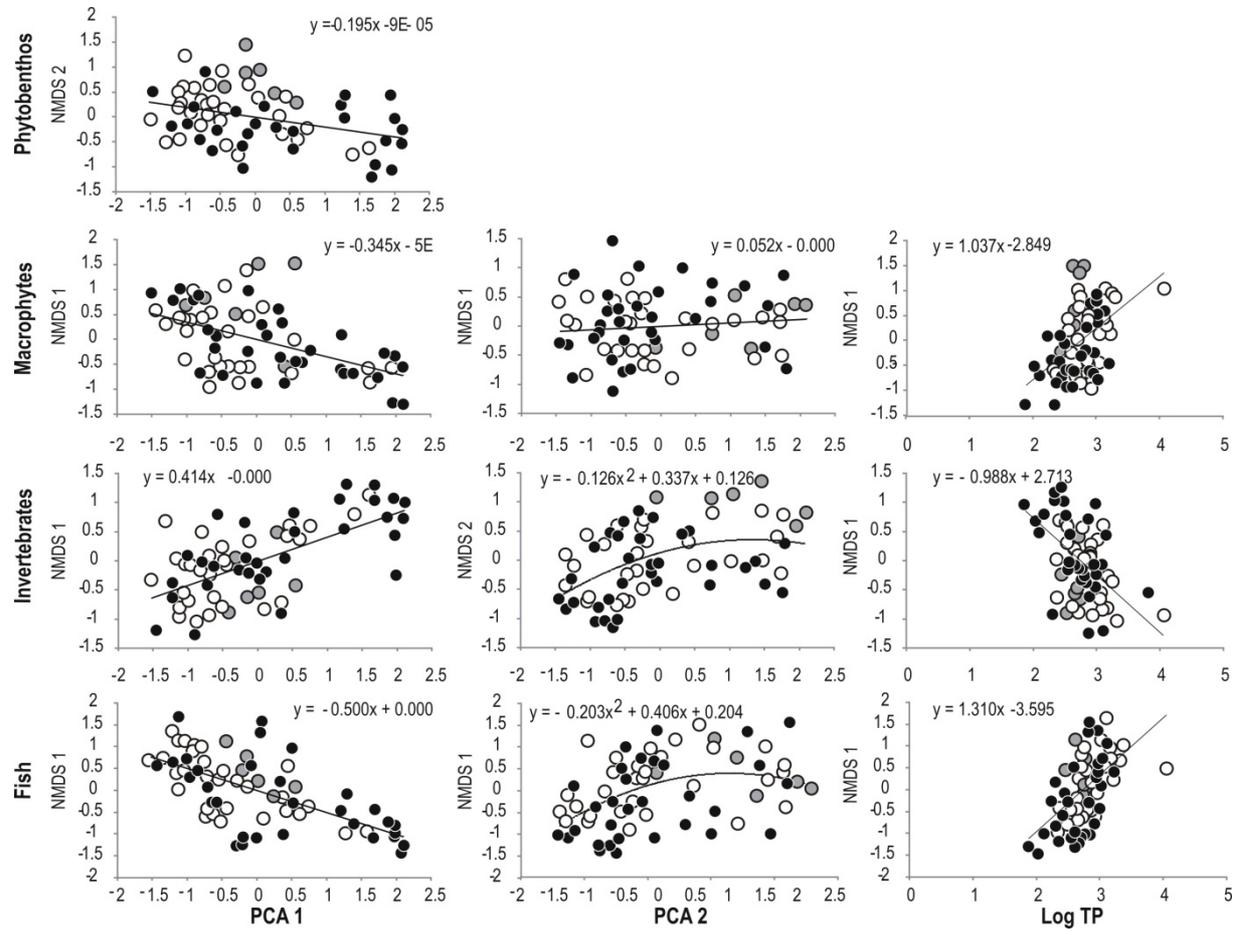
Figure 6