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# Hierarchical response of littoral macroinvertebrates to altered hydromorphology and eutrophication

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## Abstract

The composition of littoral macroinvertebrate communities in lakes is governed by multiple natural and anthropogenic environmental influences interacting at different spatial scales. Since ecological assessment methods using littoral macroinvertebrates should respond specifically to a single stressor, knowledge on the unique effects of a given stressor is necessary. To effectively disentangle the effects of hydromorphology and trophic state requires analysing macroinvertebrate communities at lake sites with the full range of both stressors. We used a dataset of 98 lakes encompassing the entire gradient of geographical locations, lake types, hydromorphological degradation and trophic states in Central European lakes. We studied the unique and joint effects of hydromorphology and trophic state on macroinvertebrate richness, community composition and the Littoral Invertebrate Multimetric Index based on Composite Sampling (LIMCO). Variation partitioning analyses were conducted to test the importance of hydromorphology relative to trophic state across and within hydromorphological states (natural shorelines, hard and soft shore modifications) and trophic states (oligotrophic to hypertrophic states). At natural, hard and soft modification sites, hydromorphology explained 10, 16 and 19 %, respectively, of the average unique variation of diversity, community composition and the LIMCO index, whereas trophic state explained on

average 2, 3 and 3 %, respectively. Similarly, in low, medium and high trophic state lakes, hydromorphology explained 10, 15 and 7 %, respectively, of the average unique variation of diversity, community composition and the LIMCO index, whereas trophic state explained on average 0.3, 3 and 6 %, respectively. Our results demonstrate that littoral hydromorphology was a more important driver of macroinvertebrate diversity, community composition and LIMCO than trophic state across hydromorphological states and trophic states. This indicates that multiple stressors in lakes act hierarchically on littoral macroinvertebrate communities and that the hydromorphological degradation of littoral zones is the primary driver for altered communities.

## 1. Introduction

The diversity and composition of benthic macroinvertebrate communities in lakes is governed by a variety of environmental factors interacting at several spatial scales (Heino, 2000; Johnson and Goedkoop, 2002; McGoff et al., 2013b). Under natural conditions, benthic communities are shaped by littoral hydromorphology, trophic state, lake morphometry, catchment geology and biogeography (Johnson and Goedkoop, 2002; White and Irvine, 2003; Donohue et al., 2009). In the upper littoral zone, the diversity and complexity of habitats represents a major governing factor for benthic macroinvertebrate communities (Strayer and Findlay, 2010; Brauns et al., 2011; Pätzig et al., 2015). Littoral hydromorphology interacts with wind exposure, as fine sediment particles and fine particulate organic matter (FPOM) are resuspended at wind-exposed shorelines and accumulate either at wind sheltered shorelines or deeper littoral areas (Bloesch, 1995; Cyr, 1998). The increased availability of nutrients derived from autochthonous or allochthonous sources, combined with the high availability of light and substrates can result in an intense benthic primary production (Vadeboncoeur et al., 2002; Ask et al., 2009; Cantonati and Lowe, 2014).

However, natural interactions of environmental drivers are often superimposed by impacts associated with human activities (Brauns et al., 2011; Pilotto et al., 2015; Siling and Urbanic, 2016). Since about half a century ago, nutrient inputs and resulting eutrophication have been recognized to represent a strong impact on lake ecosystems at the global scale (Vollenweider and Kerekes, 1982; Schindler, 2006; Smith et al., 2006; Ansari and Singh Gill, 2014). Thus, considerable efforts have been made to reduce nutrient loadings from point sources (Schindler, 2006; Ansari and Singh Gill, 2014). In spite of these efforts, surface run-off from agricultural and urban areas still constitutes a significant driver of eutrophication and its adverse ecological effects (Carpenter et al., 1998; Schindler, 2006).

Recently, human shoreline development has been recognised as a significant threat to the ecological integrity of lakes through the simplification of the natural structural heterogeneity of littoral zones (Ostendorp et al., 2004; Brauns et al., 2007b; Verdonschot et al., 2013). This recognition has led to the development of approaches to assess the hydromorphological status of lake shores based on littoral macroinvertebrate communities (Miler et al., 2013, 2015c; Urbanic, 2014). However, contemporary assessment methods for aquatic ecosystems are faced with the fact that human impacts occur simultaneously (Hecky et al., 2010; Johnson and Ringler, 2014; Noges et al., 2016). A recent meta-analysis of river, lake, transitional/coastal water and groundwater sites found that more than 40% of the analysed studies encountered combinations of two stressors (Noges et al., 2016). Of the analysed multi-stress situations, combined hydrological and nutrient stress was dominant and occurred in 53% of the rivers and 27% of the lakes (Noges et al., 2016). Multiple stressors pose significant challenges for ecological assessments since they should attribute an ecological status to a single driver even if multiple interacting drivers are present. Stressors in lakes have been previously demonstrated to act in a hierarchical manner: Johnson et al. (2018) ranked the effects of the stressors acidity, agriculture, forestry, urbanization and invasive species on littoral macroinvertebrate assemblages in order of decreasing influence, after accounting for covariance with natural factors. The first step to disentangle the effects of multiple interacting drivers is to test for the nature of the interaction of stressors, i.e. synergistic or antagonistic interactions. This requires knowledge on the relative importance of the different stressors, i.e. a stressor hierarchy, including dominating stressors.

Lotic mesocosm experiments have shown interacting effects of multiple stressors on benthic macroinvertebrates (Matthaei et al., 2010; Elbrecht et al., 2016; Beermann et al., 2018). Nutrient enrichment increased total macroinvertebrate abundances, whereas sediment and flow reduction negatively affected total macroinvertebrate abundances (Matthaei et al., 2010). Mostly additive effects on macroinvertebrate taxa were found by Elbrecht et al. (2016). Sediment addition negatively affected the abundances and richness of disturbance sensitive taxonomic groups, whereas decreased current velocity reduced several disturbance sensitive taxa metrics, but increased the abundances of some more common/disturbance tolerant taxonomic groups (Elbrecht et al., 2016).

In lentic ecosystems, hydromorphological degradation through shoreline development often occurs in lakes that are also subject to eutrophication (Brauns et al., 2007a; Latinopoulos et al., 2016). Contrary to stream ecosystems, only few studies have attempted to quantitatively disentangle the interacting effects of hydromorphological alteration and eutrophication on littoral benthic macroinvertebrate communities in lakes. Pilotto et al. (2015) studied the macroinvertebrate community composition in 14 Italian lakes and demonstrated that the effects of hydromorphological alterations were 2.5 times higher than the effects of eutrophication. The study also showed that lake type (i.e. subalpine and volcanic lakes) had a substantial impact on the community composition aside from stressor effects. Hence, sampling designs are required where the biological response variable is recorded in different lake types along the complete gradient of a given stressor while keeping the other stressor(s) constant.

Such an analysis could provide valuable information at which scales environmental processes predominantly structure littoral macroinvertebrate communities and how these compare between lotic and lentic aquatic ecosystems. Despite the well-known importance of local hydromorphological and catchment-scale trophic influences on benthic macroinvertebrate communities in lake littoral zones (Johnson and Goedkopp, 2002; Jurca et al., 2012; McGoff et al., 2013b), how these environmental variables interact with each other remains unknown. The ecological importance of lake littoral zones at the interface between terrestrial and aquatic food webs and nutrient cycles and the significant role of zoobenthos in benthic-pelagic coupling (Wetzel, 2001; Vadeboncoeur et al., 2002; Francis and Schindler, 2009; Strayer and Findlay, 2010) further warrant the study of hydromorphology and trophic state as environmental factors influencing littoral macroinvertebrate community composition and diversity.

From an ecological assessment perspective, distinguishing between the effects of hydromorphology and eutrophication is necessary in order to quantitatively and precisely analyse stressor-response relationships and to develop statistically robust assessment tools (Johnson et al., 2018). The development of EU WFD compliant ecological assessment indices requires the definition of a stressor gradient, from unimpacted (reference) sites to heavily degraded (poor) sites (Hering et al., 2006, 2011; Ofenböck et al., 2004). This is necessary to properly calibrate biotic assessment indices against the stressor gradient (Hering et al., 2006, 2011; Miler et al., 2013, 2015c). The frequent co-occurrence of both hydromorphological and eutrophication stressors in lakes (Noges et al., 2016; Poikane et al., 2016) necessitates distinguishing the effects of both on littoral macroinvertebrate communities for assessment purposes. Furthermore, stressor specific assessments are vital to ensure targeted restoration measures to improve the ecological status of lake littoral zones. For example, measurably improving the ecological condition has been formulated as one of the five criteria for successful river restoration (Palmer et al., 2005). This in turn requires the selection of appropriate ecological indicators to measure the specific types of stressors causing impaired ecological conditions (Palmer et al., 2005). Targeted restoration measures specific to the diagnosed stressors affecting an impaired ecosystem should be applied to improve its ecological condition (Palmer et al., 2005, 2010).

Hence, we quantified the interacting influences of trophic state and hydromorphology on littoral macroinvertebrate communities from 98 lakes spanning the entire gradient of geographical locations, lake types, hydromorphological states as well as trophic states characteristic for Central European lakes. We used variation partitioning analyses to test if the hydromorphology of the littoral zone represents a more important environmental factor determining benthic macroinvertebrate diversity, community composition and ecological assessment than trophic state i) across different hydromorphological states and across different trophic states, ii) within different hydromorphological states, and iii) within different trophic states.

# 2. Methods

## 2.1 Study area and sampling

We sampled 98 natural lakes in Germany (Fig. 1) covering all lake types from alpine to lowland lakes. Concomitantly, the studied lakes represent ecoregions defined by the EU WFD, i.e. the Central Plains, Central highlands and Alps ecoregions (European Commission, 2000). The data set consisted of the results of biological monitoring performed for the implementation of the EU WFD in Germany, using a standardized national sampling protocol (Brauns et al., 2007a, 2007b; Schreiber and Brauns, 2010) during spring (April to June) from 2007 to 2014. Within each lake, the total number of sampling sites was determined based on the shore length in km by the formula:

$$N_{sites} = 4 + \sqrt{shorelength} \quad \textbf{(1)}$$

Subsequently, for each lake the length of the whole shoreline was categorized into three hydromorphological states, i.e. natural, soft modification (recreational beaches) and hard modification shorelines (rip-rap, retaining walls, docks and marinas). The number of sampling sites for each hydromorphological state in a lake was calculated by multiplying the share of the respective hydromorphological state's length on the whole shoreline length with the total number of sampling sites that was calculated according to formula (1). Sampling sites for a specific hydromorphological state were only determined if the hydromorphological state's length contributed to more than 10 % of the whole shoreline length. One sampling site comprised a maximum of 50 m (recreational beaches, hard bank engineering, docks and marinas) or 100 m (natural shores) of shore length and encompassed the upper littoral zone down to 1.2 m water depth.

At each site, the percentage contribution of all littoral habitats was estimated, i.e. sand (defined as substrates < 20 mm grain diameter, i.e. ≤ medium pebbles according to Wentworth, 1922; Poppe, 2003), fine particulate organic matter (FPOM), stones (defined as substrates ≥ 20 mm grain diameter, i.e. ≥ coarse pebbles according to Wentworth, 1922; Poppe, 2003; incl. rip-rap), cliffs (natural vertical rock surfaces), submerged tree roots, coarse woody debris (CWD), emergent macrophytes, submerged macrophytes, docks and marinas and retaining walls. At each site, a total area of 1 $m^2$ was sampled and the sampling area of each habitat was calculated as a share of the total area of 1 $m^2$ based on the percentage contribution of littoral habitats. Each habitat was sampled with a minimum area of 0.1 $m^2$.



Macroinvertebrate sampling generally followed Schreiber and Brauns (2010). Briefly, samples were taken using a dip net (500 µm mesh size, rectangular opening with the dimensions 0.25 m by 0.25 m). Macroinvertebrates were brushed from stones as well as from coarse woody debris (CWD) into a dip net. Subsequently, the dimensions and surface area of the sampled stones and CWD were measured, i.e. length x height x width (stones) and diameter and length (CWD). Sand and FPOM were each sampled by dragging the dip net along the surface of the bottom substrates and collecting approximately the uppermost 5 cm of the substrate in the dip net. Sand and FPOM were subsequently sieved 20 times for macroinvertebrate taxa floating up due to their lower densities compared to the sediment. Within emergent macrophyte stands the bottom substrates located c. 1 m to 2 m from the open water into the emergent macrophyte stand were sampled. In addition, 20 emergent macrophyte stems were cut and collected from as close to the substrate surface as possible. Macroinvertebrates from larger vertical surfaces, e.g. from cliffs, retaining walls and docks and marinas, were collected with a scraper. Habitat samples from each site were stored separately and macroinvertebrates were identified in the laboratory to species level, whenever possible, except Diptera (family) and Oligochaeta (order). Generally, samples were completely processed and all macroinvertebrates sorted. Subsamples (1/2 to 1/6 of the sample volume) were only taken, if high volumes of inorganic and/or organic material were encountered within a sample. Macroinvertebrate densities of each site were calculated as individuals $m^{-2}$.

## 2.2 Environmental variables



Environmental variables were recorded in order to characterize hydromorphology, trophic state, riparian land use, lake morphometry and geographical location (Table 1). The variable class hydromorphology was parameterized by the percentages of habitat types, by the number of habitats and by the Shannon Wiener diversity of habitats (Table 1). Trophic state was parameterized by the seasonal mean total phosphorus content ($TP_{seas}$) and seasonal mean secchi depth ($SD_{seas}$) that were measured and calculated according to Mischke et al. (2009) and Riedmüller et al. (2013) (Table 1). Briefly, secchi depth was measured and water samples for TP were collected from a sampling site located at the maximum water depth of each lake. Water samples taken from the euphotic or epilimnic zone were collected on a minimum of three separate sampling occasions during the vegetation period from March to October. The trophic state of the studied lakes was classified according to Vollenweider and Kerekes (1982).

Riparian land use was quantified based on the land use 15 m landwards from the shore as the land use index:

$$\% \text{ low impact land use} + 2 \times \% \text{ high impact land use} \quad (2)$$

where low impact land use includes extensively used recreational beaches, orchards, parks and gardens, while high impact land use includes recreational beaches, camping and caravans, residential development, roads and railways, harbours, hard modification, docks and marinas, channels, clearings, tilled land and grassland (grazing) (Table 1). Lake morphometry was parameterized by surface area, mean depth and by lake type, i.e. prealpine/alpine, lowland and riverine lakes (Table 1). Geographical location was quantified via latitude and longitude (Table 1).

## 2.3 Biological response variables

We used the log10(x)-transformed number of taxa at each sampling site as a measure of diversity. Macroinvertebrate community composition, i.e. more specifically the compositional dissimilarity of macroinvertebrate communities between sites, was quantified as the Bray-Curtis dissimilarities of fourth root transformed macroinvertebrate taxa densities. We used the 2/pi arcsine-square root transformed multimetric assessment index LIMCO (Littoral Invertebrate Multimetric Index based on Composite Sampling, Miler et al., 2013) for our analyses, as it successfully indicates hydromorphological alterations across European ecoregions (Miler et al., 2013, 2015b, 2015c; Lorenz et al., 2017). LIMCO is composed of three metric types reflecting several aspects of the macroinvertebrate community that commonly respond to anthropogenic stressors, i.e. i) diversity, ii) disturbance-sensitive taxa and iii) abundance, taxonomic and functional composition (Hering et al., 2006, 2011). LIMCO was calculated according to Miler et al. (2013) as the unweighted mean value of the four metrics Margalef diversity, % abundance classes of Gatherers & Collectors, % abundance classes of Chironomidae and no. of EPTCBO (Ephemeroptera, Plecoptera, Trichoptera, Coleoptera, Bivalvia and Odonata) taxa. All metrics were normalized to values from 0 (worst ecological condition) to 1 (best ecological condition).

## 2.4 Statistical analyses

First, in many lakes, several sites exhibited natural hydromorphology, hard modification or soft modification and we thus averaged environmental and biological variables for each lake and hydromorphological state combination. Four data sets stratified by hydromorphological states were created and used for subsequent statistical analyses, encompassing i) sites from all three hydromorphological states (n = 176), ii) natural hydromorphology sites (n = 98), iii) hard modification sites (n = 55), and iv) soft modification sites (n = 23).

Second, in order to represent each lake by a single value in the statistical analyses of trophic states, we averaged all quantitative environmental and biological response variables for each lake (since each lake belongs to only one of the three trophic states, i.e. low (oligotrophic and mesotrophic), medium (eutrophic) and high (hypertrophic and polytrophic) trophic state). Consequently, four data sets stratified by trophic states were created and used for the statistical analyses, encompassing i) lakes from all three trophic states (n = 98), ii) low trophic state lakes (n = 41), iii) medium trophic state lakes (n = 38), and iv) high trophic state lakes (n = 19)



We applied a classical variation partitioning approach to disentangle the effects of ‘Hydromorphology’, ‘Riparian land use’, ‘Trophic state’, ‘Lake morphometry’ and ‘Geographical location’ using the varpart function in R (R Development Core Team, 2015; Oksanen et al., 2016). Variation partitioning has been frequently used to assess the joint/unique variation in the composition of plant and animal communities explained by environmental factors (Liu, 1997; Legendre, 2008; Göthe et al., 2013). Partial linear regressions with LIMCO as well as the number of taxa as dependent variables and 15 variables of the classes ‘Hydromorphology’, ‘Riparian land use’, ‘Trophic state’, ‘Lake morphometry’ and ‘Geographical location’ as independent variables were conducted (Table 1). For Bray-Curtis distances, we used distance based redundancy (db-RDA) analyses instead of linear models.

Starting with ‘Hydromorphology’ as the variable class of interest, we first calculated a linear model that included only the ‘Hydromorphology’ variables Sand (%), Stones (%), Xylal (%), Macrophytes (%), Fortification (%), No. habitats and Habitat diversity as independent variables. Then, we calculated a linear model that included the remaining eight variables not belonging to ‘Hydromorphology’ (Table 1). Subsequently, a variation partitioning analysis was conducted based on both linear models. The analyses resulted in five components of variation: (1) The variation of 'Hydromorphology' variables after accounting for variation of 'Riparian land use', 'Trophic state', 'Lake morphometry' and 'Geographical location' variables (unique variation), (2) the variation that is shared between 'Hydromorphology' variables and 'Riparian land use', 'Trophic state', 'Lake morphometry' and 'Geographical location' variables (shared variation), (3) the unique variation explained by 'Riparian land use', 'Trophic state', 'Lake morphometry' and 'Geographical location' variables (remaining variation), (4) the sum of unique, shared and remaining explained variation (total explained variation) and (5) the unexplained variation, i.e. 100 % - total explained variation (unexplained variation). The variation partitioning procedure was then also conducted with 'Riparian land use', 'Trophic state', 'Lake morphometry' and 'Geographical location' each specified subsequently as the variable class of interest.

This process was repeated with the four data sets stratified by hydromorphological states (across hydromorphological states, natural hydromorphology, hard modification, soft modification) and the four data sets stratified by trophic state (across trophic states, low trophic state, medium trophic state, high trophic state). We then contrasted the variation of the four levels of hydromorphological degradation with the four levels of eutrophication: 'across hydromorphological states – across trophic states', 'natural hydromorphology – low trophic state', 'hard shore modification – medium trophic state' and 'soft shore modification – high trophic state'.

## 3. Results

When all hydromorphological states were considered together, hydromorphology explained a 3.7, 37 and 6.4 times higher amount of unique variation of macroinvertebrate community composition, diversity and the LIMCO index, (6.2 %, 13.6 % and 17.4 %, respectively) than trophic state (1.7 %, 0.4 % and 2.7 %, respectively) (Table 2). With all three trophic states being considered together, hydromorphology explained a 5, 10 and 4.3 times higher amount of unique variation of macroinvertebrate community composition, diversity and LIMCO

(7.1 %, 12.3 % and 17.2 %, respectively) than trophic state (1.4 %, 1.2 % and 4 %, respectively) (Table 3).

At natural, undeveloped sites, variation in macroinvertebrate community composition. diversity and LIMCO was 5.4, 14.8 and 3.2 times better explained by hydromorphology (6.8 %, 9.5 % and 14.9 %, respectively) than trophic state (1.2 %, 0.6 % and 4.6 %, respectively) (Table 2). In oligotrophic & mesotrophic lakes, hydromorphology explained 8.2, 0.0 and 0.0 times (trophic state variation of diversity and LIMCO set to zero due to negative values) more unique variation of community composition, diversity and LIMCO (6.8 %, 14.4 % and 8.8 %, respectively) than trophic state (0.8 %, 0.0 % and 0.0 %, respectively) (Table 3).

At shorelines altered by hard modifications, hydromorphology explained 2.6, 6.1 and 2.7 times more unique variation of community composition, diversity and LIMCO (8.8 %, 18.2 % and 21.1 %, respectively) than trophic state (3.4 %, 3.0 % and 7.9 %, respectively) (Table 2). In eutrophic lakes, hydromorphology macroinvertebrate community composition, diversity and LIMCO (10.2 %, 15.7 % and 19.9 %, respectively) 4.3, 5.9 and 5.9 times better than trophic state (2.4 %, 2.7 % and 3.4 %, respectively) (Table 3).

At shorelines developed by soft modifications, hydromorphology explained macroinvertebrate community composition and LIMCO (17.6 % and 26.3 %, respectively) 6.8 and 0.0 times (trophic state variation of LIMCO set to zero due to negative values) better than trophic state (2.6 % and 0.0 %, respectively) (Table 2). However, trophic state explained 1.1 times more unique variation of diversity (12.4 %) than hydromorphology (11.6 %) (Table 2). In hypertrophic & polytrophic lakes, variation in macroinvertebrate diversity was 2.8 times better explained by hydromorphology (15.1 %) than trophic state (5.4 %) (Table 3). However, trophic state explained 3.0 times more unique variation of community composition (13.2 %) than hydromorphology (4.4 %) (Table 3). No unique variation of LIMCO was explained (set to zero due to negative values) either by hydromorphology or trophic state (Table 3).

The unique variation explained by hydromorphology when the sites are classified by trophic state, was higher than the unique variation explained by trophic state when the sites are classified by hydromorphological states (Fig. 2, Table 4, Appendix Table 1). This was true for all four comparisons ‘across hydromorphological states – across trophic states’, ‘natural hydromorphology – low trophic state’, ‘hard shore modification – medium trophic state’ and ‘soft modification – high trophic state’ (Fig. 2, Table 4, Appendix Table 1).

# 4. Discussion

## 4.1 Relative effects of hydromorphology and trophic state

Disentangling the unique effects of multiple environmental drivers of littoral macroinvertebrate communities and ranking their importance remains an important aspect of lake ecology. Across hydromorphological states as well as across trophic states, hydromorphology explained more unique variation than trophic state, irrespective of whether community composition (Bray-Curtis distances), diversity or LIMCO was used (Fig. 2, Table 2, 3 and 4, Appendix Table 1). Previous studies, with an environmental gradient of hydromorphology and trophic state comparable to our study, have also shown hydromorphology to have a stronger effect on macroinvertebrate community composition than trophic state (Brauns et al., 2007b; Jurca et al., 2012; McGoff and Sandin, 2012; McGoff et al., 2013b; Pilotto et al., 2015). However, these analyses included the effects of covariation between the co-occurring stressors hydromorphological degradation and eutrophication on littoral macroinvertebrate communities, making an unequivocal ranking of the two environmental stressors impossible. In our study, we demonstrated a hierarchical stressor response of macroinvertebrate communities, more specifically a higher importance of hydromorphology for littoral macroinvertebrates based on the unique variations of hydromorphology and trophic state disentangled from their shared variation.

## 4.2 Environmental conditions explaining the influence of hydromorphology and trophic state on littoral macroinvertebrates

When comparing the variation explained by hydromorphology within each trophic state with those from trophic state within each hydromorphological state, hydromorphology explained more variation of macroinvertebrate community composition, diversity and LIMCO (Fig. 2, Table 4, Appendix Table 1). This result is surprising as we expected trophic state to be more important than hydromorphology given the large range of TP in our study (7-788 µg $L^{-1}$, 24 % hypertrophic lakes), n = 98 lakes). Previous studies found substantial effects of trophic state on macroinvertebrate communities (Tolonen et al., 2001; Brauns et al., 2007a; Donohue et al., 2009; Tolonen and Hämäläinen, 2010) with the TP in these studies ranging from 4-23 µg $l^{-1}$ (Tolonen et al., 2001), 8-19 µg $l^{-1}$ (Tolonen and Hämäläinen, 2010) and 1-80 µg $l^{-1}$ (Donohue et al., 2009; 4 % hypertrophic lakes, n = 25 lakes) to 13-366 µg $l^{-1}$ (Brauns et al., 2007a; 29 % hypertrophic lakes, n = 7 lakes). A potential reason for the different outcome of our study could be that these studies focused on hydromorphologically undisturbed sites, while we analysed a gradient of hydromorphological degradation, ranging from natural hydromorphology to soft and hard modification sites (Table 1, Appendix Table 2). Furthermore, Tolonen et al. (2001), Brauns et al. (2007a), Donohue et al. (2009) and Tolonen and Hämäläinen (2010) did not distinguish between the unique and shared variation explained by trophic state, whereas in this study we specifically compared the unique variation explained by trophic state at constant hydromorphology relative to the unique variation explained by hydromorphology at constant trophic state.

Furthermore, previous studies focused on the effects of trophic state on macroinvertebrate community composition nested within mesohabitats (Tolonen et al., 2001; Brauns et al., 2007a; Donohue et al., 2009; Tolonen and Hämäläinen, 2010). In our study, we were less interested in capturing the diversity and taxonomic composition of macroinvertebrate taxa in specific mesohabitats. Instead, using composite samples as in our study, we were able to assess the availability and relative composition of littoral habitats at a given site and their macroinvertebrate fauna and hence to appropriately evaluate the effect of overall hydromorphological degradation on littoral macroinvertebrate community composition.

Ecological processes may be responsible for the increase in the influence of trophic state on macroinvertebrate communities at hard and soft modification sites compared to natural hydromorphology sites. At both hydromorphological states, the number of taxa was more strongly negatively correlated with $TP_{seas}$ compared to natural shores, indicating a wider range of the number of taxa values at hard and soft modification sites (Spearman-Rank; across hydromorphological states: $\rho = -0.35$, $p < 0.001$; hard modification: $\rho = -0.39$, $p = 0.003$; soft modification: $\rho = -0.70$, $p < 0.001$; natural hydromorphology: $\rho = -0.26$, $p = 0.008$). With increasing eutrophication and thus productivity, specialized, disturbance-sensitive taxa will disappear and generalist, disturbance-tolerant taxa will increase in densities, potentially resulting in a decrease of the overall number of taxa at a site (Brodersen et al., 1998; Brauns et al., 2007a; Tolonen and Hämäläinen, 2010). These results could potentially explain the larger effect of trophic state on the number of taxa, macroinvertebrate community composition and the LIMCO index (which includes the metric Margalef diversity as a measure of taxonomic diversity).



In addition, soft and hard modification sites were characterized by reduced habitat diversity (Appendix Table 2). Hereby, uniform sandy substrates were the dominant littoral habitat, especially at soft modification sites (Appendix Table 2). The littoral macroinvertebrate community composition of sandy substrates has been shown to be significantly correlated with lake TP concentrations (see Brauns et al., 2007a for North-German lowland lakes). These patterns in habitat diversity and occurrence could be responsible for the higher amount of unique variation explained by trophic state at hard and soft modification sites compared to natural hydromorphology sites.

The unique variation explained by trophic state across hydromorphological states, natural hydromorphology and hard modification sites was comparatively low (Table 2). However, these values were still higher than the zero unique variation of LIMCO explained by hydromorphology in high trophic state lakes (Table 3, downward arrows for LIMCO in Table 4). In lakes with high trophic states, in contrast to unique variation explained by hydromorphology, the shared and remaining variation was comparatively high (Table 3). This suggests a strong influence of environmental variables other than hydromorphology, more specifically riparian land use and trophic state, since the land use index and total phosphorus (µg $l^{-1}$) showed higher mean values in high trophic state compared to medium and low trophic state lakes (Table 1; Appendix Table 2).

## 4.3 Influence of hydromorphological degradation and eutrophication on lake littoral and stream macroinvertebrate communities

The influence of multiple stressors on benthic macroinvertebrate communities for ecological assessment, conservation and recovery processes has so far been more intensively studied in streams, compared to the comparatively scarce number of publications concerning lake ecosystems (Verdonschot et al., 2013; Poikane et al., 2015; Noges et al., 2016). Recent studies analysing stream macroinvertebrate data confirm the major importance of hydromorphological stressors relative to nutrient enrichment (Noges et al., 2016; Gieswein et al., 2017; Villeneuve et al., 2018). According to Noges et al. (2016) potential explanations for this are (1) the generally high ratio of bottom substrates to water volume in a stream cross-section and (2) the dilution of nutrients with water flow, thereby reducing their effect at a specific site.

Furthermore, experimental studies in stream ecosystems also identified nutrient enrichment and sedimentation/flow reduction as the two major trophic and hydromorphological stressors impacting macroinvertebrate communities, respectively (Matthaei et al., 2010; Elbrecht et al., 2016; Beermann et al., 2018; Davis et al., 2018). The results from mesocosm experiments showed hydromorphological stressors to affect total abundances, abundances of disturbance sensitive taxa and/or taxonomic richness of benthic stream macroinvertebrate communities considerably more than nutrient enrichment (Matthaei et al., 2010; Elbrecht et al., 2016; Davis et al., 2018).

The relative effects of multiple stressors also depend on the geographical scale of the studied stream ecosystem variables (Sundermann et al., 2013; Leps et al., 2015; Aschonitis et al., 2016). Local physico-chemical water quality variables as a result of catchment-scale processes were primarily responsible in shaping stream macroinvertebrate communities across Germany, overriding the considerably weaker effects of riparian land-use at the local scale (Leps et al., 2015). Catchment-scale land use and water quality were significantly more important than local hydromorphological degradation in highland rivers in Central Germany (Sundermann et al., 2013). Aschonitis et al. (2016) described a strong effect of ecoregion in lotic systems of Northern Italy (including the Po river watershed), with considerably lesser effects of hydromorphology and water quality on macroinvertebrate communities. Considering such scale-dependent effects could explain the outcomes of studies that conclude water quality to be a more significant factor than local hydromorphological degradation in determining stream macroinvertebrate community composition.



Furthermore, we could expect, with regards to the explanations put forward by Noges et al. (2016) above, in lower river reaches decreasing flow velocities and a higher water volume per stream cross-section compared to upper and middle reaches (Wetzel, 2001). This could be a potential explanation for the higher importance of water quality/nutrient stressors relative to hydromorphological stressors on macroinvertebrate communities observed in the Danube river (Rico et al., 2016), the Ebro river watershed in Spain (Herrero et al., 2018) and the Luanhe River in China (Shi et al., 2019). Urbanic et al. (2020) described a dominance of hydromorphological stressors on macroinvertebrate communities, but almost equal effects of water quality (and land use) in five large South-eastern European rivers.

The outcomes of our study suggest that overall local scale hydromorphological effects in lakes are more important than catchment scale trophic effects on macroinvertebrate communities. This is at first glance in contrast to the findings of Sundermann et al. (2013) and Leps et al. (2015) for stream macroinvertebrate communities. Generally low benthal-to-pelagial ratios of lakes together with generally high retention times would indicate a higher importance of nutrient stress compared to hydromorphology for the overall lake macroinvertebrate fauna according to Noges et al. (2016). However, hydromorphological stress has a high importance for eulittoral macroinvertebrate communities close to shorelines (Strayer and Findlay, 2010; Noges et al., 2016), which is confirmed by the results of our study. Potential reasons for this could be the commonly found higher physical habitat complexity (macrophytes, coarse woody debris, stones) and shallower water depth in the littoral zone and the presence of a land-water ecotone with riparian vegetation (Brodersen et al., 1998; Wetzel, 2001; Ostendorp et al., 2004; Strayer and Findlay, 2010), resulting in high benthal-to-pelagial ratios close to the shore comparable to stream ecosystems, in which hydromorphology has been shown to affect benthic macroinvertebrates more than nutrient enrichment (Noges et al., 2016).

Overall, the total amount of explained variation in our study ranged from 9 % to 71 % for hydromorphology and from 1 % to 71 % for trophic state. This is comparable to other studies that analysed the influence of environmental variables on littoral macroinvertebrate communities (Pinel-Alloul et al., 1996; Trigal et al., 2007; Pilotto et al., 2015; Siling and Urbanic, 2016). Other important environmental drivers may explain the residual variation, for example fish predation (Okun and Mehner, 2005), wind exposition (Scheifhacken et al., 2007), water-level fluctuations (Baumgärtner et al., 2008) and resource availability (Brauns et al., 2011). Combinations of these often difficult to quantify environmental drivers, potentially acting together with those analysed in our study (e.g. hydromorphology and trophic state), could be important in explaining macroinvertebrate community composition, diversity and LIMCO. This does however not diminish the relevance of our conclusions with respect to the relative importance of hydromorphology and trophic state.

Our results are valid for other Central European lakes given that the studied lakes encompass the most important lake types found there. For example, lowland and riverine lakes of Western Poland and Denmark contain macroinvertebrate communities similar to the lakes in our study (Miler et al., 2013, 2015a; Porst et al., 2019; Solimini et al., 2014). Concerning prealpine/alpine lakes, which are located in the Central highlands and Alps ecoregions, we covered a smaller data set (15 lakes). However, alpine lakes in Slovenia are comparable in their morphological and trophic characteristics as well as in their benthic macroinvertebrate community composition and biotic assessment method characteristics to prealpine/alpine lakes in our study (Urbanic et al., 2012; Peterlin and Urbanic, 2013; Solimini et al., 2014; Siling and Urbanic, 2016). The applicability of our results to lakes found in other ecoregions determined by the EU WFD (European Commission, 2000), e.g. Italy, Corsica and Malta (ecoregion 3), Ireland and Northern Ireland (ecoregion 17), Great Britain (ecoregion 18), Borealic uplands (ecoregion 20) and Fenno-Scandian Shield (ecoregion 22), remains restricted given the differences in macroinvertebrate communities (McGoff et al., 2013a; Miler et al., 2013; Porst et al., 2019). In conclusion, littoral macroinvertebrates specifically indicate the ecological status of lakes affected by hydromorphological alterations of lake shores even if trophic state covaries with hydromorphological impacts. This finding demonstrates that littoral macroinvertebrates fulfil the requirements of the EU WFD by responding in a stressor-specific manner. Moreover, this facilitates the definition of targeted restoration measures to improve the ecologic status of so far degraded lake ecosystems.



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# 6. References


Ansari, A.A., Singh Gill, S., 2014. Eutrophication: Causes, Consequences and Control. Springer Netherlands, Dordrecht. https://doi.org/10.1007/978-94-007-7814-6

Aschonitis, V.G., Feld, C.K., Castaldelli, G., Turin, P., Visonà, E., Fano, E.A., 2016. Environmental stressor gradients hierarchically regulate macrozoobenthic community turnover in lotic systems of Northern Italy. Hydrobiologia 765, 131–147. https://doi.org/10.1007/s10750-015-2407-x

Ask, J., Karlsson, J., Persson, L., Ask, P., Byström, P., Jansson, M., 2009. Whole-lake estimates of carbon flux through algae and bacteria in benthic and pelagic habitats of clear-water lakes. Ecology 90, 1923–1932. https://doi.org/10.1890/07-1855.1

Beermann, A.J., Elbrecht, V., Karnatz, S., Ma, L., Matthaei, C.D., Piggott, J.J., Leese, F., 2018. Multiple-stressor effects on stream macroinvertebrate communities: A mesocosm experiment manipulating salinity, fine sediment and flow velocity. Sci. Total Environ. 610–611, 961–971. https://doi.org/10.1016/j.scitotenv.2017.08.084

Bloesch, J., 1995. Mechanisms, Measurement and Importance of Sediment Resuspension in Lakes. Mar. Freshw. Res. 46, 295–304. https://doi.org/http://dx.doi.org/10.1071/MF9950295

Brauns, M., Garcia, X.F., Pusch, M.T., Walz, N., 2007a. Eulittoral macroinvertebrate communities of lowland lakes: Discrimination among trophic states. Freshw. Biol. 52, 1022–1032. https://doi.org/10.1111/j.1365-2427.2007.01750.x

Brauns, M., Garcia, X.F., Walz, N., Pusch, M.T., 2007b. Effects of human shoreline development on littoral macroinvertebrates in lowland lakes. J. Appl. Ecol. 44, 1138–1144. https://doi.org/10.1111/j.1365-2664.2007.01376.x

Brauns, M., Gücker, B., Wagner, C., Garcia, X.F., Walz, N., Pusch, M.T., 2011. Human lakeshore development alters the structure and trophic basis of littoral food webs. J. Appl. Ecol. 48, 916–925. https://doi.org/10.1111/j.1365-2664.2011.02007.x

Brodersen, K.P., Dall, P.C., Lindegaard, C., 1998. The fauna in the upper stony littoral of Danish lakes: Macroinvertebrates as trophic indicators. Freshw. Biol. 39, 577–592. https://doi.org/10.1046/j.1365-2427.1998.00298.x

Cantonati, M., Lowe, R.L., 2014. Lake benthic algae: toward an understanding of their ecology. Freshw. Sci. 33, 475–486. https://doi.org/10.1086/676140

Carpenter, S.R., Caraco, N.F., Correll, D.L., Howarth, R.W., Sharpley, A.N., Smith, V.H., 1998. Nonpoint Pollution of Surface Waters with Phosphorus and Nitrogen. Issues Ecol. 4, 1–12. https://doi.org/1092-8987

Cyr, H., 1998. Effects of wave disturbance and substrate slope on sediment characteristics in the littoral zone of small lakes. Can. J. Fish. Aquat. Sci. 55, 967–976. https://doi.org/10.1139/f97-298

Davis, S.J., O hUallachain, D., Mellander, P.-E., Kelly, A.-M., Matthaei, C.D., Piggott, J.J., Kelly-Quinn, M., 2018. Multiple-stressor effects of sediment, phosphorus and nitrogen on stream macroinvertebrate communities. Sci. Total Environ. 637–638, 577–587. https://doi.org/10.1016/j.scitotenv.2018.05.052

Donohue, I., Jackson, A.L., Pusch, M.T., Irvine, K., 2009. Nutrient enrichment homogenizes lake benthic assemblages at local and regional scales. Ecology 90, 3470–3477. https://doi.org/10.1890/09-0415.1

Elbrecht, V., Beermann, A.J., Goessler, G., Neumann, J., Tollrian, R., Wagner, R., Wlecklik, A., Piggott, J.J., Matthaei, C.D., Leese, F., 2016. Multiple-stressor effects on stream invertebrates: a mesocosm experiment manipulating nutrients, fine sediment and flow velocity. Freshw. Biol. 61, 362–375. https://doi.org/10.1111/fwb.12713

European Commission, 2000. Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy. Off. J. Eur. Communities L327, 1–82. https://doi.org/10.1039/ap9842100196

Francis, T.B., Schindler, D.E., 2009. Shoreline urbanization reduces terrestrial insect subsidies to fishes in North American lakes. Oikos 118, 1872–1882. https://doi.org/10.1111/j.1600-0706.2009.17723.x

Gieswein, A., Hering, D., Feld, C.K., 2017. Additive effects prevail: the response of biota to multiple stressors in an intensively monitored watershed. Sci. Total Environ. 593–594, 27–35. https://doi.org/10.1016/j.scitotenv.2017.03.116

Göthe, E., Angeler, D.G., Gottschalk, S., Löfgren, S., Sandin, L., 2013. The Influence of Environmental, Biotic and Spatial Factors on Diatom Metacommunity Structure in Swedish Headwater Streams. PLoS One 8, e72237. https://doi.org/10.1371/journal.pone.0072237

Hecky, R.E., Mugidde, R., Ramlal, P.S., Talbot, M.R., Kling, G.W., 2010. Multiple stressors cause rapid ecosystem change in Lake Victoria. Freshw. Biol. 55, 19–42. https://doi.org/10.1111/j.1365-2427.2009.02374.x

Heino, J., 2000. Lentic macroinvertebrate assemblage structure along gradients in spatial heterogeneity, habitat size and water chemistry. Hydrobiologia 418, 229–242. https://doi.org/10.1023/A:1003969217686

Hering, D., Birk, S., Lyche-Solheim, A., Moe, S.J., Carvalho, L., Borja, A., Hendriksen, P., Krause-Jensen, D., Lauridsen, T.L., Söndergaard, M., Pont, D., Johnson, R.K., Kolada, A., Porst, G., Marba, N., Noges, P., Ott, I., Marques, J.C., Irvine, K., Basset, A., 2011. Guidelines for indicator development. WISER Deliverable 2.2-2.

Hering, D., Feld, C.K., Moog, O., Ofenböck, T., 2006. Cook book for the development of a Multimetric Index for biological condition of aquatic ecosystems: Experiences from the European AQEM and STAR projects and related initiatives. Hydrobiologia 566, 311–324. https://doi.org/10.1007/s10750-006-0087-2

Herrero, A., Gutiérrez-Cánovas, C., Vigiak, O., Lutz, S., Kumar, R., Gampe, D., Huber-García, V., Ludwig, R., Batalla, R., Sabater, S., 2018. Multiple stressor effects on biological quality elements in the Ebro River: Present diagnosis and predicted responses. Sci. Total

Environ. 630, 1608–1618. https://doi.org/10.1016/j.scitotenv.2018.02.032

Johnson, R.K., Goedkoop, W., 2002. Littoral macroinvertebrate communities: Spatial scale and ecological relationships. Freshw. Biol. 47, 1840–1854. https://doi.org/10.1046/j.1365-2427.2002.00932.x

Johnson, R.K., Hallstan, S., Zhao, X., 2018. Disentangling the response of lake littoral invertebrate assemblages to multiple pressures. Ecol. Indic. 85, 1149–1157. https://doi.org/10.1016/j.ecolind.2017.10.075

Johnson, S.L., Ringler, N.H., 2014. The response of fish and macroinvertebrate assemblages to multiple stressors: A comparative analysis of aquatic communities in a perturbed watershed (Onondaga Lake, NY). Ecol. Indic. 41, 198–208. https://doi.org/10.1016/j.ecolind.2014.02.006

Jurca, T., Donohue, L.A., Laketic, D., Radulovic, S., Irvine, K., 2012. Importance of the shoreline diversity features for littoral macroinvertebrate assemblages. Fundam. Appl. Limnol. / Arch. für Hydrobiol. 180, 175–184. https://doi.org/10.1127/1863-9135/2012/0315

Latinopoulos, D., Ntislidou, C., Kagalou, I., 2016. Multipurpose Plans for the Sustainability of the Greek Lakes: Emphasis on Multiple Stressors. Environ. Process. 3, 589–602. https://doi.org/10.1007/s40710-016-0152-4

Legendre, P., 2008. Studying beta diversity: ecological variation partitioning by multiple regression and canonical analysis. J. Plant Ecol. 1, 3–8. https://doi.org/10.1093/jpe/rtm001

Leps, M., Tonkin, J.D., Dahm, V., Haase, P., Sundermann, A., 2015. Disentangling environmental drivers of benthic invertebrate assemblages: The role of spatial scale and riverscape heterogeneity in a multiple stressor environment. Sci. Total Environ. 536, 546–556. https://doi.org/10.1016/j.scitotenv.2015.07.083

Liu, Q., 1997. Variation partitioning by partial redundancy analysis (RDA). Environmetrics 8, 75–85. https://doi.org/10.1002/(SICI)1099-095X(199703)8:2<75::AID-ENV250>3.0.CO;2-N

Lorenz, S., Pusch, M.T., Miler, O., Blaschke, U., 2017. How much ecological integrity does a lake need? Managing the shores of a peri-urban lake. Landsc. Urban Plan. 164, 91–98. https://doi.org/10.1016/j.landurbplan.2017.04.007

Matthaei, C.D., Piggott, J.J., Townsend, C.R., 2010. Multiple stressors in agricultural streams: Interactions among sediment addition, nutrient enrichment and water abstraction. J. Appl. Ecol. 47, 639–649. https://doi.org/10.1111/j.1365-2664.2010.01809.x

McGoff, E., Aroviita, J., Pilotto, F., Miler, O., Solimini, A.G., Porst, G., Jurca, T., Donohue, L.A., Sandin, L., 2013a. Assessing the relationship between the Lake Habitat Survey and littoral macroinvertebrate communities in European lakes. Ecol. Indic. 25, 205–214. https://doi.org/10.1016/j.ecolind.2012.09.018

McGoff, E., Sandin, L., 2012. Catchment land-use effects on littoral macroinvertebrates in response to local habitat structure and trophic state. Fundam. Appl. Limnol. / Arch. für Hydrobiol. 180, 111–121. https://doi.org/10.1127/1863-9135/2012/0194

McGoff, E., Solimini, A.G., Pusch, M.T., Jurca, T., Sandin, L., 2013b. Does lake habitat alteration and land-use pressure homogenize European littoral macroinvertebrate communities? J. Appl. Ecol. 50, 1010–1018. https://doi.org/10.1111/1365-2664.12106

Miler, O., Czarnecka, M., Jäger, A., Garcia, X.F., Pusch, M.T., 2015a. Lake shore assessment and macroinvertebrate community composition in near-natural fluvial lakes, in: Erweiterte Zusammenfassungen Der Jahrestagung 2015 Der Deutschen Gesellschaft Für Limnologie (DGL) Und Der Deutschen Und Österreichischen Sektion Der Societas Internationalis Limnologiae (SIL), Essen, 21. - 25. Sept. 2015. pp. 64–68.

Miler, O., Ostendorp, W., Brauns, M., Porst, G., Pusch, M.T., 2015b. Ecological assessment of morphological shore degradation at whole lake level aided by aerial photo analysis. Fundam. Appl. Limnol. / Arch. für Hydrobiol. 186, 353–369. https://doi.org/10.1127/fal/2015/0658

Miler, O., Porst, G., Mcgoff, E., Pilotto, F., Donohue, L.A., Jurca, T., Solimini, A.G., Sandin, L., Irvine, K., Aroviita, J., Clarke, R.T., Pusch, M.T., 2015c. An index of human alteration of lake shore morphology. Aquat. Conserv. Mar. Freshw. Ecosyst. 25, 353–364. https://doi.org/10.1002/aqc.2534

Miler, O., Porst, G., McGoff, E., Pilotto, F., Donohue, L.A., Jurca, T., Solimini, A.G., Sandin, L., Irvine, K., Aroviita, J., Clarke, R.T., Pusch, M.T., 2013. Morphological alterations of lake shores in Europe: A multimetric ecological assessment approach using benthic macroinvertebrates. Ecol. Indic. 34, 398–410. https://doi.org/10.1016/j.ecolind.2013.06.002

Mischke, U., Hoehn, E., Riedmüller, U., 2009. Feinabstimmungsprojekt zum deutschen Bewertungsverfahren für Phytoplankton in Seen zur Umsetzung der EU-Wasserrahmenrichtlinie. Bund-/Länderarbeitsgemeinschaft Wasser, Schwerin, Mecklenburg-Vorpommern, Germany.

Noges, P., Argillier, C., Borja, A., Garmendia, J.M., Hanganu, J., Kodes, V., Pletterbauer, F., Sagouis, A., Birk, S., 2016. Quantified biotic and abiotic responses to multiple stress in freshwater, marine and ground waters. Sci. Total Environ. 540, 43–52. https://doi.org/10.1016/j.scitotenv.2015.06.045

Ofenböck, T., Moog, O., Gerritsen, J., Barbour, M.T., 2004. A stressor specific multimetric approach for monitoring running waters in Austria using benthic macro-invertebrates. Hydrobiologia 516, 251–268. https://doi.org/10.1023/B:HYDR.0000025269.74061.f9

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O’Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., Szoecs, E., Wagner, H., 2016. vegan: Community Ecology Package (R package). R Foundation for Statistical Computing, Vienna, Austria.

Okun, N., Mehner, T., 2005. Distribution and feeding of juvenile fish on invertebrates in littoral reed (Phragmites) stands. Ecol. Freshw. Fish 14, 139–149. https://doi.org/10.1111/j.1600-0633.2005.00087.x

Ostendorp, W., Schmieder, K., Jönk, K., 2004. Assessment of human pressures and their hydromorphological impacts on lakeshores in Europe. Ecohydrol. Hydrobiol. 4, 380–395.

Pätzig, M., Grüneberg, B., Brauns, M., 2015. Water depth but not season mediates the effects of human lakeshore modification on littoral macroinvertebrates in a large lowland lake. Fundam. Appl. Limnol. / Arch. für Hydrobiol. 186, 311–321. https://doi.org/10.1127/fal/2015/0652

Peterlin, M., Urbanic, G., 2013. A Lakeshore Modification Index and its association with benthic invertebrates in alpine lakes. Ecohydrology 6, 297–311. https://doi.org/10.1002/eco.1269

Pilotto, F., Bazzanti, M., di Vito, V., Frosali, D., Livretti, F., Mastrantuono, L., Pusch, M.T., Sena, F., Solimini, A.G., 2015. Relative impacts of morphological alteration to shorelines and eutrophication on littoral macroinvertebrates in Mediterranean lakes. Freshw. Sci. 34, 410–422. https://doi.org/10.1086/680523

Pinel-Alloul, B., Methot, G., Lapierre, L., Willsie, A., 1996. Macroinvertebrate community as a biological indicator of ecological and toxicological factors in Lake Saint-Francois (Quebec). Environ. Pollut. 91, 65–87.

Poppe, L.J., Paskevich, V.F., Williams, S.J., Hastings, M.E., Kelley, J.T., Belknap, D.F., Ward, L.G., FitzGerald, D.M., Larsen, P.F., 2003. Surficial sediment data from the Gulf of Maine, Georges Bank, and vicinity; a GIS compilation, USGS Open-File Report 03-001. https://doi.org/10.3133/ofr031

Porst, G., Brauns, M., Irvine, K., Solimini, A.G., Sandin, L., Pusch, M.T., Miler, O., 2019. Effects of shoreline alteration and habitat heterogeneity on macroinvertebrate community composition across European lakes. Ecol. Indic. 98, 285–296. https://doi.org/10.1016/j.ecolind.2018.10.062

R Development Core Team, 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Australia.

Rico, A., van den Brink, P.J., Leitner, P., Graf, W., Focks, A., 2016. Relative influence of chemical and non-chemical stressors on invertebrate communities: a case study in the Danube River. Sci. Total Environ. 571, 1370–1382. https://doi.org/10.1016/j.scitotenv.2016.07.087

Riedmüller, U., Hoehn, E., Mischke, U., 2013. Trophie-Klassifizierung von Seen - Handbuch Trophie-Index. Bund-/Länderarbeitsgemeinschaft Wasser, Schwerin, Mecklenburg-Vorpommern, Germany.

Scheifhacken, N., Fiek, C., Rothhaupt, K.-O., 2007. Complex spatial and temporal patterns of littoral benthic communities interacting with water level fluctuations and wind exposure in the littoral zone of a large lake. Fundam. Appl. Limnol. / Arch. für Hydrobiol. 169, 115–129. https://doi.org/10.1127/1863-9135/2007/0169-0115

Schindler, D.W., 2006. Recent advances in the understanding and management of eutrophication. Limnol. Oceanogr. 51, 356–363. https://doi.org/10.4319/lo.2006.51.1_part_2.0356

Schreiber, J., Brauns, M., 2010. How much is enough? Adequate sample size for littoral macroinvertebrates in lowland lakes. Hydrobiologia 649, 365–373. https://doi.org/10.1007/s10750-010-0284-x

Shi, X., Liu, J., You, X., Bao, K., Meng, B., 2019. Shared effects of hydromorphological and physico-chemical factors on benthic macroinvertebrate integrity for substrate types. Ecol. Indic. 105, 406–414. https://doi.org/10.1016/j.ecolind.2018.02.028

Siling, R., Urbanic, G., 2016. Do lake littoral benthic invertebrates respond differently to eutrophication, hydromorphological alteration, land use and fish stocking? Knowl. Manag. Aquat. Ecosyst. 417, 35. https://doi.org/10.1051/kmae/2016022

Smith, V.H., Joye, S.B., Howarth, R.W., 2006. Eutrophication of freshwater and marine ecosystems. Limnol. Oceanogr. 51, 351–355. https://doi.org/10.4319/lo.2006.51.1_part_2.0351

Solimini, A.G., Argillier, C., Bohmer, J., Gevrey, M., Urbanic, G., Wolfram, G., 2014. Water Framework Directive Intercalibration Technical Report: Alpine Lake Benthic invertebrate ecological assessment methods. European Commission, Joint Research Centre, Institute for Environment and Sustainability, Ispra, Italy. https://doi.org/10.2788/74387

Sundermann, A., Gerhardt, M., Kappes, H., Haase, P., 2013. Stressor prioritisation in riverine ecosystems: Which environmental factors shape benthic invertebrate assemblage metrics? Ecol. Indic. 27, 83–96. https://doi.org/10.1016/j.ecolind.2012.12.003

Tolonen, K.T., Hämäläinen, H., Holopainen, I.J., Karjalainen, J., 2001. Influences of habitat type and environmental variables on littoral macroinvertebrate communities in a large lake system. Fundam. Appl. Limnol. / Arch. für Hydrobiol. 152, 39–67. https://doi.org/10.1127/archiv-hydrobiol/152/2001/39

Tolonen, K.T., Hämäläinen, H., 2010. Comparison of sampling methods and habitat types for detecting impacts on lake littoral macroinvertebrate assemblages along a gradient of human disturbance. Fundam. Appl. Limnol. / Arch. für Hydrobiol. 176, 43–59. https://doi.org/10.1127/1863-9135/2010/0176-0043

Trigal, C., Garcia-Criado, F., Fernandez-Alaez, C., 2007. Macroinvertebrate communities of mediterranean ponds (North Iberian Plateau): Importance of natural and human-induced variability. Freshw. Biol. 52, 2042–2055. https://doi.org/10.1111/j.1365-2427.2007.01805.x

Urbanic, G., 2014. A Littoral Fauna Index for assessing the impact of lakeshore alterations in Alpine lakes. Ecohydrology 7, 703–716. https://doi.org/10.1002/eco.1392

Urbanic, G., Mihaljevic, Z., Petkovska, V., Urbanic, M.P., 2020. Disentangling the Effects of Multiple Stressors on Large Rivers Using Benthic Invertebrates—A Study of Southeastern European Large Rivers with Implications for Management. Water 12, 621. https://doi.org/10.3390/w12030621

Urbanic, G., Petkovska, V., Pavlin, M., 2012. The relationship between littoral benthic invertebrates and lakeshore modification pressure in two alpine lakes. Fundam. Appl. Limnol.

/ Arch. für Hydrobiol. 180, 157–173. https://doi.org/10.1127/1863-9135/2012/0207

Vadeboncoeur, Y., Vander Zanden, M.J., Lodge, D.M., 2002. Putting the Lake Back Together: Reintegrating Benthic Pathways into Lake Food Web Models. Bioscience 52, 44–54. https://doi.org/10.1641/0006-3568(2002)052[0044:PTLBTR]2.0.CO;2

Verdonschot, P.F.M., Spears, B.M., Feld, C.K., Brucet, S., Keizer-Vlek, H.E., Borja, A., Elliott, M., Kernan, M., Johnson, R.K., 2013. A comparative review of recovery processes in rivers, lakes, estuarine and coastal waters. Hydrobiologia 704, 453–474. https://doi.org/10.1007/s10750-012-1294-7

Villeneuve, B., Piffady, J., Valette, L., Souchon, Y., Usseglio-Polatera, P., 2018. Direct and indirect effects of multiple stressors on stream invertebrates across watershed, reach and site scales: A structural equation modelling better informing on hydromorphological impacts. Sci. Total Environ. 612, 660–671. https://doi.org/10.1016/j.scitotenv.2017.08.197

Vollenweider, R., Kerekes, J., 1982. Eutrophication of waters. Monitoring, assessment and control. OECD, Paris.

Wentworth, C.K., 1922. A Scale of Grade and Class Terms for Clastic Sediments. J. Geol. 30, 377–392. https://doi.org/10.1086/622910

Wetzel, R.G., 2001. Limnology: Lake and River Ecosystems. Academic Press.

White, J., Irvine, K., 2003. The use of littoral mesohabitats and their macroinvertebrate assemblages in the ecological assessment of lakes. Aquat. Conserv. Mar. Freshw. Ecosyst. 13, 331–351. https://doi.org/10.1002/aqc.586

Table 1: Environmental variables used in statistical analyses.

| Environ-mental variable | Variable | Description | Mean ± SD | Range |
| --- | --- | --- | --- | --- |
| Hydro-morphology | Sand (%) | Grain size ≤ 2 cm including fine particulate organic matter | 56 ± 32 | 0 - 100 |
| | Stones (%) | Grain size > 2 cm including natural vertical cliffs | 9 ± 20 | 0 - 100 |
| | Xylal (%) | Sum of submerged tree roots and coarse woody debris | 6 ± 12 | 0 - 50 |
| | Macrophytes (%) | Sum of emergent and submerged aquatic vegetation | 26 ± 31 | 0 - 100 |
| | Fortification (%) | Rip-rap, retaining walls, including docks and marinas | 3 ± 14 | 0 - 100 |
| | No. habitats | | 2 ± 1 | 0 - 6 |
| | Habitat diversity | Shannon-Wiener diversity of littoral habitats | 1 ± 0 | 0 - 2 |
| Riparian land use | Land use index | % low impact land use + 2 x % high impact land use ) (15 m landwards from the shoreline) | 1 ± 1 | 0 - 2 |
| Trophic state | Total phosphorus (µg $l^{-1}$) | Seasonal mean | 73 ± 113 | 7 - 788 |

| | | | | |
|---|---|---|---|---|
| | Secchi depth (m) | Seasonal mean | [illegible] | [illegible] |
| Lake morpho-metry | Lake type | Prealpine/alpine, lowland and riverine lakes | | |
| | Surface area (km$^2$) | | 9 ± 17 | 1 - 103 |
| | Mean water depth (m) | | 11 ± 14 | 1 - 98 |
| Geographi-cal location | Latitude (dd) | | | |
| | Longitude (dd) | | | |

**Table 2:** Variation partitioning of the effects of the environmental variables 'Hydromorphology' and 'Trophic state' on the biotic variables macroinvertebrate community composition (Bray-Curtis dissimilarity, **Bray-Curtis**), diversity (number of taxa, **No. taxa**) and the multimetric assessment index LIMCO. Results are given for the analysis across hydromorphological states and within each of the hydromorphological states.

| | | | Source of variation | | | | |
|---|---|---|---|---|---|---|---|
| Environ-mental variable | Classification | Biotic Variable | unique | shared | remain-ing | total ex-plained | unex-plained |
| Hydro-morphology | Across hydro-morphological states | Bray-Curtis | 6.2 | 5.4 | 12.4 | 24.0 | 76.0 |
| Hydro-morphology | Across hydro-morphological states | No. taxa | 13.6 | 0.9 | 20.4 | 34.9 | 65.1 |
| Hydro-morphology | Across hydro-morphological states | LIMCO | 17.4 | 1.0 | 19.0 | 37.4 | 62.6 |
| Hydro-morphology | Natural hydro-morphology | Bray-Curtis | 6.8 | 7.2 | 8.4 | 22.3 | 77.7 |
| Hydro-morphology | Natural hydro-morphology | No. taxa | 9.5 | 4.2 | 12.7 | 26.4 | 73.6 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Hydro-morphology | Natural hydro-morphology | LIMCO | 14.9 | 4.3 | 8.6 | 27.7 | 72.3 |
| Hydro-morphology | Hard modification | Bray-Curtis | 8.8 | 0.0 | 14.3 | 23.1 | 76.9 |
| Hydro-morphology | Hard modification | No. taxa | 18.2 | 0.0 | 16.3 | 34.5 | 65.5 |
| Hydro-morphology | Hard modification | LIMCO | 21.1 | 0.0 | 15.7 | 36.8 | 63.2 |
| Hydro-morphology | Soft modification | Bray-Curtis | 17.6 | 9.6 | 12.1 | 39.3 | 60.7 |
| Hydro-morphology | Soft modification | No. taxa | 11.6 | 43.1 | 15.1 | 69.9 | 30.1 |
| Hydro-morphology | Soft modification | LIMCO | 26.3 | 32.8 | 11.7 | 70.8 | 29.2 |
| Trophic state | Across hydro-morphological states | Bray-Curtis | 1.7 | 1.5 | 20.8 | 24.0 | 76.0 |
| Trophic state | Across hydro-morphological states | No. taxa | 0.4 | 3.5 | 31.0 | 34.9 | 65.1 |
| Trophic state | Across hydro-morphological states | LIMCO | 2.7 | 6.9 | 27.8 | 37.4 | 62.6 |
| Trophic state | Natural hydro-morphology | Bray-Curtis | 1.2 | 1.0 | 19.9 | 22.1 | 77.9 |
| Trophic state | Natural hydro-morphology | No. taxa | 0.6 | 1.4 | 24.0 | 26.1 | 73.9 |
| Trophic state | Natural hydro-morphology | LIMCO | 4.6 | 3.4 | 15.6 | 23.6 | 76.4 |
| Trophic state | Hard modification | Bray-Curtis | 3.4 | 1.3 | 18.1 | 22.8 | 77.2 |
| Trophic state | Hard modification | No. taxa | 3.0 | 2.8 | 25.7 | 31.4 | 68.6 |
| Trophic state | Hard modification | LIMCO | 7.9 | 5.4 | 22.0 | 35.3 | 64.7 |
| Trophic state | Soft modification | Bray-Curtis | 2.6 | 12.0 | 24.7 | 39.3 | 60.7 |
| Trophic state | Soft modification | No. taxa | 12.4 | 38.5 | 18.9 | 69.9 | 30.1 |
| Trophic state | Soft modification | LIMCO | 0.0 | 30.8 | 40.3 | 71.0 | 29.0 |

**Table 3.** Variation partitioning of the effects of the environmental variables 'Hydromorphology' and 'Trophic state' on the biotic variables macroinvertebrate community composition (Bray-Curtis dissimilarity, **Bray-Curtis**), diversity (number of taxa, **No. taxa**) and the multimetric assessment index LIMCO. Results are given for the analysis across trophic states and within each of the trophic states.

| | | | Source of variation | | | | |
|---|---|---|---|---|---|---|---|
| Environ-mental variable | Classification | Biotic Variable | unique | shared | remain-ing | total ex-plained | unex-plained |
| Hydro-morphology | Across trophic states | Bray-Curtis | 7.1 | 6.8 | 11.5 | 25.4 | 74.6 |
| Hydro-morphology | Across trophic states | No. taxa | 12.5 | 2.6 | 17.0 | 32.1 | 67.9 |
| Hydro-morphology | Across trophic states | LIMCO | 17.2 | 1.5 | 12.9 | 31.6 | 68.4 |
| Hydro-morphology | Low trophic state | Bray-Curtis | 6.8 | 7.0 | 11.3 | 25.1 | 74.9 |
| Hydro-morphology | Low trophic state | No. taxa | 14.4 | 0.0 | 7.9 | 22.2 | 77.8 |
| Hydro-morphology | Low trophic state | LIMCO | 8.8 | 0.0 | 0.0 | 8.8 | 91.2 |
| Hydro-morphology | Medium trophic state | Bray-Curtis | 10.2 | 11.2 | 10.7 | 32.1 | 67.9 |
| Hydro-morphology | Medium trophic state | No. taxa | 15.7 | 9.9 | 26.0 | 51.7 | 48.3 |
| Hydro-morphology | Medium trophic state | LIMCO | 19.9 | 5.5 | 28.3 | 53.7 | 46.3 |
| Hydro-morphology | High trophic state | Bray-Curtis | 4.4 | 13.6 | 15.1 | 33.1 | 66.9 |
| Hydro-morphology | High trophic state | No. taxa | 15.1 | 18.6 | 26.5 | 60.1 | 39.9 |
| Hydro-morphology | High trophic state | LIMCO | 0.0 | 11.7 | 58.1 | 69.7 | 30.3 |
| Trophic state | Across trophic states | Bray-Curtis | 1.4 | 1.1 | 23.4 | 26.0 | 74.0 |
| Trophic state | Across trophic states | No. taxa | 1.2 | 1.8 | 30.2 | 33.3 | 66.7 |
| Trophic state | Across trophic states | LIMCO | 4.0 | 5.2 | 22.7 | 31.9 | 68.1 |
| Trophic state | Low trophic state | Bray-Curtis | 0.8 | 5.5 | 18.6 | 24.9 | 75.1 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Trophic state | Low trophic state | No. taxa | 0.0 | 0.0 | 22.8 | 22.8 | 77.2 |
| Trophic state | Low trophic state | LIMCO | 0.0 | 1.3 | 0.0 | 1.3 | 98.7 |
| Trophic state | Medium trophic state | Bray-Curtis | 2.4 | 2.7 | 27.0 | 32.1 | 67.9 |
| Trophic state | Medium trophic state | No. taxa | 2.7 | 7.6 | 41.4 | 51.7 | 48.3 |
| Trophic state | Medium trophic state | LIMCO | 3.4 | 10.2 | 40.1 | 53.7 | 46.3 |
| Trophic state | High trophic state | Bray-Curtis | 13.2 | 0.0 | 29.6 | 42.8 | 57.2 |
| Trophic state | High trophic state | No. taxa | 5.4 | 0.0 | 58.6 | 64.1 | 35.9 |
| Trophic state | High trophic state | LIMCO | 0.0 | 15.1 | 35.9 | 51.0 | 49.0 |

**Table 4**: Synthesis of the variation partitioning approach analysing the variables trophic state with hydromorphology kept constant and hydromorphology when trophic state was kept constant. Constant hydromorphology is indicated by the classification into hydromorphological states (natural hydromorphology, hard modification, soft modification, across hydromorphological states) at the left side of the table. Constant trophic state is indicated by the classification into trophic states (low, medium, high, across trophic states) at the top of the table. The direction of each arrow indicates the unique variation explained by the variable hydromorphology relative to trophic state, i.e. upward arrows = hydromorphology more important than trophic state & downward arrow = hydromorphology less important than trophic state. Biotic variables are separated in each cell by / in the format: community composition/number of taxa/LIMCO.

| | | Trophic state | | | |
|---|---|---|---|---|---|
| | | Low trophic state | Medium trophic state | High trophic state | Across trophic states |
| Hydro-morpho logical state | Natural hydromorphology | ↑/↑/↑ | ↑/↑/↑ | ↑/↑/↓ | ↑/↑/↑ |
| | Hard modification | ↑/↑/↑ | ↑/↑/↑ | ↑/↑/↓ | ↑/↑/↑ |
| | Soft modification | ↑/↑/↑ | ↑/↑/↑ | ↑/↑/= | ↑/=/↑ |
| | Across hydromorphological states | ↑/↑/↑ | ↑/↑/↑ | ↑/↑/↓ | ↑/↑/↑ |

# Figure headers

**Figure 1**: Location of 98 studied lakes sampled for littoral macroinvertebrates in Germany. Circles indicate lowland lakes, stars indicate riverine lakes and triangles indicate prealpine/alpine lakes.

**Figure 2**: Percentage of unique (black bars) and joint variation (grey bars) in littoral macroinvertebrate community composition (**A)**, in littoral macroinvertebrate diversity (**B)** and in the multimetric biotic assessment (LIMCO) (**C)**. Each figure contains the unique and joint variation explained by trophic state in the four classifications 'across hydromorphological states', 'natural hydromorphology', 'hard shore modification' and 'soft shore modification' and the unique and joint variation explained by hydromorphology in the four classifications 'across trophic states', 'low trophic state', 'medium trophic state' and 'high trophic state'.

Declaration of competing interest

The Authors declare that there is no conflict of interest.

# CRediT author statement

**Oliver Miler:** Conceptualization, Methodology, Data analysis, Writing- Original draft preparation, Writing - Reviewing and Editing

**Mario Brauns:** Conceptualization, Methodology, Data analysis, Writing- Original draft preparation, Writing - Reviewing and Editing

Graphical abstract

Highlights

- Variation partitioning of littoral macroinvertebrate assessment & community metrics
- Natural, soft & hard modification lake shores, oligotrophic to hypertrophic lakes
- Hydromorphology explained more unique variation than trophic state
- Consistent findings across hydromorphological and trophic states
- Littoral macroinvertebrates suitable for assessment of hydromorphology

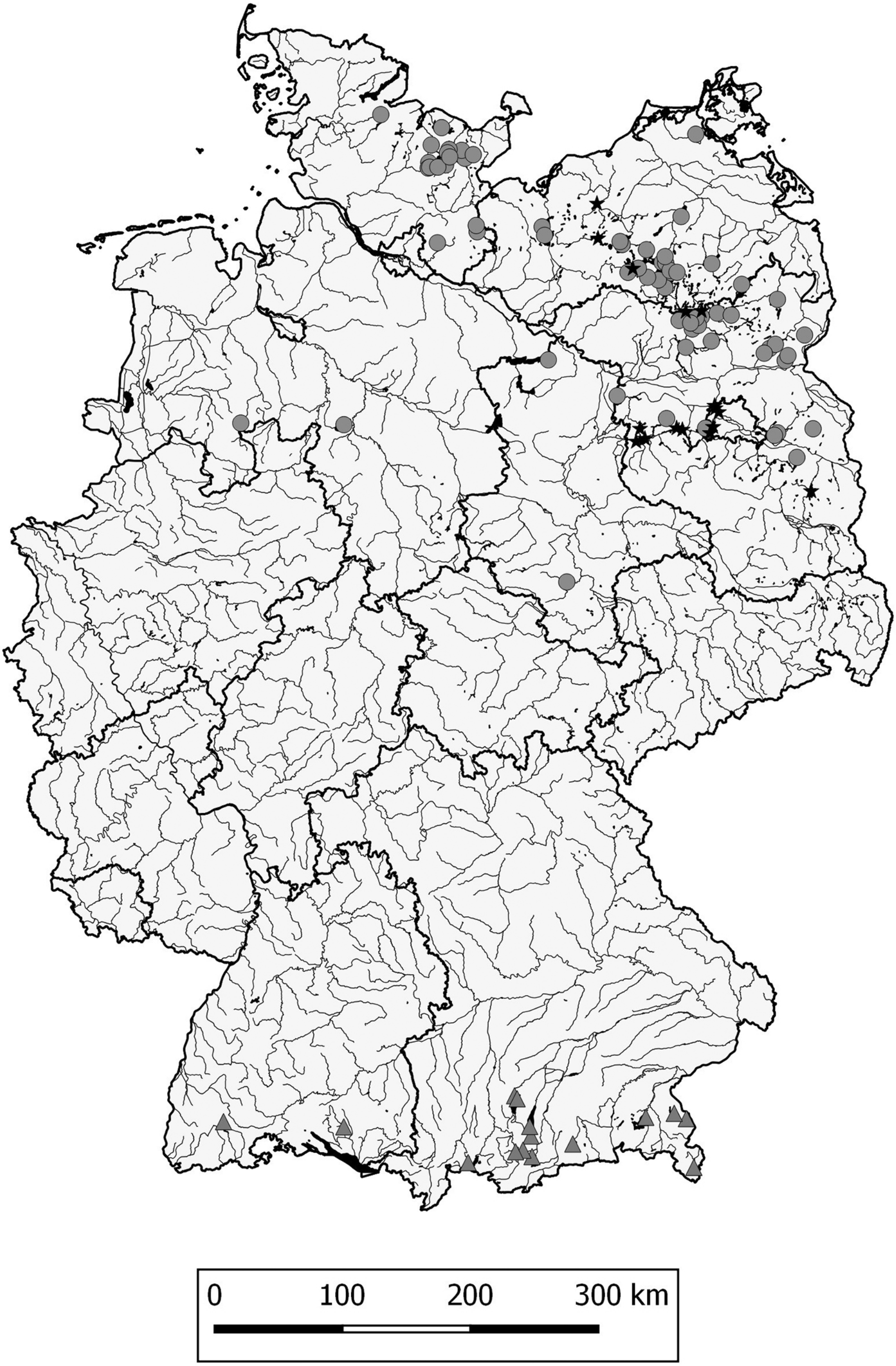


Figure 1

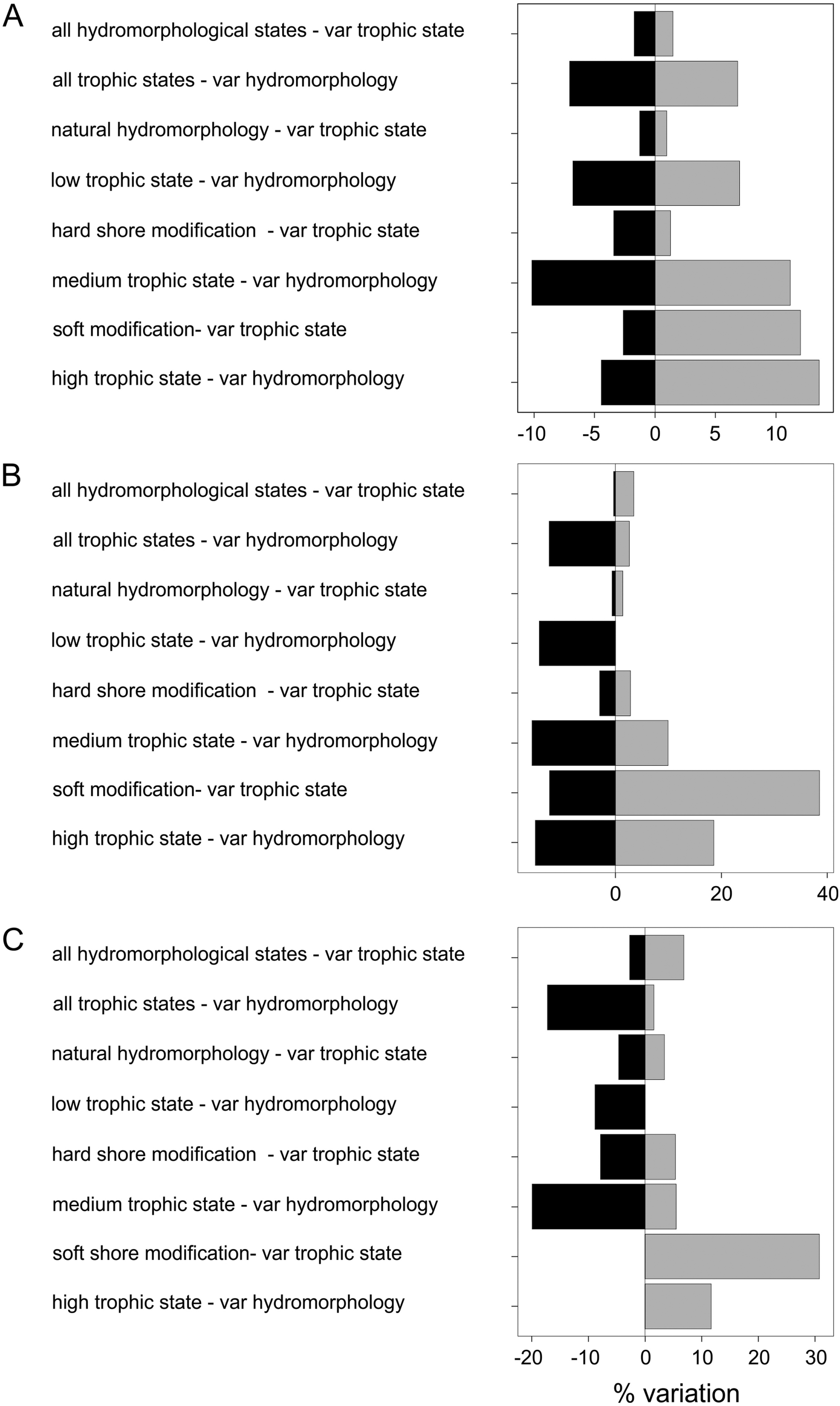
A
all hydromorphological states - var trophic state
all trophic states - var hydromorphology
natural hydromorphology - var trophic state
low trophic state - var hydromorphology
hard shore modification - var trophic state
medium trophic state - var hydromorphology
soft modification- var trophic state
high trophic state - var hydromorphology
-10
-5
0
5
10
B
all hydromorphological states - var trophic state
all trophic states - var hydromorphology
natural hydromorphology - var trophic state
low trophic state - var hydromorphology
hard shore modification - var trophic state
medium trophic state - var hydromorphology
soft modification- var trophic state
high trophic state - var hydromorphology
0
20
40
C
all hydromorphological states - var trophic state
all trophic states - var hydromorphology
natural hydromorphology - var trophic state
low trophic state - var hydromorphology
hard shore modification - var trophic state
medium trophic state - var hydromorphology
soft shore modification- var trophic state
high trophic state - var hydromorphology
-20
-10
0
10
20
30
% variation

Figure 2