

# Original Article

**Title:** Nonlinear higher-order abiotic interactions explain riverine biodiversity

**Short running-title:** Higher-order interactions predict diversity

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## STRUCTURED ABSTRACT

**Aim** Theory and experiments strongly support the importance of interactive effects of multiple factors shaping biodiversity, although their importance rarely has been investigated at biogeographically relevant scales. In particular, the importance of higher-order interactions among environmental factors at such scales is largely unknown. We investigated higher-order interactions of environmental factors to explain diversity patterns in a meta-community of aquatic invertebrates at a biogeographically relevant scale and discuss the findings in an environmental management context.

**Location** All major drainage basins in Switzerland (Rhine, Rhone, Ticino and Inn; 41,285 km<sup>2</sup>).

**Methods** Riverine  $\alpha$ -diversity patterns at two taxonomic levels (family richness of all benthic macroinvertebrates and species richness of Ephemeroptera, Plecoptera and Trichoptera) were examined at 518 sites across the basins. We applied a novel machine learning technique to detect key three-way interactions of explanatory variables by comparing the relative importance of 1140 three-way combinations for family richness and 680 three-way combinations for species richness.

**Results** Relatively few but important three-way interactions were meaningful for predicting biodiversity patterns among the numerous possible combinations. Specifically, we found that interactions among elevational gradient, prevalence of forest coverage in the upstream basin and biogeoclimatic regional classification were distinctly important.

**Main conclusion** Our results indicated that a high prevalence of terrestrial forest generally sustains riverine benthic macroinvertebrate diversity, but this relationship varies considerably with biogeoclimatic and elevational conditions likely due to community composition of forests and macroinvertebrates changing along climatic and geographical gradients. An adequate management of riverine ecosystems at relevant biogeographical scales requires the identification of such interactions and a context-dependent implementation.

### **Keywords:**

Context dependency, conservation, ecological surprises, freshwater, land use, machine learning, macroinvertebrates, meta-ecosystem, metacommunity, multiple stressors.

## INTRODUCTION

Interactions among ecological drivers represent a major source of uncertainty in predicting species distributions (Araújo & Guisan, 2006; Guisan *et al.*, 2006) and biodiversity patterns (Sala *et al.*, 2000) because it is impossible to predict effects by studying each driver independently. This imprecision can lead to ‘ecological surprises’ (*sensu* King, 1995), which are defined as an unexpected outcome based on current ecological knowledge (King 1995). Interacting ecological drivers either can amplify or weaken individual effects through synergy or antagonism, respectively, depending on the prevailing context (Harvey *et al.*, 2017). For instance, interactions among multiple stressors likely accelerate biodiversity loss (Sala *et al.* 2000) and even can be more important than additive effects in freshwater, marine and terrestrial communities, as reviewed in Darling & Côté, (2008) and Jackson *et al.* (2016).

Current evidence relating to water use and the extent at which hydrological processes can spread stressors suggests that issues of multiple stressors are especially acute in freshwater ecosystems (Ormerod *et al.*, 2010). River ecosystems are not only among the most diverse but also among the most threatened ecosystems globally (Dudgeon *et al.*, 2006; Vörösmarty *et al.*, 2010). Indeed, local biodiversity in running waters is affected by various factors across multiple spatial scales, ranging from local to regional scales (Frissell *et al.*, 1986; O’Neill *et al.*, 1986; Poff 1997). These factors include catchment hydrological processes that reflect upstream terrestrial conditions (Richards *et al.*, 1997), connections with adjacent riparian ecosystems (Vannote *et al.*, 1980; Loreau, 2003; Soininen *et al.*, 2015; Harvey *et al.*, 2016), and linkages of local environments in dendritic river networks (Vannote *et al.*, 1980; Ward, 1989; Altermatt, 2013; Altermatt *et al.*, 2013; Tonkin *et al.*, 2018). Previous studies reported that major ecological surprises sometimes emerge, as these multiple factors often cause nonlinear interactive effects in freshwater ecosystems (e.g. Hecky *et al.* 2010; Ormerod *et al.*, 2010).

Whereas theory and experiments strongly support the importance of interactive effects of multiple factors in shaping biodiversity (Darling & Côté, 2008; Jackson *et al.*, 2016), their importance rarely has been investigated at biogeographically relevant scales (Gieswein *et al.*, 2017). In particular, the importance of higher-order interactions (HOI) among environmental factors at such scales is largely unknown. We refer to HOI as the interactions among three or more variables whose effects cannot be explained by any subset of the tested variables. Not taking HOI into account can lead to a perceived context-dependency in observed biodiversity

patterns akin to an ecological surprise (Sala *et al.*, 2000; Tonkin *et al.* 2016; Mayfield & Stouffer, 2017). A solution to dissipate ecological surprises caused by HOI could be to build a statistical model including all possible interaction combinations, but this is not feasible when several factors simultaneously determine such patterns (Côté *et al.* 2016; Mayfield & Stouffer, 2017; Gieswein *et al.* 2017). For instance, the independent effects of 10 drivers can be reasonably tested, but their three-way interaction effects accounting for 120 combinations are difficult to statistically test (cf. as a rule of thumb, at least 5 to 10 independent data points are needed for each interaction and main factor to be considered; Burnham & Anderson, 2002). Machine learning algorithms can offer an alternative approach to study HOI (Hochachka *et al.*, 2007; Kelling *et al.*, 2009). Machine learning algorithms have been developed to account for nonlinearity and HOI among variables without the requirement that the user specifies a priori which variables interact.

Here, we investigated HOI of environmental factors across multiple spatial scales to better explain diversity patterns in a riverine meta-community. We asked the following questions: (i) are key HOI of environmental factors detectable from the numerous possible combinations using a machine learning technique? (ii) which environmental factors play a major interactive role? and (iii) how can interactive effects among environmental factors be considered for effective environmental management?

Specifically, we investigated the effects of 76 environmental factors across regional (landscape) and local scales on  $\alpha$ -diversity patterns of benthic aquatic macroinvertebrates (family and species level) among rivers (518 sites) in Switzerland. First, we performed variable selection, and estimated the effects of environmental factors individually, using a random forest (RF) algorithm (Breiman, 2001; Cutler *et al.*, 2007). Then, we ranked the relative importance of all the three-way interactions of the selected variables (1140 and 680 combinations for family and species level, respectively) and examined interactive effects.

This study focused on three-way interactions only, because HOI characteristics are largely unknown even at that minimal order (i.e. three-way). In addition, comparisons between different orders of interactions (e.g., three-way versus four-way) are very difficult because interactive effects can differ radically at each order as was shown for three-way versus two-way interactions (e.g. Billick and Case, 1994 and reference therein).

## MATERIALS AND METHODS

Our study used presence-absence data of aquatic macroinvertebrates in Switzerland from a governmental monitoring program (“Biodiversity Monitoring in Switzerland BDM”; BDM Coordination Office, 2014). The program is managed by the Federal Office for the Environment (BAFU/FOEN). Based on a systematic sampling grid across Switzerland, stream macroinvertebrates were collected by trained field biologists using a standardized protocol (BDM Coordination Office, 2014).

### Biogeography of Switzerland

Switzerland is a relatively small country (41,285 km<sup>2</sup>) in the center of Europe (Fig. 1) composed of different biogeographical units. A large part of the country consists of the Alps (50% of the area) and Jura mountains (10% of the area). North of the Alps, a large, densely populated central valley extends from east to west (30% of the area), whereas several smaller valleys extend into sub-Mediterranean climates south of the Alps. Switzerland covers a large elevational gradient, ranging from 193 to 4634 m a.s.l. The country has a typical temperate climate with moderate to high precipitation. Several large European rivers originate in Switzerland, including the Rhine basin (draining 71% of the country, flowing into the North Sea), the Rhone basin (draining 20% of the country, flowing into the Mediterranean Sea), the Po basin (draining 5% of the country, flowing into the Adriatic Sea), the Danube basin (draining 3.5% of the country, flowing into the Black Sea), and the Etsch basin (draining 0.5% of the country, flowing into the Adriatic Sea) (Fig. 1). Due to its small size, the Etsch data were pooled with the Po data in the present study.

### Study sites and sampling methods

The BDM currently monitors 518 study sites across Switzerland (Fig. 1), representing the diversity of stream macroinvertebrates in the country (see also Altermatt *et al.* 2013; Kaelin & Altermatt 2016; Seymour *et al.*, 2016a, Seymour *et al.*, 2016b). Sampling was conducted in wadeable streams, 2<sup>nd</sup> order or larger in size, and excluded standing waterbodies, 1<sup>st</sup> order streams and large rivers inaccessible by wading (Stucki, 2010). Each site was sampled once between 2009–2014 with seasonal timing of sampling adjusted with respect to elevation. For instance, the sampling period for a site was based on local phenology so as to collect as many macroinvertebrate taxa as possible for a given elevation (Stucki, 2010).

The survey was completed using a standard kick-net (25 x 25 cm, 500 µm mesh) sampling procedure defined in the Swiss “Macrozoobenthos Level I” module for stream benthic

macroinvertebrates (BDM Coordination Office, 2014; Stucki, 2010; Altermatt *et al.*, 2013). Briefly, eight kick-net samples were taken at each site to cover all major microhabitats within an area (10x the average width) and composited. Different habitat types (including various sediment types such as rocks, pebbles, sand, mud, submerged roots, macrophytes, leaf litter and artificial river-beds) at different water velocities were sampled. Samples were preserved in 80% ethanol and returned to the laboratory for processing. In the laboratory, all benthic macroinvertebrates were sorted and identified to the family level. The Ephemeroptera, Plecoptera and Trichoptera (EPT taxa) were identified further to species level by experts using standardized keys as found in BDM Coordination Office (2014).

### **Diversity (response variables)**

We used the number of families (all macroinvertebrates) and the number of EPT species as response variables. Macroinvertebrate family richness is a commonly used indicator for assessing the ecological state of running waters (Lenat, 1988), whereas EPT species richness is one of the most commonly used variables in biodiversity studies. Because species level identifications are often unattainable, higher-order taxa richness is commonly used as a substitute. We conducted separate analyses for the two levels of taxonomic richness to better infer general patterns.

### **Environmental factors (explanatory variables)**

We used 76 environmental factors (see Appendix S1 in Supporting Information). Only subsets of these factors were used in previous studies to explain biodiversity patterns in Swiss rivers (Altermatt *et al.*, 2013; Kaelin & Altermatt, 2016; Seymour *et al.*, 2016a). For subsequent interpretation purposes only, we grouped factors into four categories targeting different spatial scales and realms. Sample collection year was the only variable not falling into any category, but was included as a covariate to correct for any confounding effects of time. The four categories included:

- 1) Regional category — factors determined by the geographical coordinates of a biological sampling site (5 variables). This category included two altitude measures (elevation at the site and the mean elevation of the catchment upstream of the site), two catchment classifications (3 classes for major catchments and 9 classes for sub-catchments), and a biogeoclimatic classification (6 classes).

- 2) Landscape category — terrestrial conditions of the upstream catchment of a biological

sampling site (35 variables). Local instream habitat is regarded as the outlet of a catchment affected by upstream hydrological processes and terrestrial conditions in the catchment (Allan, 2004). Analysis considered catchment size and the relative proportion of land cover types. We used two land cover classifications. One classification distinguished 23 classes from the entire upstream catchment area (Kaelin & Altermatt, 2016) and the other distinguished 6 classes that considered influences of the adjacent upstream catchment area to the local site at lateral buffer distances of 500 m and 5 km (Seymour *et al.*, 2016a).

3) Riverscape category — instream and geometry conditions of the river network in the upstream catchment of a biological sampling site (13 variables). This category included size and length of the river network, a network fragmentation intensity, and geomorphological (e.g., riverbed slope), hydrological (e.g., mean discharge) and chemical (e.g., inflowing wastewater volume) conditions.

4) Local category — Instream habitat conditions observed *in-situ* at a biological sampling site (22 variables). This category considered geomorphological features of channel cross-sections (e.g., width, depth, and their variability), riverbed conditions (e.g., mud deposition and attached algae), and aquatic conditions (e.g., turbidity and dissolved iron sulfide concentration).

### **Random Forest modeling with variable selection**

We did not exclude any explanatory variable before analysis because the approach employed can (i) perform variable selection, (ii) evaluate the relative importance among highly correlated variables (Nicodemus *et al.*, 2010; Bradter *et al.*, 2013; Ryo *et al.*, 2017; Bergmann *et al.* 2017), and (iii) fairly assesses the relative importance between continuous and categorical variables without bias (Hothorn *et al.*, 2006; Strobl *et al.*, 2008). We used the RF machine learning algorithm for performing multiple regressions with variable selection (Hapfelmeier & Ulm, 2013).

In short, the RF algorithm uses a model ensemble approach that constructs a large number of decision tree models (Breiman *et al.*, 1984) and then takes an average from their outputs as a final output of the algorithm (Breiman, 2001). A decision tree is a nonparametric approach that partitions a sample into subsamples to minimize variation within each subsample. The model searches for an explanatory variable and its threshold value to partition a sample into two subsamples. The searching and partitioning procedure is done recursively until no better split is found. Employing the RF algorithm is beneficial when there are too many explanatory variables and interactions to model statistically (Breiman, 2001).

The RF algorithm with variable selection by Hapfelmeier & Ulm (2013) takes two modeling steps. First, it performs a multiple regression using all explanatory variables to estimate a

statistical significance for each variable. For each variable, the RF algorithm estimates a  $p$ -value that is defined as the probability that the observed increase in validation accuracy could be due to chance alone (Hapfelmeier & Ulm, 2013). We set the significance level to 0.01 with Bonferroni correction by 76 variables (i.e.  $\alpha = 0.000132$ ) to account for Type I error. Second, using only significant variables, the RF algorithm performs a multiple regression to build the final RF model and to estimate a relative importance score for each variable. The relative importance score of each variable is quantified by evaluating how much model accuracy would decrease if the model removes the effect of a focal variable (Breiman 1996; Breiman, 2001).

After variable selection, we ranked the relative importance scores of the explanatory variables and visualized their modeled relationships to each response variable. Partial dependence plots were used for visualization (Hastie *et al.*, 2009), which delineate modeled associations between a few variables (and their interactions if specified) while marginalizing (averaging) out the effects of all the other variables. The procedure calculates a partial dependence score that indicates the relative extent of the response variable. In our case, the higher the score, the higher taxonomic richness.

Explanatory power is evaluated based on the coefficient of determination by comparing observed with fitted values as explained variance. In addition, validation accuracy is evaluated based also on the coefficient of determination using 1/3 of the samples that were omitted for parameter fitting, following standard RF procedures (Breiman, 1996). The RF algorithm avoids over-fitting by averaging a large number of decision tree models, which in turn, minimizes bias (Breiman, 2001).

The entire script we used is available at github ([https://github.com/masahiroryo/R\\_HOI](https://github.com/masahiroryo/R_HOI)). We used the R script available in Hapfelmeier and Ulm (2013), which is based on ‘ctree’ and ‘cforest’ functions of the ‘party’ package (Strobl *et al.*, 2009) in R 3.3.2 (R Development Core Team, 2016). All parameters in the functions were set to default settings. We set 1,000 decision trees in the RF model, after confirming that this amount satisfactorily stabilizes a performance of RF models in comparison to 100 and 500 decision trees in preliminary analyses. For  $p$ -value estimation, each variable was permuted 5,000 times. The explanatory power was evaluated using the ‘cforeststats’ function of the ‘caret’ package (Kuhn, 2015). We used the ‘mlr’ package for partial dependence plots (Bishl *et al.*, 2016).

#### **Assessment and visualization of HOI effects**

We quantified the relative importance of three-way interactions of all possible combinations among the selected variables (see results; of 76 variables, the variable selection approach chose 20 variables that accounted for 1140 combinations ( $= {}_{20}C_3$ ) for macroinvertebrate family richness and 17 variables that accounted for 680 combinations ( $= {}_{17}C_3$ ) for EPT species richness). We employed the approach of Kelly & Okada (2012) that quantifies the relative importance of variable interactions based on permutation with RF. As Kelly & Okada (2012) was limited to two-way interactions, we extended their work to three-way interactions based on mutual information theory (McGill, 1954; Anastassiou, 2007; Williams & Beer, 2010). The relative



importance score, which quantifies the degree of effect of the three-way combinations of variables A, B, and C, is defined as:

$$E(A \cap B \cap C) = E(A) + E(B) + E(C) - \{E(A \cup B) + E(A \cup C) + E(B \cup C)\} + E(A \cup B \cup C)$$

where,  $E(\ )$  represents the importance score based on the permutation approach (Kelly & Okada, 2012).  $A \cap B$  is the effects of the interaction between variables A and B, excluding their independent effects.  $A \cup B$  is the total effects of variables A and B, including both independent and interactive effects.

$E(A \cup B)$  was calculated by simultaneously permuting variables A and B and then calculating the mean decrease in validation accuracy (Kelly & Okada, 2012).  $E(\ )$  is quantified for each tree model and then averaged across all tree models. Eventually,  $E(A \cap B \cap C)$  equals the difference between synergistic and redundant information (Anastassiou 2007; Williams & Beer, 2010). Redundant information means that both variables partially share the same information (cf. correlation). A value can be either negative (redundant) or positive (synergistic), and being close to 0 indicates no interaction. The R function *intimp* we developed is also available at github ([https://github.com/masahiroryo/R\\_HOI](https://github.com/masahiroryo/R_HOI)).

After assessing the relative importance for all possible three-way combinations, we focused on some of the highest values (i.e. the most synergetic combinations) and visualized some representatives to confirm interaction patterns, again using partial dependence plots. We focused on the top 10 combinations. We decided to set this threshold as an absolute value instead of relative value such as percentile because the total number of combinations was unknown before performing variable selection (e.g., 70,300 combinations would appear if all 76 variables remain, but only 10 combinations would appear if 5 variables remain). Note that the mutual information theory approach does not estimate confidence interval and statistical significance, meaning that we cannot rely on null hypothesis testing to assess importance. For visualization, we avoided variable combinations where value combinations are physically impossible. For instance, the elevation at a site cannot be higher than the mean elevation over the upstream catchment.

## RESULTS

Macroinvertebrate family richness among sites ranged from 1 to 39 taxa with a median of 20, while EPT species richness ranged from 0 to 36 with a median of 16 (Fig. 1). Macroinvertebrate family and EPT species richness was highly correlated (Pearson's  $r = 0.81$ ). Of 76 explanatory variables, 20 and 17 variables were finally selected (Fig. 2) for the RF models of macroinvertebrate family and EPT species richness, respectively, and their association patterns were individually estimated (Fig. S1 in Appendix S2). Overall, the explanatory power was 58% of the variation in macroinvertebrate family and EPT species richness (validation accuracy: 40% and 35%, respectively).

According to the relative importance of individual factors, regional and landscape factors were dominant drivers (Fig. 2). Elevation, the relative proportion of forest land cover, and biogeoclimatic classifications were ranked within the top 5 for both richness measures (Fig. 2). Specifically, both richness measures were monotonically declining above 1000 m, were decreasing where the relative proportion of forest land cover within any buffer distance was lower than 20–30%, and were lower in the central Alps regions than in other regions (Fig. 3 and Fig. S1).

More than 97% of the possible three-way combinations had importance scores near zero, i.e., between  $-0.1$  and  $0.1$  (1124 out of 1140 combinations for macroinvertebrate family richness and 663 out of 680 combinations for EPT species richness). Less than 20 combinations exceeded an importance score  $\geq 0.1$  for both richness measures (Fig. 4). This indicates that only a few three-way interactions explained both richness measures meaningfully. Same as the relative importance of individual factors (Fig. 2), elevation, the relative proportion of forest land cover, and biogeoclimatic regions were the most important factors interacting for explaining both richness measures (Table 1). For instance, the top combination for family richness revealed a score of 1.2%, which is 13.3 times higher than the random expectation ( $100\% \times 1/1140 = 0.088\%$ ).

The impact of key factors (Table 1) on diversity patterns was nonlinear and interactive, as shown in representative examples for diversity patterns explained by the interactions of biogeoclimatic regions, elevation, and the relative proportion of forest land cover (Fig. 5). Most distinctly, negative synergetic effects were found commonly where the relative proportion of forest land cover (5 km-buffer) was less than 20–30%, together with the conditions of over 2000 m of elevation (at the bottom-foreground corner of each cube in Fig. 5). These interaction patterns were dependent on biogeoclimatic region. Variability in richness along these gradients was highest in the north flank of the Alps, Jura, and Central plains (Fig. 5a and Fig. S2), moderate in the south flank of the Alps (Fig. 5b), and lowest in the eastern and western Central Alps (Fig. 5c and Fig. S2). The variation caused by the interactions cannot be explained by their individual effects (Fig. 3).

## DISCUSSION

Theory and experiments strongly suggest that interactions of multiple drivers, especially HOI, are a major source of uncertainty as ecological surprises (*sensu* King 1995) in predicting species

distributions and biodiversity (Sala *et al.*, 2000; Araújo & Guisan, 2006; Guisan *et al.*, 2006). However, HOI of environmental factors shaping biodiversity patterns at biogeographically relevant scales have been rarely systematically investigated because of too many possible factor interactions (Côté *et al.* 2016; Gieswein *et al.* 2017). Answering the first two study questions, the results showed that (i) a machine learning algorithm with mutual information theory can extract a few key HOI of environmental factors from numerous possible three-way interactions, and (ii) the three-way interactions of elevation, terrestrial land cover, and biogeoclimatic region were most important in explaining riverine macroinvertebrate diversity patterns across Switzerland.

Our results suggest that a vast majority of possible three-way combinations are negligible (as shown by importance scores near zero; Fig. 4), while only a few may play a role as ecological surprises in shaping observed biodiversity patterns. Thus, a key aspect for understanding freshwater communities is to identify which of all possible factor combinations are relevant; this selection can be guided by the approach used herein. Our results are in agreement with Gieswein *et al.* (2017), who used a different machine learning approach to conclude that non-additive effects certainly exist but additive effects may prevail in structuring diversity patterns in streams at similar geographical scales. Neither study, however, compared models with and without interaction effects because of the nature of the applied techniques. The relative importance of interaction effects vs. individual effects still remains untested.

The interaction effects of elevation-forest-biogeoclimatic combinations might be explained by the underlying ecological significance of riparian forests on streams in terms of the meta-ecosystem concept (Loreau *et al.*, 2003; Gounand *et al.* 2018). Dense riparian forest coverage generally increases local macroinvertebrate diversity (e.g., Rios & Bailey, 2006). Riparian forests provide leaf litter as a nutritious resource and large woody debris that creates local habitat heterogeneity (Hilderbrand *et al.*, 1997; Feld & Hering, 2007). Further, roots in soil influence biogeochemical conditions together with root-associated microbes (Schade *et al.*, 2001). Plant community composition, which shows turnover along an elevational gradient, can also be important for these functions. Further, plant community composition also is dependent on the available regional species pool, which, in turn, reflects biogeoclimatic conditions. Another possible explanation for an effect of elevation is a direct thermal influence on macroinvertebrates. As aquatic organisms tend to be more sensitive to stressors near their

thermal tolerance limits (Heugens *et al.*, 2001), it is reasonable to assume that the negative effects of low forest coverage become stronger above 2000 m elevation.

Biodiversity conservation requires the selective management of pivotal factors to effectively allocate limited resources and time (Pimm *et al.*, 2001). Answering the last study question, our results suggest that the preservation of forest coverage is a priority to conserve riverine biodiversity. This is consistent with previous field-based studies (Kautza & Sullivan, 2015; Krell *et al.*, 2015; Kaelin & Altermatt, 2016; Seymour *et al.*, 2016a) and theoretical and experimental studies that predict the importance of cross-ecosystem exchange processes (Loreau *et al.*, 2003) and patterns across landscapes (Harvey *et al.*, 2016). Considering cross-ecosystem subsidies, such as nutrients, along land-use types in rivers (Kautza & Sullivan, 2015; Krell *et al.*, 2015), disruptions or alterations to these subsidy exchanges are key mechanisms explaining how changes in the terrestrial matrix can spatially affect aquatic assemblages (Soininen *et al.*, 2015). Considering the interactive effects that we found, it is important to develop a better understanding of how the contributions of forest on riverine biodiversity change along elevational gradients and among biogeoclimatic regions.

Another implication for management is to consider the appropriate spatial scale. For EPT species richness, the negative effect of low forest coverage was amplified where forest coverage was low within both 500 m and 5 km-buffered distances (1<sup>st</sup> rank for EPT in Table 1 and Fig. S2 in Appendix S2). Ignoring this interaction in management practice may lead to an unexpectedly stronger reduction in diversity. To avoid this interaction, forest coverage within either 500 m or 5 km-buffered distance needs to be preserved at >30% (Jackson *et al.*, 2016). For instance, even if there is no forest coverage within 5 km-buffered distance, the negative effect may be compensated with >30% forest coverage within 500 m-buffered distance. Such cross-scale interactions are an emerging topic in ecology (Peters *et al.*, 2007; Soranno *et al.*, 2014) but have received little attention in multi-scale land use studies (Allan, 2004).

Our approach captured the multiple biological patterns within the dataset much more accurately than previous modeling attempts. The explanatory power was two to three-fold higher than that reported in previous studies that analyzed subsets of variables from the same dataset (20–30%; e.g., Altermatt *et al.*, 2013; Seymour *et al.*, 2016a). Therefore, the limited power of explaining biodiversity in riverine ecosystems may not be necessarily due to inherent limitations of the system (Heino *et al.*, 2015) and missing key processes such as species interactions,

large-scale dispersal dynamics, and demography (e.g., Urban *et al.*, 2016), but also due to inherent limitations of the analytical methods applied. For example, the use of multi-process hierarchical or network-based statistical assumptions in ecology also can offer new insights into ecological analyses (Cressie *et al.*, 2009; Grace *et al.*, 2012, 2016; Harvey & MacDougall, 2015).

A recent review by Jackson *et al.* (2016) concluded that multiple stressors often interact with each other in freshwater experiments. This study and Gieswein *et al.* (2017), conducted at a much larger scale, also found some interactive effects on macroinvertebrate richness. However, Gieswein *et al.* (2017) found no interactive effects of environmental factors on diversity patterns of fishes and macrophytes. Such inconsistency highlights the urgent need to accumulate much more empirical evidence on interactive effects of multiple drivers at biogeographically relevant scales, especially HOI, toward concluding the importance of interactive effects across scales, organisms, and ecological levels.

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## REFERENCES

- Allan, J.D. (2004) Landscapes and Riverscapes: The influence of land use on stream ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, **35**, 257–284.
- Altermatt, F. (2013) Diversity in riverine metacommunities: A network perspective. *Aquatic Ecology*, **47**, 365–377.

- 406 Altermatt, F., Seymour, M. & Martinez, N. (2013) River network properties shape  $\alpha$ -diversity  
 407 and community similarity patterns of aquatic insect communities across major drainage  
 408 basins. *Journal of Biogeography*, **40**, 2249–2260.
- 409 Anastassiou, D. (2007) Computational analysis of the synergy among multiple interacting genes.  
 410 *Molecular Systems Biology*, **3**, 83, 1–8.
- 411 Araújo, M.B. & Guisan, A. (2006) Five (or so) challenges for species distribution modelling.  
 412 *Journal of Biogeography*, **33**, 1677–1688.
- 413 BDM Coordination Office (2014) *Swiss biodiversity monitoring BDM. Description of methods*  
 414 *and indicators*, Bern, Switzerland.
- 415 Bergmann, J., Ryo, M., Prati, D., Hempel, S., & Rillig, M.C. (2017) Root traits are more than  
 416 analogues of leaf traits: the case for diaspore mass. *New Phytologist*, **216**, 1130–1139.
- 417 Billick, I. & Case, T.J. (1994) Higher order interactions in ecological communities: What are they  
 418 and how can they be detected? *Ecology*, **75**, 1529–1543.
- 419 Bishl, B., Lang, M., Kotthoff, L., Richter, J., Jones, Z., Casalicchio, G., Bossek, J., Studerus, E.,  
 420 Judt, L., Kuehn, T., Kerschke, P. & Fendt, F. (2016) Package “mlr.”
- 421 Bradter, U., Kunin, W.E., Altringham, J.D., Thom, T.J., & Benton, T.G. (2013) Identifying  
 422 appropriate spatial scales of predictors in species distribution models with the random forest  
 423 algorithm. *Methods in Ecology and Evolution*, **4**, 167–174.
- 424 Breiman, L. (1996) *Out-of-bag estimation*, Berkeley.
- 425 Breiman, L. (2001) Random forests. *Machine learning*, **45**, 5–32.
- 426 Breiman, L., Friedman, J., Stone, C.J. & Olshen, R.A. (1984) *Classification and regression trees*,  
 427 Chapman and Hall/CRC.
- 428 Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: A practical*  
 429 *information-theoretic approach*, 2nd Edition. Springer.
- 430 Côté, I.M., Darling, E.S., & Brown, C.J. (2016) Interactions among ecosystem stressors and their  
 431 importance in conservation. *Proceedings of the Royal Society B: Biological Sciences*, **283**,  
 432 20152592.
- 433 Cressie, N., Calder, C.A., Clark, J.S., Hoef, J.M. Ver & Wikle, C.K. (2009) Accounting for  
 434 uncertainty in ecological analysis: The strengths and limitations of hierarchical statistical  
 435 modeling. *Ecological Applications*, **19**, 553–570.

- 436 Cutler, D.R., Edwards, T.C., Beard, K.H., Cutler, A., Hess, K.T., Gibson, J. & Lawler, J.J.  
 437 (2007) Random forests for classification in ecology. *Ecology*, **88**, 2783–2792.
- 438 Darling, E.S. & Côté, I.M. (2008) Quantifying the evidence for ecological synergies. *Ecology*  
 439 *Letters*, **11**, 1278–1286.
- 440 Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.-I., Knowler, D.J., Lévêque, C.,  
 441 Naiman, R.J., Prieur-Richard, A.-H., Soto, D., Stiassny, M.L.J. & Sullivan, C.A. (2006)  
 442 Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological*  
 443 *Reviews*, **81**, 163–182.
- 444 Feld, C.K. & Hering, D. (2007) Community structure or function: Effects of environmental stress  
 445 on benthic macroinvertebrates at different spatial scales. *Freshwater Biology*, **52**, 1380–  
 446 1399.
- 447 Frissell, C.A., Liss, W.J., Warren, C.E. & Hurley, M.D. (1986) A hierarchical framework for  
 448 stream habitat classification: viewing streams in a watershed context. *Environmental*  
 449 *Management*, **10**, 199–214.
- 450 Gieswein, A., Hering, D., & Feld, C.K. (2017) Additive effects prevail: The response of biota to  
 451 multiple stressors in an intensively monitored watershed. *Science of the Total Environment*,  
 452 **593–594**, 27–35.
- 453 Gounand, I., Harvey, E., Little, C.J., & Altermatt, F. (2018) Meta-ecosystems 2.0: Rooting the  
 454 theory into the field. *Trends in Ecology & Evolution*. *in press* doi:  
 455 <http://dx.doi.org/10.1016/j.tree.2017.10.006>
- 456 Grace, J.B., Anderson, T.M., Seabloom, E.W. *et al.* (2016) Integrative modelling reveals  
 457 mechanisms linking productivity and plant species richness. *Nature*, **529**, 390–393.
- 458 Grace, J.B., Schoolmaster, D.R., Guntenspergen, G.R., Little, A.M., Mitchell, B.R., Miller, K.M.  
 459 & Schweiger, E.W. (2012) Guidelines for a graph-theoretic implementation of structural  
 460 equation modeling. *Ecosphere*, **3**, art73.
- 461 Guisan, A., Lehmann, A., Ferrier, S., Austin, M., Overton, J.M.C., Aspinall, R., & Hastie, T.  
 462 (2006) Making better biogeographical predictions of species' distributions. *Journal of*  
 463 *Applied Ecology*, **43**, 386–392.
- 464 Hapfelmeier, A. & Ulm, K. (2013) A new variable selection approach using random forests.  
 465 *Computational Statistics and Data Analysis*, **60**, 50–69.

- 466 Harvey, E., Gounand, I., Ganesanandamoorthy, P. & Altermatt, F. (2016) Spatially cascading  
 467 effect of perturbations in experimental meta-ecosystems. *Proceedings of the Royal Society*  
 468 *of London B*, **283**, 1–9.
- 469 Harvey, E., Gounand, I., Ward, C. & Altermatt, F. (2017) Bridging ecology and conservation:  
 470 from ecological networks to ecosystem function. *Journal of Applied Ecology*, **54**, 371–379.
- 471 Harvey, E. & MacDougall, A.S. (2015) Spatially heterogeneous perturbations homogenize the  
 472 regulation of insect herbivores. *American Naturalist*, **186**, 623–633.
- 473 Hastie, T., Tibshirani, R. & Friedman, J. (2009) *The elements of statistical learning: Data*  
 474 *mining, inference, and prediction*, 2nd Edition. Springer.
- 475 Hecky, R.E., Mugidde, R., Ramlal, P.S., Talbot, M.R., & Kling, G.W. (2010) Multiple stressors  
 476 cause rapid ecosystem change in Lake Victoria. *Freshwater Biology*, **55**, 19–42.
- 477 Heino, J., Melo, A., Bini, L.M., Altermatt, F., Al-Shami, S.A., Angeler, D.G., Bonada, N., Brand,  
 478 C., Callisto, C., Cottenie, C., Dangles, O., Dudgeon, D., Encalada, A., Göthe, E., Grönroos,  
 479 M., Hamada, N., Jacobsen, D., Landeiro, V., Ligeiro, R., Martins, R., Miserendino, M.L.,  
 480 Md Rawi, C.S., Rodrigues, M., Roque, F., Sandin, L., Schmera, D., Sgarbi, L., Simaika, J.,  
 481 Siqueira, T., Thompson, R.M. & Townsend, C.R. (2015) A comparative analysis reveals  
 482 weak relationships between ecological factors and beta diversity of stream insect  
 483 metacommunities at two spatial levels. *Ecology and Evolution*, **6**, 1235–1248.
- 484 Heugens, E.H.W., Hendriks, A.J., Dekker, T., van Straalen, N.M., & Admiraal, W. (2001) A  
 485 review of the effects of multiple stressors on aquatic organisms and analysis of uncertainty  
 486 factors for use in risk assessment. *Critical reviews in toxicology*, **31**, 247–284.
- 487 Hilderbrand, R.H., Lemly, A.D., Dolloff, C.A. & Harpster, K.L. (1997) Effects of large woody  
 488 debris placement on stream channels and benthic macroinvertebrates. *Canadian Journal of*  
 489 *Fisheries and Aquatic Sciences*, **54**, 931–939.
- 490 Hochachka, W.M., Caruana, R., Fink, D., Munson, A., Riedewald, M., Sorokina, D. & Kelling,  
 491 S. (2007) Data-mining discovery of pattern and process in ecological systems. *Journal of*  
 492 *Wildlife Management*, **71**, 2427–2437.
- 493 Hothorn, T., Hornik, K. & Zeileis, A. (2006) Unbiased recursive partitioning : A conditional  
 494 inference framework. *Journal of Computational and Graphical Statistics*, **15**, 651–674.



- 495 Jackson, M.C., Loewen, C.J.G., Vinebrooke, R.D., & Chimimba, C.T. (2016) Net effects of  
 496 multiple stressors in freshwater ecosystems: A meta-analysis. *Global Change Biology*, **22**,  
 497 180–189.
- 498 Kaelin, K. & Altermatt, F. (2016) Landscape-level predictions of diversity in river networks  
 499 reveal opposing patterns for different groups of macroinvertebrates. *Aquatic Ecology*, **50**,  
 500 283–295.
- 501 Kautza, A. & Sullivan, S.M.P. (2015) Shifts in reciprocal river-riparian arthropod fluxes along  
 502 an urban-rural landscape gradient. *Freshwater Biology*, **60**, 2156–2168.
- 503 Kelling, S., Hochachka, W.M., Fink, D., Riedewald, M., Caruana, R., Ballard, G. & Hooker, G.  
 504 (2009) Data-intensive science: A new paradigm for biodiversity studies. *BioScience*, **59**,  
 505 613–620.
- 506 Kelly, C. & Okada, K. (2012) Variable interaction measures with random forest classifiers.  
 507 *Proceedings - International Symposium on Biomedical Imaging*, 154–157.
- 508 King, A. (1995) Avoiding ecological surprise: Lessons from long-standing communities.  
 509 *Academy of Management Review*, **20**, 961–985.
- 510 Krell, B., Röder, N., Link, M., Gergs, R., Entling, M.H. & Schäfer, R.B. (2015) Aquatic prey  
 511 subsidies to riparian spiders in a stream with different land use types. *Limnologia*, **51**, 1–7.
- 512 Kuhn, M. (2015) Package “caret”, Classification and regression training.
- 513 Lenat, D.R. (1988) Water quality assessment of streams using a qualitative collection method for  
 514 benthic macroinvertebrates. *Journal of the North American Benthological Society*, **7**, 222–  
 515 233.
- 516 Loreau, M., Mouquet, N. & Holt, R.D. (2003) Meta-ecosystems: A theoretical framework for a  
 517 spatial ecosystem ecology. *Ecology Letters*, **6**, 673–679.
- 518 Mayfield, M. M. & Stouffer, D. B. (2017) Higher-order interactions capture unexplained  
 519 complexity in diverse communities. *Nature Ecology & Evolution*, **1**, 1–7.
- 520 McGill, W.J. (1954) Multivariate information transmission. *Transactions of the IRE Professional*  
 521 *Group on Information Theory*, **4**, 93–111.
- 522 Nicodemus, K.K., Malley, J.D., Strobl, C., & Ziegler, A. (2010) The behaviour of random forest  
 523 permutation-based variable importance measures under predictor correlation. *BMC*  
 524 *bioinformatics*, **11**, 110.

- O'Neill, R.V., DeAngelis, D.L., Waide, J.B. & Allen, T.F.H. (1986) *A hierarchical concept of ecosystems*, Princeton University Press.
- Ormerod, S. J., M. Dobson, A. G. Hildrew, and C. R. Townsend. (2010) Multiple stressors in freshwater ecosystems. *Freshwater Biology*, **55**, 1–4.
- Peters, D.P.C., Bestelmeyer, B.T. & Turner, M.G. (2007) Cross-scale interactions and changing pattern-process relationships: Consequences for system dynamics. *Ecosystems*, **10**, 790–796.
- Pimm, S.L., Ayres, M., Balmford, A., *et al.* (2001) *Can We Defy Nature's End?*
- Poff, N.L. (1997) Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society*, **16**, 391–409.
- R Development Core Team (2016) R: A language and environment for statistical computing.
- Richards, C., Haro, R., Johnson, L.B. & Host, G.E. (1997) Catchment and reach-scale properties as indicators of macroinvertebrate species traits. *Freshwater Biology*, **37**, 219–230.
- Rios, S.L. & Bailey, R.C. (2006) Relationship between riparian vegetation and stream benthic communities at three spatial scales. *Hydrobiologia*, **553**, 153–160.
- Ryo, M., Yoshimura, C., & Iwasaki, Y. (2017) Importance of antecedent environmental conditions in modeling species distributions. *Ecography*, doi: 10.1111/ecog.02925.
- Sala, O.E., Chapin III, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A.P., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., & Wall, D.H. (2000) Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770–1774.
- Schade, J.D., Fisher, S.G., Grimm, N.B. & Seddon, J.A. (2001) The influence of a riparian shrub on nitrogen cycling in a Sonoran desert stream. *Ecology*, **82**, 3363–3376.
- Seymour, M., Deiner, K. & Altermatt, F. (2016a) Scale and scope matter when explaining varying patterns of community diversity in riverine metacommunities. *Basic and Applied Ecology*, **17**, 134–144.
- Seymour, M., Seppälä, K., Mächler, E. & Altermatt, F. (2016b) Lessons from the macroinvertebrates: species-genetic diversity correlations highlight important dissimilar relationships. *Freshwater Biology*, **61**, 1819–1829.

- Soranno, P.A., Cheruvilil, K.S., Bissell, E.G., Bremigan, M.T., Downing, J.A., Fergus, C.E., Filstrup, C.T., Henry, E.N., Lottig, N.R., Stanley, E.H., Stow, C.A., Tan, P.N., Wagner, T. & Webster, K.E. (2014) Cross-scale interactions: Quantifying multi-scaled cause-effect relationships in macrosystems. *Frontiers in Ecology and the Environment*, **12**, 65–73.
- Strobl, C., Boulesteix, A.-L., Kneib, T., Augustin, T. & Zeileis, A. (2008) Conditional variable importance for random forests. *BMC bioinformatics*, **9**, 1–11.
- Strobl, C., Hothorn, T. & Zeileis, A. (2009) Party on! A new, conditional variable-importance measure for random forests available in the party package. *R Journal*, **1**, 14–17.
- Stucki, P. (2010) *Methoden zur Untersuchung und Beurteilung der Fließgewässer. Makrozoobenthos Stufe F*, Bern, Switzerland.
- Soininen, J., Bartels, P., Heino, J., Luoto, M. & Hillebrand, H. (2015) Toward more integrated ecosystem research in aquatic and terrestrial environments. *BioScience*, **65**, 174–182.
- Tonkin, J.D., Heino, J., Sundermann, A., Haase, P. & Jähnig, S.C. (2016) Context dependency in biodiversity patterns of central German stream metacommunities. *Freshwater Biology*, **61**, 607–620.
- Tonkin, J.D., Altermatt, F., Finn, D., Heino, J., Olden, J.D., Steffen, U.P. & Lytle, D.A. (2018) The role of dispersal in river network metacommunities: patterns, processes, and pathways. *Freshwater Biology*. In Press. DOI: 10.1111/fwb.13037
- Urban, M.C., Bocedi, G., Hendry, A.P. *et al.* (2016) Improving the forecast for biodiversity under climate change. *Science*, **353**, aad8466.
- Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R. & Cushing, C.E. (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 130–137.
- Vörösmarty, C.J., McIntyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S.E., Sullivan, C.A., Liermann, C.R., & Davies, P.M. (2010) Global threats to human water security and river biodiversity. *Nature*, **467**, 555–561.
- Ward, J.V. (1989) The four-dimensional nature of lotic ecosystems. *Journal of the North American Benthological Society*, **8**, 2–8.
- Williams, P.L. & Beer, R.D. (2010) Nonnegative decomposition of multivariate information. *arXiv*, **1004.2515v**, 1–14.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Detailed list of variables.

**Appendix S2** Additional results.

## **DATA ACCESSIBILITY**

The macroinvertebrate data are available with permission by the Swiss Biodiversity Monitoring BDM Coordination Office, while the data sources of explanatory variables are listed in Appendix S1.

## **BIOSKETCHES:**

**Masahiro Ryo** is interested in discovering patterns using advanced analytical tools (<http://masahiroryo.jimdo.com/>): In particular, spatial and temporal ecology and biodiversity.

**Eric Harvey** is interested in meta-community and food web ecology. He focuses on the impacts of global changes and the structure and stability of communities and ecosystem services (<http://ericharvey.weebly.com/>).

**Christopher T. Robinson** is a stream ecologist specializing in alpine streams, ranging from microbial functioning to ecosystem processes, including the eco-evolutionary dynamics of aquatic insects in relation to environmental change (<http://www.eawag.ch/en/aboutus/portrait/organisation/staff/profile/christopher-robinson/show/>) .

**Florian Altermatt** is a professor of community ecology and is interested in processes shaping diversity patterns in riverine ecosystems, using a combined approach of theory, conceptual microcosm experiments and comparative analyses of empirical datasets (<http://homepages.eawag.ch/~altermfl/Home.html>).

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610 Table 1 The 10 most important three-way interactions for local taxonomic richness of aquatic  
 611 invertebrates in Switzerland. Combinations in bold are visualized in Figure 5.

Rank	Explanatory variables			Score
<i>(a) Macroinvertebrate family richness: 1140 combinations among the 20 variables</i>				
1	Elevation	Elevation (mean)	Biogeoclimatic class	1.17
2	<b>Elevation</b>	<b>Biogeoclimatic class</b>	<b>% forest cover (5 km)</b>	<b>0.84</b>
3	Elevation	Biogeoclimatic class	Carbonate rock/silicate rock	0.82
4	Elevation	Biogeoclimatic class	% forest cover	0.81
5	Elevation (mean)	Biogeoclimatic class	% forest cover (5 km)	0.74
6	Elevation	Biogeoclimatic class	% aquatic cover (500 m)	0.70
7	Elevation	Elevation (mean)	% forest cover (5 km)	0.68
8	Elevation (mean)	% agriculture cover (5 km)	% forest cover (5 km)	0.65
9	Elevation	% agriculture cover (5 km)	% forest cover (5 km)	0.65
10	Elevation	Biogeoclimatic class	% agriculture cover (5 km)	0.60
<i>(b) EPT species richness: 680 combinations among the 17 variables</i>				
1	% forest cover (500 m)	% forest cover (5 km)	Biogeoclimatic class	1.67
2	% forest cover (500 m)	% forest cover (5 km)	Elevation	1.27
3	% forest cover (500 m)	% forest cover (5 km)	% settlement cover (5 km)	1.15
4	% forest cover (500 m)	Elevation	Biogeoclimatic class	0.94
5	% forest cover (5 km)	% forest cover	Biogeoclimatic class	0.94
6	% forest cover (500 m)	% forest cover	Biogeoclimatic class	0.94
7	<b>% forest cover (5 km)</b>	<b>Elevation</b>	<b>Biogeoclimatic class</b>	<b>0.93</b>
8	% forest cover (500 m)	% forest cover (5 km)	deciduous/coniferous forest	0.89
9	% forest cover (500 m)	Elevation (mean)	Biogeoclimatic class	0.84
10	% forest cover (500 m)	% settlement cover (5 km)	Biogeoclimatic class	0.80

612 Footnote: 500 m and 5 km as buffer distance from the sampling site to the upstream catchment

## FIGURE LEGENDS

Figure 1. Local taxonomic richness ( $\alpha$ -diversity) of riverine macroinvertebrates in Switzerland among 518 biodiversity monitoring sites: (a) family richness and (b) EPT species richness. Large lakes and main rivers are in dark blue. The different major drainage basins are color-coded on the map (see also inset): the river Rhine (light blue) drains into the North Sea, the river Rhone (pink) drains into the Mediterranean Sea, the river Danube drains into the Black Sea (salmon), and the remaining rivers (green) drain into the Adriatic Sea.

Figure 2. Relative importance scores of selected explanatory variables (out of 76 variables) for local taxonomic richness ( $\alpha$ -diversity) of riverine macroinvertebrates in Switzerland: (a) family richness and (b) EPT species richness. See Appendix S1 for variable description.

Figure 3. Representative modeled relationships of explanatory variables for macroinvertebrate family richness: C, Central plain; J, Jura; N, North flank of Alps; S, South flank of Alps; E, eastern Central Alps; and W, western Central Alps. See Appendix S2 for all the variables.

Figure 4. Frequency distributions of the relative importance measures of all possible three-way interactions.

Figure 5. Representative interactive effects of biogeoclimatic region, elevation, and the relative proportion of forest cover within 5 km-buffer distance on macroinvertebrate family richness. The higher partial dependence score reflects a higher richness. See Appendix S2 for other examples.

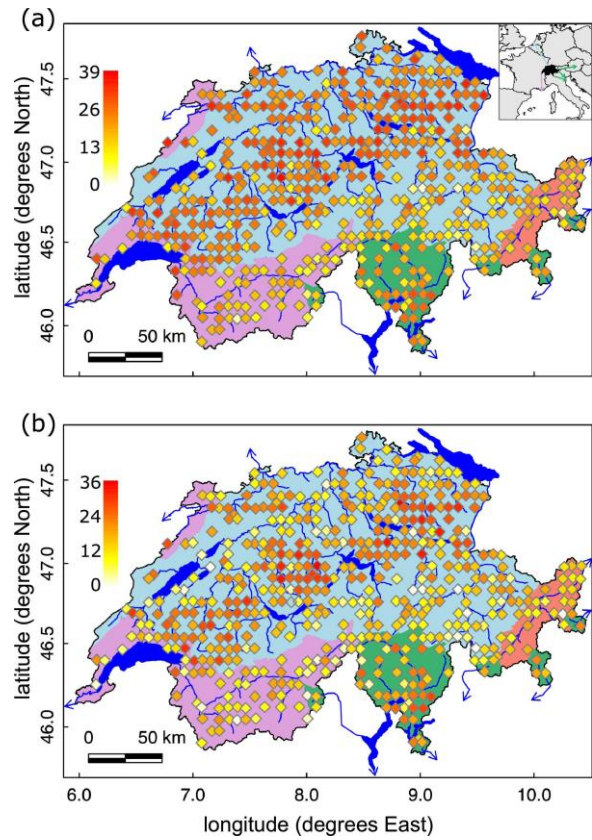


Figure 1.

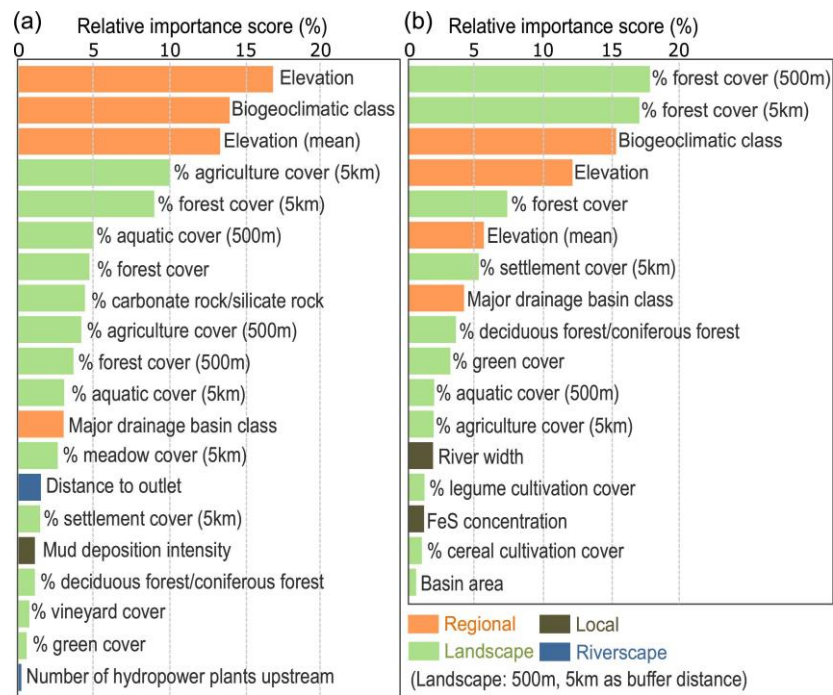


Figure 2.

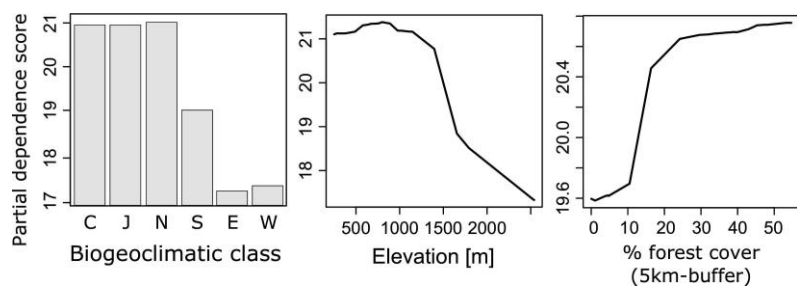


Figure 3.

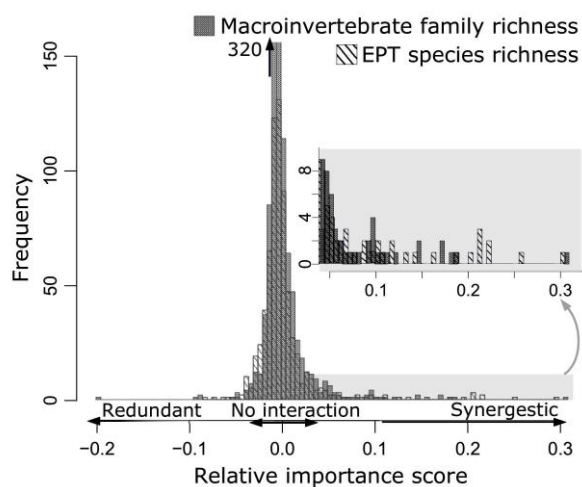


Figure 4.

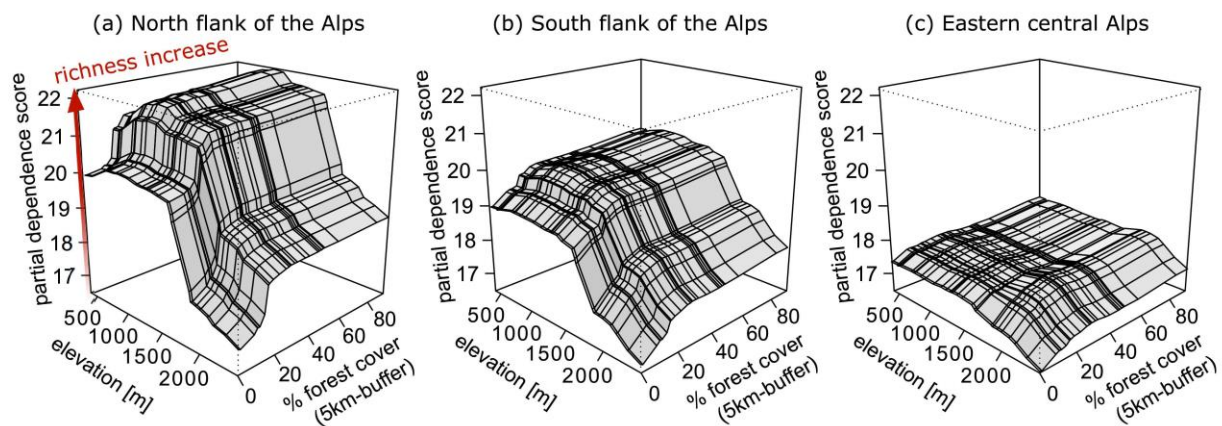


Figure 5.