ORIGINAL ARTICLE

Nonlinear higher order abiotic interactions explain riverine biodiversity

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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 metacommunity 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^2).

Methods: Riverine α-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 1,140 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
conservation, context dependency, ecological surprises, freshwater, land use, machine learning, macroinvertebrates, metacommunity, meta-ecosystem, multiple stressors

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1 | 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, Gounand, Ward, & Altermatt, 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 and Côté (2008) and Jackson, Loewen, Vinebrooke, and Chimimba (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, Dobson, Hildrew, & Townsend, 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, Liss, Warren, & Hurley, 1986; O'Neill, DeAngelis, Waide, & Allen, 1986; Poff, 1997). These factors include catchment hydrological processes that reflect upstream terrestrial conditions (Richards, Haro, Johnson, & Host, 1997), connections with adjacent riparian ecosystems (Harvey, Gounand, Ganesanandamoorthy, & Altermatt, 2016; Loreau, Mouquet, & Holt 2003; Soininen, Bartels, Heino, Luoto, & Hillebrand, 2015; Vannote, Minshall, Cummins, Sedell, & Cushing, 1980) and linkages of local environments in dendritic river networks (Altermatt, 2013; Altermatt, Seymour, & Martinez, 2013; Tonkin et al., 2018; Vannote et al., 1980; Ward, 1989). Previous studies reported that major ecological surprises sometimes emerge, as these multiple factors often cause nonlinear interactive effects in freshwater ecosystems (e.g. Hecky, Mugidde, Ramlal, Talbot, & Kling, 2010; Ormerod et al., 2010).

Although 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, Hering, & Feld, 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 (Mayfield & Stouffer, 2017; Sala et al., 2000; Tonkin, Heino, Sundermann, Haase, & Jähnig, 2016). 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, Darling, & Brown, 2016; Gieswein et al., 2017; Mayfield & Stouffer, 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 test statistically (cf. as a rule of thumb, at least 5–10 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; Ryo & Rillig, 2017). 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 metacommunity. We asked the following questions: (1) are key HOI of environmental factors detectable from the numerous possible combinations using a machine learning technique? (2) which environmental factors play a major interactive role? and (3) 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 α-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 (1,140 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 interactions) 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 & Case, 1994 and reference therein).

2 | MATERIALS AND METHODS

Our study used presence–absence data of aquatic macroinvertebrates in Switzerland, from a governmental monitoring programme ("Biodiversity Monitoring in Switzerland BDM"; BDM Coordination Office, 2014). The programme 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).

2.1 | Biogeography of Switzerland

Switzerland is a relatively small country (41,285 km^2) in the centre of Europe (Figure 1) composed of different biogeographical units. A large
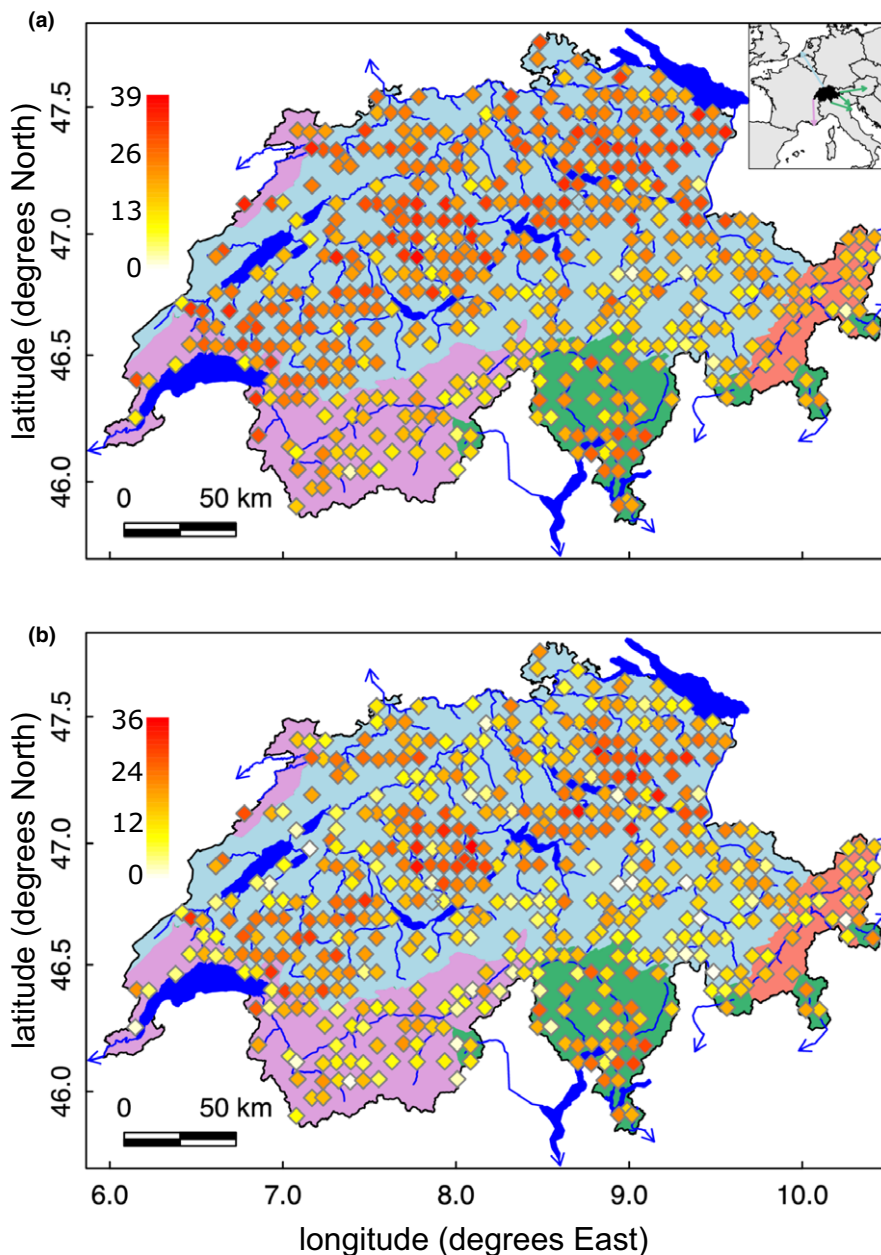
FIGURE 1 Local taxonomic richness (α-diversity) of riverine macroinvertebrates in Switzerland, among 518 biodiversity monitoring sites: (a) family richness and (b) EPT species richness. Large lakes and main rivers are in dark blue. The different major drainage basins are colour coded on the map (see 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 [Color figure can be viewed at wiley onlinelibrary.com]

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 submediterranean climates, south of the Alps. Switzerland covers a large elevational gradient, ranging from 193 to 4,634 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) (Figure 1). Due to its small size, the Etsch data were pooled with the Po data in the present study.

2.2 | Study sites and sampling methods

The BDM currently monitors 518 study sites across Switzerland (Figure 1), representing the diversity of stream macroinvertebrates in the country (see also Altermatt et al., 2013; Kaelin & Altermatt, 2016; Seymour, Deiner, & Altermatt, 2016; Seymour, Seppälä, Mächler, & Altermatt, 2016). Sampling was conducted in wadeable streams, second order or larger in size, and excluded standing waterbodies, first order streams and large rivers inaccessible by wading (Stucki, 2010). Each site was sampled once between 2009 and 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 × 25 cm, 500 μm mesh) sampling procedure defined in the Swiss "Macrozoobenthos Level I" module for stream benthic macroinvertebrates (Altermatt et al., 2013; BDM Coordination Office, 2014; Stucki, 2010). Briefly, eight kick-net samples were taken at each site to cover all major microhabitats within an area (10× 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 riverbeds) 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).

2.3 | 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. As 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.

2.4 | 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, Deiner, et al., 2016). 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 (five variables). This category included two elevation measures (elevation at the site and the mean elevation of the catchment upstream of the site), two catchment classifications (three classes for major catchments and nine classes for subcatchments) and a biogeoclimatic classification (six 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 six 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, Deiner, et al., 2016).

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 sulphide concentration).

2.5 | Random forest modelling with variable selection

We did not exclude any explanatory variable before analysis because the approach employed can (1) perform variable selection, (2) evaluate the relative importance among highly correlated variables (Bergmann, Ryo, Prati, Hempel, & Rillig, 2017; Bradter, Kunin, Altringham, Thom, & Benton, 2013; Nicodemus, Malley, Strobl, & Ziegler, 2010; Ryo, Yoshimura, & Iwasaki, 2017) and (3) fairly assess the relative importance between continuous and categorical variables without bias (Hothorn, Hornik, & Zeileis, 2006; Strobl, Boulesteix, Kneib, Augustin, & Zeileis, 2008). We used the RF machine learning algorithm for performing multiple regressions with variable selection (Hapfelmeier & Ulm, 2013; Ryo & Rillig, 2017).

In short, the RF algorithm uses a model ensemble approach that constructs a large number of decision tree models (Breiman, Friedman, Stone, & Olshen, 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 and Ulm (2013) takes two modelling 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, 2001).

After variable selection, we ranked the relative importance scores of the explanatory variables and visualized their modelled relationships to each response variable. Partial dependence plots were used for visualization (Hastie, Tibshirani, & Friedman, 2009), which delineate modelled 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 and 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 overfitting 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). We used the R script available in Hapfelmeier and Ulm (2013), which is based on "ctree" and "cforest" functions of the "party" package (Strobl, Hothorn, & Zeileis, 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).

2.6 | 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 1,140 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 and Okada (2012) that quantifies the relative importance of variable interactions based on permutation with RF. As Kelly and Okada (2012) were limited to two-way interactions, we extended their work to three-way interactions based on mutual information theory (Anastassiou, 2007; McGill, 1954; 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∩B is the effect of the interaction between variables A and B, excluding their independent effects. A∪B is the total effects of variables A and B, including both independent and interactive effects.

E(A∪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∩B∩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 zero indicates no interaction. The R function *intimp* we developed is also available at github (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.

3 | 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 (Figure 1). Macroinvertebrate family and EPT species richness were highly correlated (Pearson's $r = .81$). Of 76 explanatory variables, 20 and 17 variables were finally selected (Figure 2) for the RF models of macroinvertebrate family and EPT species richness, respectively, and their association patterns were individually estimated (Figure 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 (Figure 2). Elevation, the relative proportion of forest land cover and biogeoclimatic

FIGURE 2 Relative importance scores of selected explanatory variables (of 76 variables) for local taxonomic richness (α-diversity) of riverine macroinvertebrates in Switzerland: (a) family richness and (b) EPT species richness. See Appendix S1 for variable description [Color figure can be viewed at wileyonlinelibrary.com]
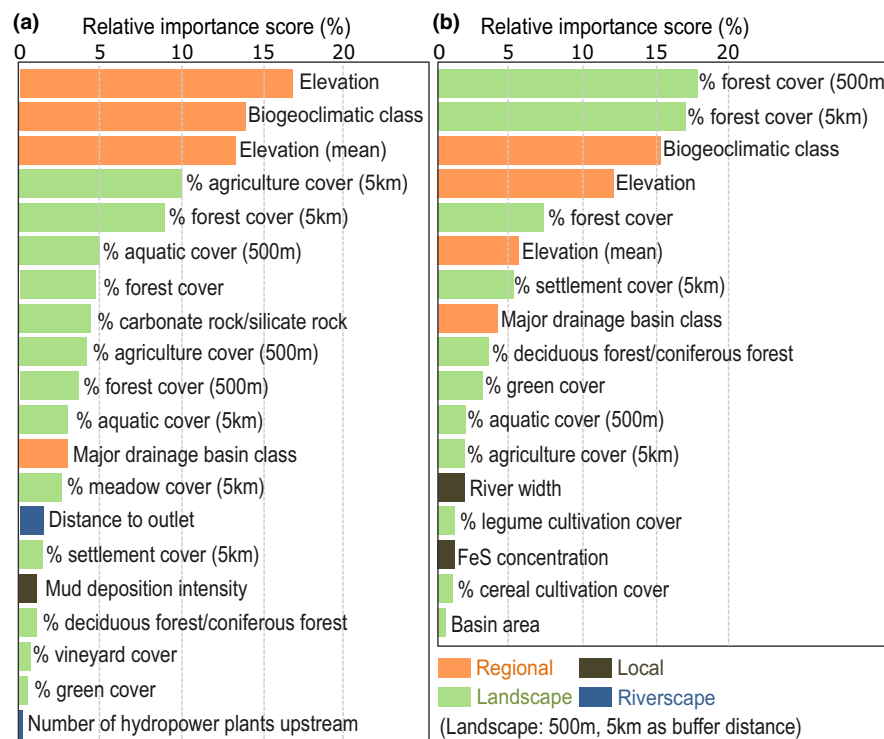
classifications were ranked within the top five for both richness measures (Figure 2). Specifically, both richness measures were monotonically declining above 1,000 m, were decreasing where the relative proportion of forest land cover within any buffer distance was lower than 20%–30% and were lower in the central Alps regions than in other regions (Figure 3 and Figure S1).

More than 97% of the possible three-way combinations had importance scores near zero, that is, between −0.1 and 0.1 (1,124 of 1,140 combinations for macroinvertebrate family richness and 663 of 680 combinations for EPT species richness). Less than 20 combinations exceeded an importance score ≥0.1 for both richness

measures (Figure 4). This indicates that only a few three-way interactions explained both richness measures meaningfully. Same as the relative importance of individual factors (Figure 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% × 1/1,140 = 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
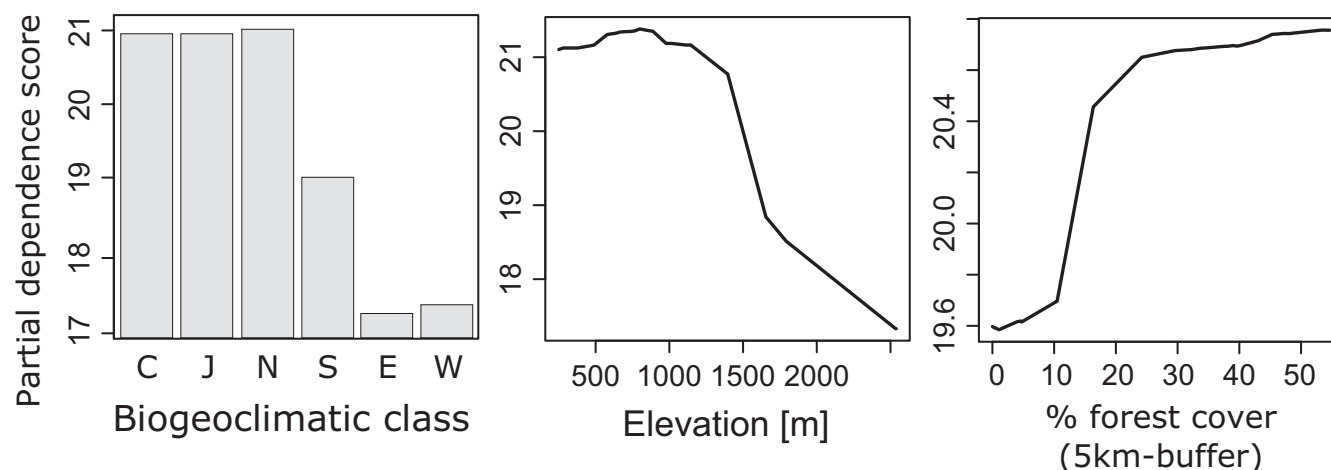

FIGURE 3 Representative modelled relationships of explanatory variables for macroinvertebrate family richness: C, Central plain; J, Jura; N, North flank of Alps; S, South flank of Alps; E, eastern Central Alps and W, western Central Alps. See Appendix S2 for all the variables
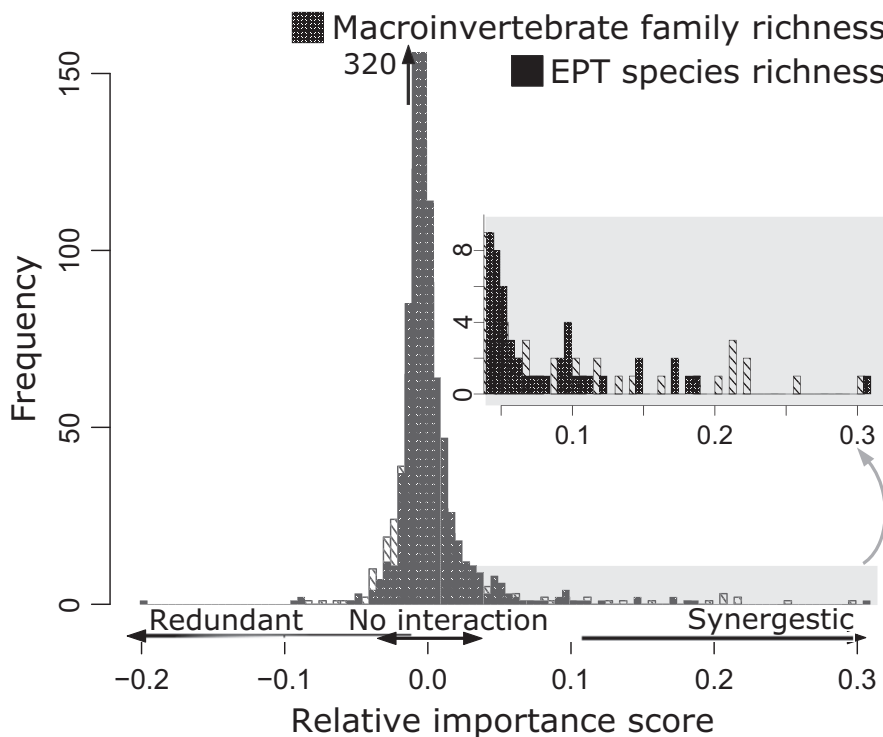
FIGURE 4 Frequency distributions of the relative importance measures of all possible three-way interactions

regions, elevation and the relative proportion of forest land cover (Figure 5). Most distinctly, negative synergetic effects were found commonly where the relative proportion of forest land cover (5 km buffer) was <20%–30%, together with the conditions of over 2,000 m of elevation (at the bottom foreground corner of each cube in Figure 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 (Figure 5a and Figure S2), moderate in the south flank of the Alps (Figure 5b) and lowest in the eastern and western Central Alps (Figure 5c and Figure S2). The variation caused by the interactions cannot be explained by their individual effects (Figure 3).

4 | 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 (Araújo & Guisan, 2006; Guisan et al., 2006; Sala et al., 2000). 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 (1) a machine learning algorithm with mutual information theory can extract a few key HOI of environmental factors from numerous possible three-way interactions and (2) 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; Figure 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 versus 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 (Gounand, Harvey, Little, & Altermatt, 2018; Loreau et al., 2003). 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 (Feld & Hering, 2007; Hilderbrand, Lemly, Dolloff, & Harpster, 1997). Furthermore, roots in soil influence biogeochemical conditions together with root-associated microbes (Schade, Fisher, Grimm, & Seddon, 2001). Plant community composition, which shows turnover along an elevational gradient, can also be important for these functions. Furthermore,

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

Rank	Explanatory variables			Score
(a) Macroinvertebrate family richness: 1140 combinations among the 20 variables				
1	Elevation	Elevation (mean)	Biogeoclimatic class	1.17
2	**Elevation**	**Biogeoclimatic class**	**% forest cover (5 km)**	**0.84**
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
(b) EPT species richness: 680 combinations among the 17 variables				
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	**% forest cover (5 km)**	**Elevation**	**Biogeoclimatic class**	**0.93**
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

500 m and 5 km as buffer distance from the sampling site to the upstream catchment.
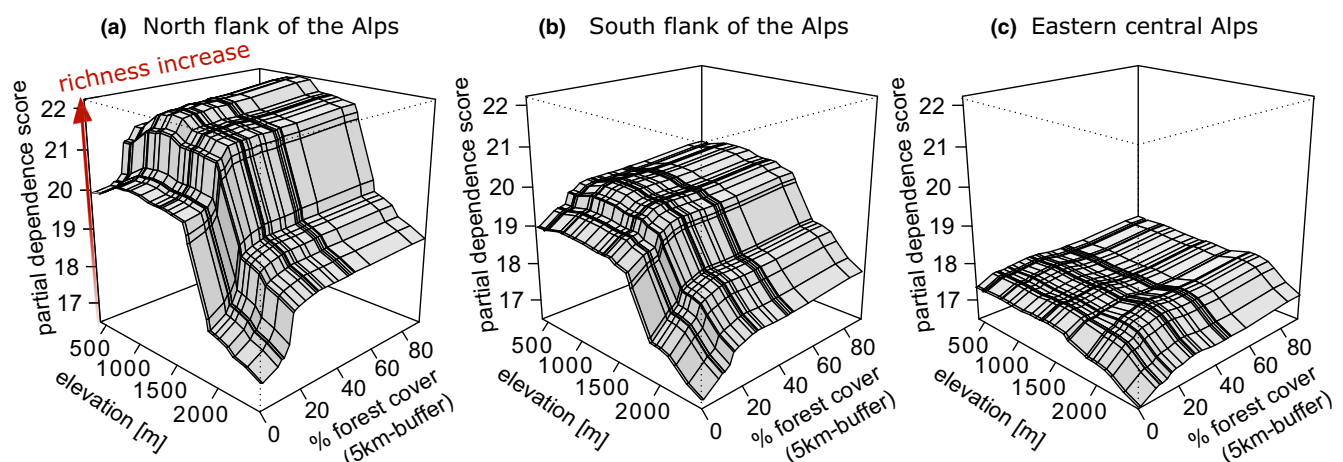

FIGURE 5 Representative interactive effects of biogeoclimatic region, elevation and the relative proportion of forest cover within 5 km-buffer distance on macroinvertebrate family richness. The higher partial dependence score reflects a higher richness. See Appendix S2 for other examples [Color figure can be viewed at wileyonlinelibrary.com]

plant community composition also dependents 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, Hendriks, Dekker, van Straalen, & Admiraal, 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 (Kaelin & Altermatt, 2016; Kautza & Sullivan, 2015; Krell et al., 2015; Seymour, Deiner, et al., 2016) 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 (first rank for EPT in Table 1 and Figure 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, Bestelmeyer, & Turner, 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 modelling attempts. The explanatory power was two- to threefold higher than that reported in previous studies that analysed subsets of variables from the same dataset (20%–30%; e.g. Altermatt et al., 2013; Seymour, Deiner, et al., 2016). Therefore, the limited power of explaining biodiversity in riverine ecosystems may not necessary, not only 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 multiprocess hierarchical or network-based statistical assumptions in ecology also can offer new insights into ecological analyses (Cressie, Calder, Clark, Ver Hoef, & Wikle, 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, towards concluding the importance of interactive effects across scales, organisms and ecological levels.

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.

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BIOSKETCHES

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

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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).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.