Landscape level predictions of diversity in river networks reveal opposing patterns for different groups of macroinvertebrates

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Abstract

Aquatic biodiversity in rivers and streams is threatened in many regions worldwide. As biodiversity loss has severe consequences on ecosystem functioning, it is important to understand the causes of decline and to predict biodiversity in space and time. In order to achieve this, the identification of the driving factors and the appropriate choice of indicator groups is needed. We developed a spatially explicit habitat distribution model for aquatic macroinvertebrates in Swiss watercourse networks using national biodiversity monitoring data from 410 randomly selected sampling sites. We specifically looked at two worldwide frequently used macroinvertebrate indicator groups. Using generalized linear models, we related firstly species richness of mayfly, stonefly, and caddisfly (Ephemeroptera, Plecoptera, Trichoptera; EPT) and secondly richness of all macroinvertebrate families and higher order taxa (macroinvertebrate family richness) to 38 nationwide available environmental variables. We then predicted richness of both indicator groups at the landscape scale, providing the first nationwide prediction of EPT species and macroinvertebrate family richness. Consistent with previous work, we found that variables describing land-use and topology were most important for explaining richness at the landscape level. However, the two indicator groups showed opposing patterns of richness and a different sensitivity to land-use variables. This indicates that the sole use of one of these groups may be misleading with respect to water quality assessments and to the identification of overall diversity hotspots. We conclude that commonly used richness patterns derived from aggregated groups, such as family level macroinvertebrate richness, may be less appropriate for conservation strategies.

Key words: Biodiversity, dendritic networks, habitat modeling, environmental niche modeling, landscape-scale, up-scaling.

Introduction

The distribution of biodiversity is typically highly spatially heterogeneous (Clarke et al. 2008). According to the metacommunity concept, the spatial distribution of taxa is shaped by the interaction between environmental factors (environmental niche) and spatial patterns (dispersal; Holyoak et al. 2005). The application of this concept is especially important in riverine ecosystems (e.g., Brown et al. 2011, Altermatt 2013, Carrara et al. 2014, Mari et al. 2014, Seymour et al. 2015), which have a characteristic dendritic network structure, to which environmental factors are inherently linked. While in the past environmental variables have been cited as primary determinants of taxa richness distribution (for reviews see Clarke et al. 2008 and Altermatt 2013), the relative importance of these determinants is now thought to vary across communities and regions (e.g., Lin et al. 2013) and to depend on the scale of observation (e.g., Seymour et al. 2016).

Changes in taxa richness alter ecosystem processes and affect the resistance of ecosystems to environmental changes (Chapin et al. 2000). Hence, improving the understanding of taxa richness distribution is important, especially with regard to the multifaceted anthropogenic impacts on taxa richness distribution (e.g., O'Connor et al. 2012). Currently observed environmental changes, such as land-use change, pollution or climate change, have an especially large impact on freshwater taxa richness distribution. 65% of the global watercourse habitats are threatened (Vörösmarty et al. 2010) and freshwater habitats have experienced a far greater decline than the most affected terrestrial habitats (Dudgeon et al. 2006). Freshwater ecosystems are particularly fragile because the dispersion of organisms is limited. Artificial structures fragment watercourses and terrestrial land-use alters the biogeochemical freshwater dynamics via the hydrological cycle at the landscape level (Allan, 2004). Given that freshwater supports almost 6% of all described species, despite only covering 0.8% (Dudgeon et al. 2006) of the earth's surface,

it is important to understand the state of biodiversity and the possible causes of biodiversity decline.

Watercourse macroinvertebrates (hereafter referred to as macroinvertebrates) are of key interest with respect to biodiversity patterns in riverine ecosystems (e.g., Heino et al. 2015) and they are often used as bioindicators. Their sampling and identification is relatively easy, their sensitivity and generally low mobility make them vulnerable to unfavorable local environments and their role in the aquatic food web is vital (e.g., Tachet 2010). Most studies on biodiversity or water quality assessments investigate macroinvertebrates either at family, genus or species richness level (e.g., Astorga et al. 2012, Grönroos & Heino 2012, Altermatt et al. 2013, Tonkin 2014, Heino et al. 2015). Family or genus richness level of macroinvertebrates is commonly used as its application is simple and as it requires relatively low taxonomic skills (e.g., Bouchard 2004, Tachet 2010). It is also the standard of many governmental richness assessments (e.g., indice biologique global normalisé IBGN; Tachet 2010). Assessments at the species richness level are also widely used, but generally focus on a few macroinvertebrate orders, such as Ephemeroptera, Plecoptera, Trichoptera (often summarized as EPT), or Odonata (for a meta-analysis that uses this kind of data see e.g., Heino et al. 2015). The identification to the species level is less commonly used than the identification to a higher taxonomic level. This is mostly attributed to the lack of appropriate identification tools and/or the lack of personnel or expertise needed for the identification. It is often assumed that the insights from one macroinvertebrate group (e.g., species level of EPT) can be transferred to other groups of macroinvertebrates (e.g., macroinvertebrate family level) (e.g., Tachet 2010).

Nowadays, advances in statistics and available GIS data and methods (Guisan & Zimmermann 2000, Guisan & Thuiller 2005) allow the inclusion of many environmental variables at the landscape level. This substantially improves taxa habitat distribution

models. A series of previous studies in the river Rhine catchment in Switzerland found that spatial patterns explain most of the variation in community composition, while environmental variables and their interaction with spatial patterns explained less (Altermatt et al. 2013, Seymour et al. 2016). However, these studies only used a subset of available environmental variables and the overall amount of variation explained in these models was not satisfactory (~20%) for predicting spatial heterogeneity of EPT and macroinvertebrate family richness at the landscape level.

In this study, we carried out a spatially explicit nationwide macroinvertebrate habitat distribution model for the EPT species richness and the macroinvertebrate family and higher order taxa richness in Swiss watercourse networks, with the help of regression analyses. We used an extensive set of environmental variables (including hydraulic conditions, land use variables, and topological variables; see Table 1 for the full list of variables) to firstly predict taxa richness at the landscape level, and to secondly compare the diversity patterns among these two major macroinvertebrate indicator groups. The latter aim is important, as it clarifies if biomonitoring approaches, which use different taxa level identifications, draw the same conclusions regarding biodiversity distribution and potential biodiversity drivers.

Material and Methods

To model taxa richness-distribution, we used macroinvertebrate family richness and EPT species richness from 410 randomly selected and monitored watercourse sites within Switzerland. These sites are monitored by the nationwide federal biodiversity monitoring program (Biodiversity Monitoring Switzerland, BDM). Details regarding the study sites, sampling procedure and methodologies used in the BDM can be found in Stucki (2010) and Altermatt et al. (2013). As explanatory variables, we used 38 environmental variables

(Table 1), which were available nationwide at the landscape level. Firstly, we modeled diversity-distributions and secondly, we predicted the nationwide richness patterns of both indicator groups to 22,169 sub-catchments at the landscape level, covering all of Switzerland. The modeling steps included the definition of the study areas, the selection of appropriate environmental variables and the model building, selection, prediction and evaluation (Figure 1).

Response variable: diversity of macroinvertebrates

In Switzerland, the BDM has monitored macroinvertebrates in watercourses at 570 randomly distributed sampling sites since 2009 (Stucki 2010, Altermatt et al. 2013, Koordinationsstelle BDM 2014). Only wadable watercourses with a Strahler order ≥ 2 which appear on maps with a 1:25,000 scale are considered. Yearly, a distinct and random subset of all sites is monitored with equal sampling effort. At the time our study was carried out, data from 410 sampling sites were available (dots in Fig. 2). Each sampling site consists of an area defined by the width of the stream x 10 times the width (giving the length). At each site, macroinvertebrates are sampled based on well-defined procedures using the kicknet method (for details see Stucki 2010, Altermatt et al. 2013). In total eight samples were taken at all habitat types found within the sampling site (for details see Stucki 2010) and subsequently pooled. Macroinvertebrates belonging to the orders of mayfly, stonefly or caddisfly (Ephemeroptera, Plecoptera and Trichoptera; abbreviated as EPT) are identified to the species level. The sum of these species per site is henceforward referred to as “EPT species richness”. All other macroinvertebrates are identified to the family or higher taxa level (Stucki, 2010). The sum of these higher taxa level per site is henceforward referred to as “macroinvertebrate family richness”.

Definition and use of sub-catchments

To up-scale diversity patterns from the sampling site-level to the landscape level, we linked sampling site diversity patterns to environmental variables that were available at the landscape level. We assumed that the environmental niche is homogenous within a sub-catchment unit at small scale. We thus used the nationwide available catchment datasets (BAFU 2012) at the 2 km² scale. For this dataset many environmental variables are available (Tables 1 and S1). The nationwide landscape-level prediction was carried for 22,169 sub-catchments covering all of Switzerland (BAFU 2012).

Explanatory variables: environmental variables

We only considered environmental variables for which nationwide landscape-level spatial data were available at the resolution of our 2 km² sub-catchments. Many previous studies primarily related macroinvertebrates to locally measured in-stream habitat features such as pH or water temperature (e.g. Miserendino 2001, Aguiar et al. 2002, Heino et al. 2003). As these variables are generally not available at the landscape level it is not possible to use them for landscape-level predictions. We initially selected 38 environmental variables. These variables are characterized by ecological relevance and previous usage in literature (e.g. Richards et al. 1997, Sliva & Williams 2001, Sawyer et al. 2004, Egler et al. 2012, Wahl et al. 2013, Seymour et al. 2016) (Supplement Table S1 and Fig. S7). To avoid a multicollinearity problem, we had to select a subset of variables for the analysis. Firstly, variables that correlated with each other ($|r| > 0.7$) were grouped (Supplement Table S2). We retained the most powerful explanatory variable per correlation group considering the quality of the spatial datasets and using tree models. Tree models give guidance about which explanatory variables to include by indicating which explanatory variables have the biggest explanatory power. Secondly, a tree model was carried out for all correlating

explanatory variables with the highest explanatory power and all non-correlating explanatory variables (Supplement Fig. S1 and S2). We thereby ended up with a set of 11 variables for the EPT species and a set of 10 variables for the macroinvertebrate families, which we used for the final model-building (Table 2 and 3).

Statistical analysis: generalized linear model

We conducted generalized linear models (GLMs) using Poisson error distribution. To avoid over-parameterization, we only considered main effects and all two-way interactions. To reduce redundant variables we used two independent model selection procedures. Firstly, we used a stepwise selection method based on Akaike's Information Criteria (backward stepwise selection method, in the following referred to as "step model"). Secondly, we used a model shrinkage method (lasso model selection method, in the following referred to as "lasso model"). The model building and selection was carried out for EPT species and macroinvertebrate family richness on the basis of the 410 BDM sub-catchments. We then used these models to predict the nationwide richness at the landscape level. For the model evaluation we used the standard error and the residuals between the mean of the lasso and the step prediction and the recorded macroinvertebrate richness values.

All modeling steps were carried out with programmed scripts in Python (Python team 2014) and R (R Core team 2014) with R packages *tree* (Ripley, 2015) and *glmnet* (Friedman et al. 2010), to automate repetitive steps and ensure reproducibility.

Results

Across all watercourses in Switzerland, the average richness of EPT taxa was 15.2 (range 0–35) and the average richness of macroinvertebrate families was 19.8 (range 1–39; for

more details on these richness distributions, see also Altermatt et al. 2013 and Seymour et al. 2016). The environmental variables explaining EPT species richness include, from most significant to least, *proportion of forest area*, *proportion of green area*, *proportion of corn cultivation area*, *proportion of street area*, *proportion of deciduous forest relative to total forest area*, *proportion of carbonate rock* and *total length of watercourses* (if not specified differently, all proportions relative to total sampling catchment area; for details, see Table 2). The environmental variables explaining macroinvertebrate family richness are, from most significant to least, *proportion of green area*, *mean meters above sea level*, *proportion of forest area*, *proportion of building facade area*, *proportion of vegetable cultivated area*, *mean watercourse gradient*, *proportion of vineyard area* and *proportion of orchard area* (if not specified differently, all proportions relative to total sampling catchment area; for details, see Table 3). Although some environmental variables are significant for both macroinvertebrate indicator groups, there are substantial differences in the environmental variables contributing significantly to the explanation of the respective macroinvertebrate indicator group. Important differences between the EPT species richness and macroinvertebrate family richness models were found in related but distinct arable land-use categories (captured by *proportion of corn cultivation area* in the EPT species and by *proportion of vegetable cultivated area* in the macroinvertebrate family model) and in developed area land-use categories (*proportion of street area* for EPT species and *proportion of building facade area* for macroinvertebrate family richness, respectively). The environmental variables *proportion of forest area* and *proportion of green area*, in contrast, were important for both the EPT species and the macroinvertebrate family. For the EPT species, agriculture (*proportion of corn cultivation area*) reduced a more significant amount of deviance of the recorded macroinvertebrate richness than man-made constructions (*proportion of street area*). The opposite holds true for the

macroinvertebrate taxa: settlements (*proportion of building facade area*) reduced a more significant amount of deviance of the recorded macroinvertebrate richness than agriculture (*proportion of vegetable cultivated area*). *Meters above sea level* and *mean watercourse gradient* did not reduce a significant amount of deviance on their own, but only reduced a significant amount of deviance of the recorded EPT species richness in interactions with other variables. *Proportion of carbonate rock* and *proportion of deciduous forest relative to total forest area* reduced a significant amount of deviance for the EPT species recorded but not for the macroinvertebrate family taxa recorded.

The nationwide predictions of EPT species and macroinvertebrate richness showed highly distinct and diverging patterns (EPT species richness Fig. 2 and Supplement Fig. S3; macroinvertebrate family richness Fig. 3 and Supplement Fig. S4). The nationwide EPT species prediction maps suggest that the EPT species mostly occur in wooded and livestock farming areas at intermediate elevation (compare richness predictions in Figs. 2 and 3 with the spatial distribution of all environmental variables given in Fig. S7). Distinctly fewer EPT species occur in highly cultivated lowland areas or at high-altitude regions of the Alps. The nationwide predicted distribution of the macroinvertebrate family richness shows an opposing pattern. It is mainly driven by decreasing richness with increasing elevation. There are some exceptions to this conclusion (e.g., the “Wallis” in southern Switzerland). The Wallis is characterized by high values of the land-use variables *proportion of orchard area* and *proportion of vineyard area*. When comparing the nationwide predictions of the EPT species richness and of the macroinvertebrate family richness two observations can be made. Firstly, the nationwide EPT species predictions show a wider range of predicted values than the nationwide macroinvertebrate family richness prediction. Secondly, based on visual inspection, the predicted EPT species richness values and macroinvertebrate family richness values do not correlate spatially.

The range of the estimated standard error is larger for the macroinvertebrate family richness prediction than for the EPT species richness prediction (Fig. S5). High estimated standard errors are often found at lake inflows and outflows for both taxa groups. When comparing the individual predictions (EPT species richness and macroinvertebrate family richness with the step and lasso model respectively) with the monitored values, we found that the macroinvertebrate indicator group richness is over-predicted by the models when few macroinvertebrates are present and under-predicted by the models when numerous macroinvertebrates are present (Supplement Fig. S6).

Discussion

We here present the first nationwide prediction of the EPT species and macroinvertebrate family richness for Switzerland (Figs. 2 & 3). We find highly diverging diversity patterns and thus question the common interchangeable use of these groups as ecological indicators (e.g., Bouchard 2004, Tachet 2010). In our analysis, we only used land-use variables that are available at the landscape level. This allows the nationwide prediction of the macroinvertebrate indicator group richness at the landscape-level. Such an approach has been rarely applied before. Most studies from other regions (including major catchments in North America, Europe and Asia; e.g., Heino et al. 2003, Maloney et al. 2011, Astorga et al. 2012, Grönroos & Heino 2012, Tonkin 2014, Heino et al. 2015, Tonkin et al. 2015, but see Richards et al. 1997) have related macroinvertebrate diversity to locally measured environmental variables (see also similar studies on fish, e.g. Blanchet et al. 2012). While the latter approach allows the identification of relevant local variables, it generally prohibits landscape level predictions, which are, for example, commonly conducted for terrestrial plants or animals (Guisan & Zimmermann 2000, Guisan & Thuiller 2005). Such landscape level predictions and visualizations, however, are crucial for the planning and

communication of conservation strategies and management actions in freshwater ecosystems, and allow to disentangle the effect of local environmental variables versus network structure as drivers of diversity in dendritic networks (Altermatt 2013, Carrara et al. 2014). Whereas landscape-level predictions exist at national or continental scales for marine or terrestrial organisms (e.g., Guisan & Zimmermann, 2000; Tittensor et al. 2010), there are very few examples for freshwater invertebrates. Moreover, they are mostly restricted to a small set of taxa (e.g., amphipods or groundwater crustaceans, Altermatt et al. 2014, Zgamaister et al. 2014).

Diversity and richness of macroinvertebrates in freshwater are, among others, affected by human land use change and chemical pollution. Our up-scalable landscape-level environmental variables (Table 1, Fig. S7) were chosen to closely match previously identified relevant environmental variables affecting macroinvertebrates. In accordance to past local-scale studies (e.g., Roy et al. 2003, Moore & Palmer 2005, Egler et al. 2012, Wahl et al. 2013), the nationwide model predicted that EPT species richness is highest in woodlands, followed by grasslands and pastures during our landscape-level approach. In contrast to past studies, however, the model predicted the lowest EPT species richness in cultivated areas (especially vine- and fruit-growing areas) and not in populated areas. This suggests that pollutants from cultivated land (e.g., Wittmer et al. 2014) may be having a greater effect on the EPT species richness in Switzerland than urban pollution. This observation is supported by the fact that arable land variables reduce more residual deviance of the recorded EPT species richness than urban site variables. In accordance, a study found that a significant proportion of chemicals found in rivers can be attributed to plant protection products used in agriculture (Wittmer et al. 2014). This indicates that agriculture impacts water quality more than populated areas, corroborating the observed and the predicted diversity patterns at the landscape level.

In contrast, the nationwide macroinvertebrate family richness prediction does not strictly follow the land-use ranking found in literature (e.g., Heino et al. 2003, Grönroos & Heino 2012) and is mainly determined by the topological variables elevation and mean watercourse gradient (i.e., steepness). A pattern of highest richness at mid-elevation has recently also been attributed to the topographic structure of landscapes only (Bertuzzo et al. 2016). Nevertheless, the statistical results (Table 3) indicate that land-use variables significantly reduce the residual deviance of the recorded macroinvertebrate family richness. As the macroinvertebrate family is a conglomerate of numerous orders (Stucki 2010), they are characterized by a variety of different ecological niches. Thus it is likely that there is a larger variance among the sensitivity of the macroinvertebrate family towards land-use variables than among the EPT species. As a consequence, the effects that were observed for the EPT species richness may be blurred for the macroinvertebrate family richness. This might also explain why the developed area land-use variable reduces more residual deviance of the recorded macroinvertebrate family species richness during the BDM than the cultivated land-use variables. Different cultivated-land-use variables (EPT species richness: *proportion of corn cultivation area*; macroinvertebrate family richness: *proportion of vegetable cultivated area*) and developed area land-use variables (EPT richness: *proportion of street area*; macroinvertebrate family richness: *proportion of building facade area*) explained the largest amount of deviance in the response variable for the EPT species richness and macroinvertebrate family taxa richness. This reinforces the idea that different macroinvertebrate orders are characterized by distinct sensitivities and habitat preferences.

The observed over- and under-predictions in the models (Supplement Fig. S6) indicate that additional explanatory variables may need to be considered in the models. We are aware that in-stream habitat features, such as riverbed substrate or flow rate, would

improve the model. But for a landscape-level prediction they would need to be available nationwide, which is unfortunately rarely the case. The observed macroinvertebrate richness values reflect the realized niche, while the models only considers the fundamental niche by including environmental variables. Thereby they neglect interspecific competition and predation (Wrona & Dixon 1991), and assume simplistic assumptions regarding dispersal and spatial network configuration (e.g., 2D lattice instead of dendritic networks for riverine systems; Altermatt 2013). This may explain some of the observed over- and under-prediction.

Conclusion

Understanding the relationship between environmental variables and macroinvertebrate diversity is an important milestone in understanding ecosystem processes in aquatic systems. It is the basis for evaluating potential river restoration successes (Jähnig et al. 2011, Sundermann et al. 2011). We here present the first landscape level predictions of macroinvertebrate diversity in Swiss rivers. Furthermore, we show that different land-use variables (forest, pasture, cultivated land and developed area) and topology variables (elevation and slope) have distinct impacts on different macroinvertebrate indicator groups. Specifically, we found that the distribution of the sensitive EPT species richness is clearly different from the more diverse macroinvertebrate family richness. The latter are a conglomerate of different species per family and have a much less well-defined ecological niche. We conclude that a more causal understanding of the environmental variable-macroinvertebrate indicator group richness relationship is gained when the focus is placed on a few sensitive macroinvertebrate taxa identified to the species level, than when numerous macroinvertebrate taxa are considered at the family level.

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