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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 are 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.

Keywords Biodiversity · Dendritic networks · Habitat modeling · Environmental niche modeling · Landscape scale · Upscaling

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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; 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 alter 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 are 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 at either family, genus or species richness level (e.g., Grönroos and 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 and Zimmermann 2000; Guisan and 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 ($\sim$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,

Table 1 Summary of the explanatory variables used in this study

No.	Definition [unit]	Abbreviation
1	Area of BDM catchment [m2]	area_bdm_m2
2	Area of total catchment [m2]	area_total_m2
3	Length of canal watercourse within sampling area [m]	canal_percentage
4	Proportion of carbonate rock in sampling area [%]	carbonate_per_carbonatesilicate
5	Proportion of cereal cultivation area within sampling area [%]	cereal_percentage
6	Proportion of corn cultivation area within sampling area [%]	corn_percentage
7	Number of dams within sampling area [count]	dam_count
8	Proportion of deciduous forest area in sampling area [%]	decidious_per_forest
9	Proportion of disposal site area within sampling area [%]	disposalsite_190207_percentage
10	Proportion of disposal site area within sampling area [%]	disposalsite_2004_percentage
11	Proportion of building facade area within sampling area [%]	facade_percentage
12	Proportion of building shell area within sampling area [%]	facaderoof_percentage
13	Proportion of cultivated area within sampling area [%]	field_percentage
14	Proportion of floodplains and wetlands within sampling area [%]	floodplain wetland_percentage
15	Proportion of forest area within sampling area [%]	forest_percentage
16	Proportion of orchard area within sampling area [%]	fruit_percentage
17	Proportion of green area (pastures and meadows) within sampling area [%]	green_percentage
18	Number of hydropower plants within sampling area [count]	hydropower_count
19	Proportion of legume cultivation area within sampling area [%]	legume_percentage
20	Mean meters above sea level of sampling area [m a.s.l.]	Masl
21	Proportion of potato cultivation area within sampling area [%]	potato_percentage
22	Maximum annual discharge within sampling area [%]	Q_amax_m3.s
23	Mean annual discharge within sampling area [%]	Q_amean_m3.s
24	Mean annual discharge variability within sampling area [%]	Qvar_amean_m3.s
25	Proportion of rapeseed cultivation area within sampling area [%]	rapeseed_percentage
26	Proportion of roof area within sampling area [%]	roof_percentage
27	Proportion of root vegetables cultivation area within sampling area [%]	root vegetable_percentage
28	Proportion of settlement area within sampling area [%]	settlement_percentage
29	Maximum watercourse gradient within sampling area [%]	slope_percentage
30	Mean watercourse gradient within sampling area [%]	slope_mean
31	Storm sewage quantity which is annually conveyed into watercourse [m3/a]	stormsewage_m3.a
32	Proportion of street area within sampling area [%]	street_percentage
33	Proportion of railway track area within sampling area [%]	track_percentage
34	Proportion of vegetable cultivated area within sampling area [%]	vegetable_percentage
35	Proportion of vineyard area within sampling area [%]	vine_percentage
36	Wastewater quantity which is annually conveyed into watercourse [m3/a]	wastewater_m3.a
37	Length of watercourses within sampling area [m]	watercourse_bdm_m
38	Length of watercourses within total catchment [m]	watercourse_total_m

Table S1 and Fig. S7 give more information on the origin of the data and the spatial distribution of the data

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 whether biomonitoring

approaches, which use different taxa level identifications, draw the same conclusions regarding biodiversity distribution and potential biodiversity drivers.

Materials 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 (Fig. 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 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 $\times$ 10 times the width (giving the length). At each site, macroinvertebrates are sampled based on well-defined procedures using the kick-net 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 upscale 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 km^2 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 km^2 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 the literature (e.g., Richards et al. 1997; Sliva and 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

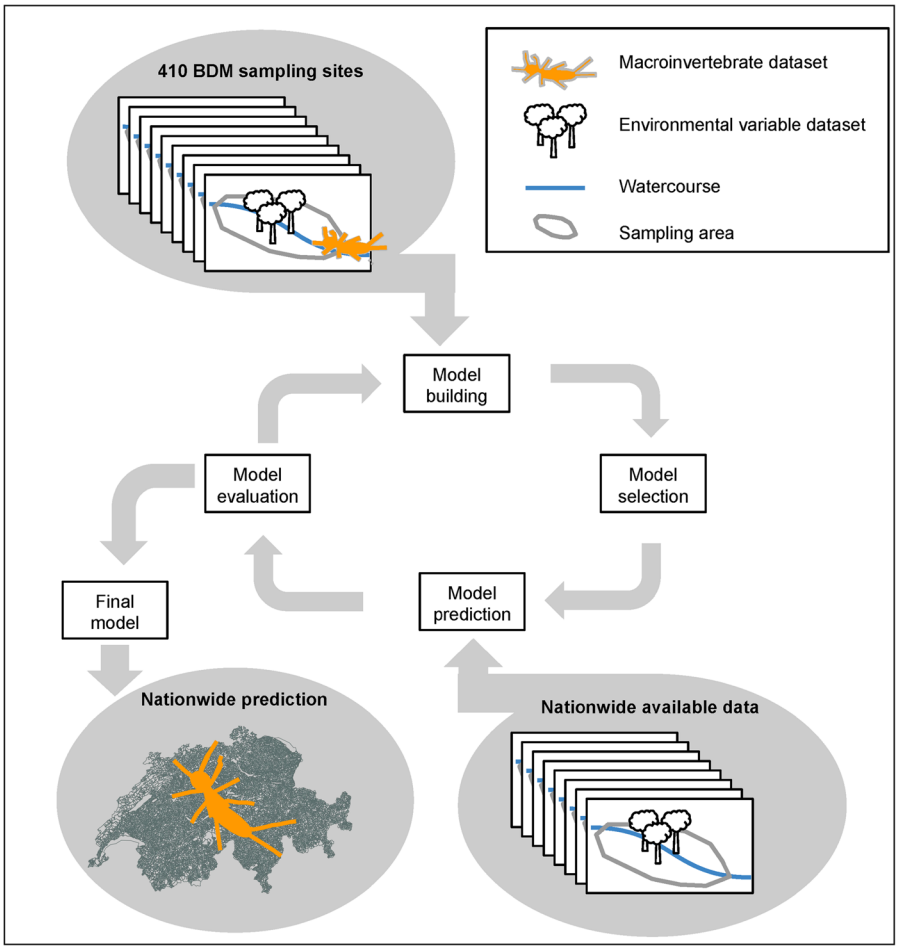

Fig. 1 Workflow of the nationwide prediction of macroinvertebrate richness. Data on macroinvertebrate richness (family and EPT species richness level) and environmental variables were available for 410 sampling sites. We built regression models describing diversity based on environmental variables and their interactions, carried out model selection and then predicted the nationwide macroinvertebrate richness for 22,169 sub-catchments using the most parsimonious model

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 therefore 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 (Tables 2, 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 were 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

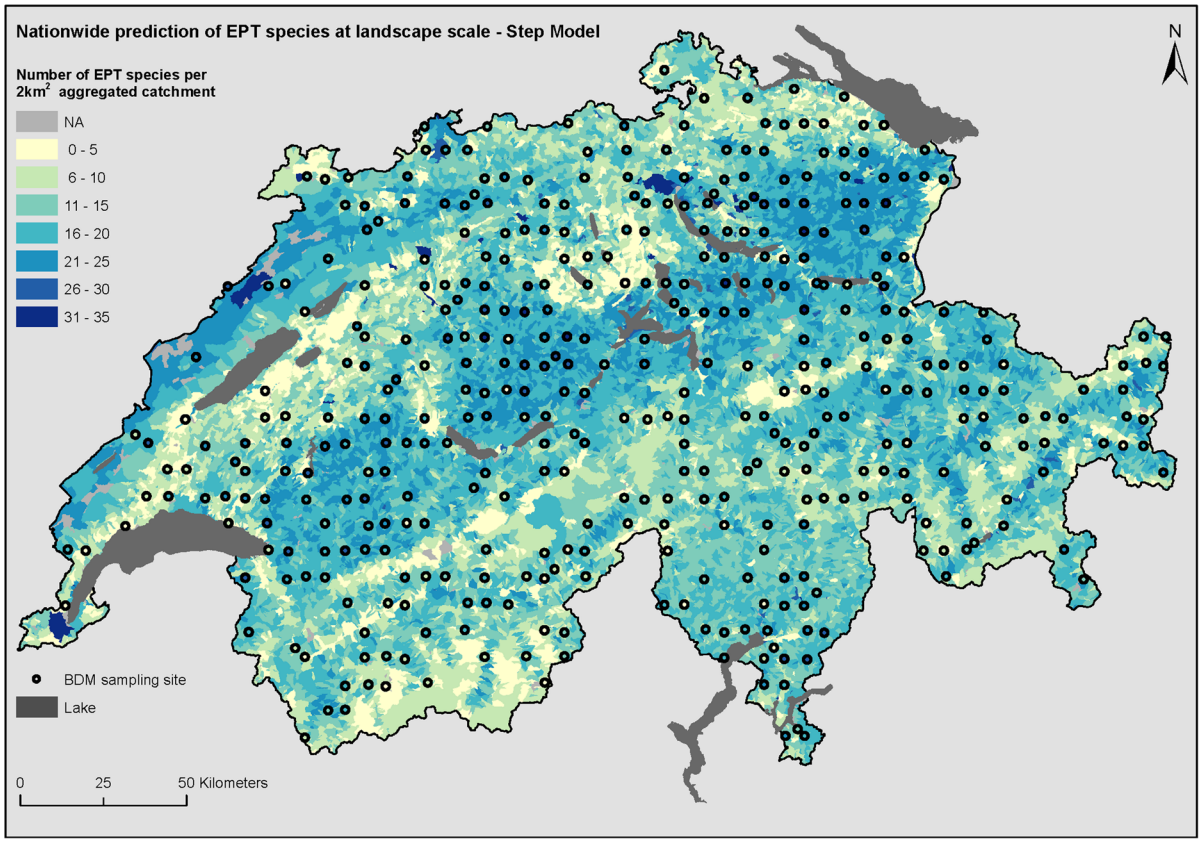

Fig. 2 Predicted EPT species richness across the whole of Switzerland for aggregated catchments at the 2 km^2 level. No predictions were made for lakes (*dark gray areas*). Source of map layout (also for subsequent figures): EZGG-CH (BAFU 2015); Vector 25 Primärfläche (Swisstopo); BDM Sites (Koordinationsstelle BDM)

(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

Table 2 Generalized linear model, explaining local EPT richness by different environmental variables

Estimate	*df*	Deviance	Residual *df*	Residual deviance	*F* value	*P* value
forest_percentage	1	2196.2	408	20,601	62.56	<0.00001
green_percentage	1	2211.5	407	18,389	62.99	<0.00,001
decidious_per_forest	1	378.9	406	18,011	10.79	0.001
street_percentage	1	455.5	405	17,555	12.97	0.0004
slope_mean	1	116.4	404	17,439	3.32	0.069
Masl	1	27.3	403	17,411	0.78	0.378
carbonate_per_carbonatesilicate	1	250.3	402	17,161	7.13	0.008
watercourse_bdm_m	1	189.5	401	16,972	5.40	0.021
roof_percentage	1	93.3	400	16,878	2.66	0.104
wastewater_m3.a	1	19.3	399	16,859	0.55	0.459
corn_percentage	1	601.8	398	16,257	17.14	<0.0001
forest_percentage * green_percentage	1	579.4	397	15,678	16.50	<0.0001
forest_percentage * street_percentage	1	91.6	396	15,586	2.61	0.107
forest_percentage * Masl	1	86.3	395	15,500	2.46	0.118
forest_percentage * wastewater_m3.a	1	394.5	394	15,105	11.24	0.0009
green_percentage * street_percentage	1	0.9	393	15,104	0.03	0.872
green_percentage * Masl	1	6.8	392	15,098	0.19	0.661
green_percentage * corn_percentage	1	2.9	391	15,095	0.08	0.773
decidious_per_forest * street_percentage	1	5.0	390	15,090	0.14	0.707
decidious_per_forest * slope_mean	1	434.9	389	14,655	12.39	0.0005
street_percentage * corn_percentage	1	521.3	388	14,134	14.85	0.0001
slope_mean * Masl	1	103.2	387	14,030	2.94	0.0873
Masl * carbonate_per_carbonatesilicate	1	204.5	386	13,826	5.82	0.016
Masl * roof_percentage	1	81.7	385	13,744	2.33	0.128
Masl * corn_percentage	1	159.0	384	13,585	4.53	0.0339
carbonate_per_carbonatesilicate * roof_percentage	1	139.1	383	13,446	3.96	0.047
NULL	409	22,797.0				

Final model after a stepwise model selection. For explanations of the environmental variables, see Table S1 in the supplementary information

(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.

Table 3 Generalized linear model, explaining local macroinvertebrate family richness by different environmental variables

Estimate	*df*	Deviance	Residual *df*	Residual deviance	*F* value	*P* value
area_bdm_m2	1	3.5	408	7925.8	0.33	0.568
facade_percentage	1	488.0	407	7437.8	45.19	<0.00001
vegetable_percentage	1	173.3	406	7264.5	16.05	<0.0001
disposalsite_2004_percentage	1	11.6	405	7252.9	1.07	0.301
forest_percentage	1	539.5	404	6713.4	49.95	<0.00001
fruit_percentage	1	59.4	403	6654	5.50	0.019
green_percentage	1	876.5	402	5777.5	81.16	<0.00001
Masl	1	812.8	401	4964.7	75.26	<0.00001
slope_mean	1	91.3	400	4873.4	8.45	0.004
vine_percentage	1	42.2	399	4831.2	3.90	0.049
area_bdm_m2 * disposalsite_2004_percentage	1	4.2	398	4827	0.39	0.534
area_bdm_m2 * slope_mean	1	19.6	397	4807.4	1.81	0.179
facade_percentage * vegetable_percentage	1	13.8	396	4793.7	1.27	0.259
facade_percentage * disposalsite_2004_percentage	1	11.3	395	4782.4	1.04	0.308
facade_percentage * vine_percentage	1	5.8	394	4776.7	0.53	0.465
vegetable_percentage * forest_percentage	1	6.5	393	4770.2	0.60	0.438
vegetable_percentage * green_percentage	1	2.2	392	4767.9	0.21	0.651
vegetable_percentage * Masl	1	42.0	391	4726	3.89	0.049
disposalsite_2004_percentage * forest_percentage	1	57.7	390	4668.3	5.34	0.021
disposalsite_2004_percentage * fruit_percentage	1	149.5	389	4518.8	13.84	0.0002
disposalsite_2004_percentage * slope_mean	1	80.8	388	4438	7.48	0.007
disposalsite_2004_percentage * vine_percentage	1	16.9	387	4421.1	1.56	0.212
forest_percentage * fruit_percentage	1	8.1	386	4413.1	0.75	0.388
forest_percentage * green_percentage	1	69.1	385	4344	6.40	0.012
fruit_percentage * green_percentage	1	12.1	384	4331.9	1.12	0.291
fruit_percentage * Masl	1	74.3	383	4257.6	6.88	0.009
green_percentage * vine_percentage	1	83.1	382	4174.5	7.69	0.006
Masl * slope_mean	1	59.8	381	4114.8	5.53	0.019
NULL	409	7929.4				

The model was simplified using a stepwise model selection method. For more details on the environmental variables, see Table S1 in the supplementary information

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

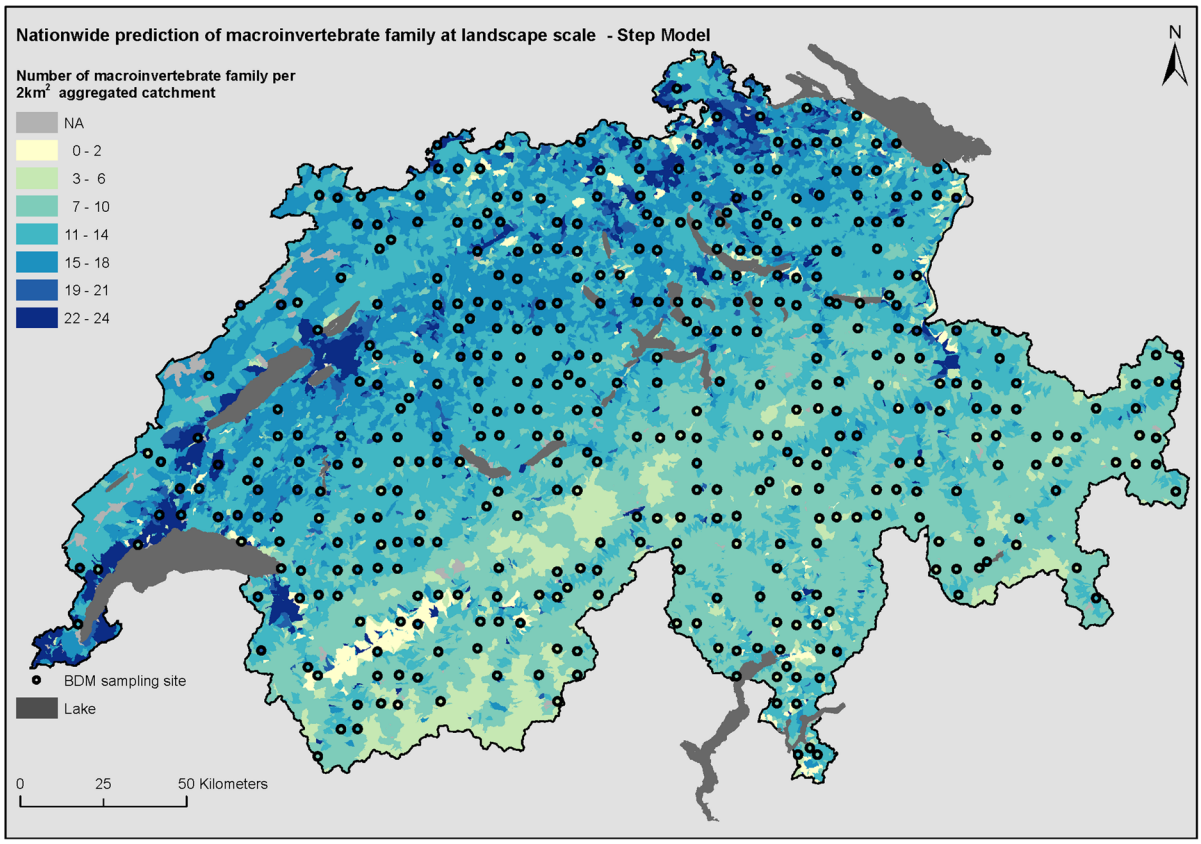

Fig. 3 Predicted macroinvertebrate family richness across the whole of Switzerland for aggregated catchments at the 2 km^2 level (step model; for the Lasso model see supplement). No predictions were made for lakes (*dark gray areas*): EZGG-CH (BAFU 2015); Vector 25 Primärfläche (Swisstopo); BDM Sites (Koordinationsstelle BDM)

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; Grönroos and 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. 2014). 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 and Zimmermann 2000; Guisan and 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 and 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; Zagmajster et al. 2014).

Diversity and richness of macroinvertebrates in freshwater are, among others, affected by human land-use change and chemical pollution. Our upscalable landscape-level environmental variables (Table 1; Fig. S7) were chosen to closely match previously identified relevant environmental variables affecting macroinvertebrates. In accordance with past local-scale studies (e.g., Roy et al. 2003; Moore and 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 accord, 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 the literature (e.g., Heino et al. 2003; Grönroos and 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 toward 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 consider the fundamental niche by including environmental variables. Therefore, they neglect interspecific competition and predation (Wrona and 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 underprediction.

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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