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River network properties shape α -diversity and community similarity patterns of aquatic insect communities across major drainage basins

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ABSTRACT

Aim Spatial dynamics and habitat connectivity affect community composition and diversity in many ecosystems. For a long time, diversity patterns in riverine ecosystems were related to local environmental conditions. Recent theoretical work suggests that diversity in rivers is strongly affected by dispersal along the dendritic landscape structure and that environmental conditions are intrinsically linked to the network position. Here, we test these hypotheses by relating river network geometry and connectivity to multi-level biodiversity patterns across large scales.

Location This study was carried out in Switzerland, Central Europe. Three major alpine drainage basins were considered (Rhine, Rhone, Ticino), extending over an elevation gradient of >2500 m and covering in total 41,285 km².

Methods We sampled all may-, stone- and caddisfly species in 217 sites. The sites representatively cover the three river networks. Using generalized additive models, we related diversity patterns in aquatic insects to centrality within the network as a direct river network property, and catchment area and elevation, which are related to network position.

Results Centrality within the river network, catchment area, and elevation had significant and interacting effects on α -diversity and community similarity. α -diversity was lowest in peripheral headwaters and at high elevations. Species richness generally increased with increasing catchment area. Well-connected, central communities within the river network had greater α -diversity compared to more peripheral communities. Elevation was a strong predictor of α -diversity, with the most diverse communities found at mid-elevation sites. Community similarity decayed with increasing along-stream distance between sites.

Main conclusions Our results highlight that diversity patterns of aquatic insects in river systems are related to local factors such as elevation, but interact with network properties and connectivity along waterways, and differ among insect orders. These findings are consistent

with dispersal-limited processes and implicate that riverine diversity should be addressed and protected in a network perspective.

Key Words: dendritic river network, dispersal, Ephemeroptera, macroinvertebrates, metacommunity, Plecoptera, Trichoptera

INTRODUCTION

Most species live in spatially heterogeneous landscapes, with habitat area, species interactions and connectivity shaping local community composition (Holyoak *et al.*, 2005, Logue *et al.*, 2011, De Bie *et al.*, 2012). Metapopulation and metacommunity theory provide a conceptual framework to describe the effect of spatially heterogeneous landscapes on species distributions and diversity. In general, local species richness increases with habitat area, as predicted by theoretical models and commonly observed in nature (Hanski & Gaggiotti, 2004, Holyoak *et al.*, 2005). Isolation often results in low diversity and connectivity promotes local richness by increasing dispersal (Gonzalez *et al.*, 1998, Altermatt *et al.*, 2011). However, the effect of connectivity and dispersal on diversity may be rather intricate (Labonne *et al.*, 2008, Lynch *et al.*, 2011), and local richness is predicted to have a unimodal relationship with dispersal rates (Mouquet & Loreau, 2003).

A large number of studies on diversity patterns and dynamics in metacommunities have been focusing on two-dimensional lattice landscapes, such as forests, meadows or ponds, where dispersers may have many possible dispersal routes between sites (Harrison *et al.*, 1988, Cottenie *et al.*, 2003, Altermatt & Ebert, 2010, Altermatt *et al.* 2012). This approach, however, does not represent all natural systems, and patterns and processes may be very different especially in dendritic habitat systems (Grant *et al.*, 2007, Labonne *et al.*, 2008, Fagan *et al.*, 2009, Morrissey & de Kerckhove, 2009). Streams and watersheds are typical

75 natural systems that have a dendritic structure (Rodriguez-Iturbe & Rinaldo, 1997, Benda *et*
76 *al.*, 2004). These habitats are not only structured in a hierarchic way, but landscape structure
77 and physical flows often dictate distance and directionality of dispersal (Lancaster *et al.*,
78 1996, Elliott, 2003). Understanding diversity patterns in dendritic riverine habitats is
79 important because even though rivers and riparian areas cover a small proportion of the earth
80 (0.8%), they contain an over-proportionate number of species (>6%) (Vorosmarty *et al.*,
81 2010). To protect this diversity, an understanding of ecological processes in dendritic systems
82 is crucial.

83 In the past, rivers were generally seen in a linear habitat concept (Vannote *et al.*, 1980,
84 Benda *et al.*, 2004), even though the dendritic structure has been long recognized (Rodriguez-
85 Iturbe & Rinaldo, 1997). Also, many local environmental factors were used to explain
86 riverine diversity patterns in a niche-driven perspective (reviewed by Richards *et al.*, 1997,
87 Vinson & Hawkins, 1998, Heino *et al.*, 2003). Recently, a paradigm shift in community
88 ecology has started to acknowledge the importance of spatial dynamics (Holyoak *et al.*,
89 2005). In the specific case of riverine ecosystems, a series of recent theoretical papers
90 addressed the origin of the characteristic diversity patterns (e.g., Labonne *et al.*, 2008,
91 Muneepeerakul *et al.*, 2008, Morrissey & de Kerckhove, 2009, Goldberg *et al.*, 2010, Lynch
92 *et al.*, 2011). These theoretical studies explicitly considered the inherent hierarchical spatial
93 structure of dendritic networks, and generally suggest that diversity patterns are strongly
94 driven by limited dispersal along the network. Also, individual drainage basins confine the
95 pool of species that are potential dispersers within them.

96 The combination of these theoretical, empirical and experimental studies increased our
97 understanding of diversity patterns in river systems. However, past empirical studies were
98 either focusing on diversity patterns in small catchment areas (e.g., Angermeier & Winston,
99 1998, Heino *et al.*, 2012), or over a small range of catchment area size and small ranges in

elevation (e.g., Richards *et al.*, 1997). Recent studies indicate that environmental factors are important at small spatial scales (Heino *et al.*, 2012), but their combined effect with dispersal on large-scale diversity patterns is unknown (Grant *et al.*, 2007, Muneeppeerakul *et al.*, 2008). Empirical large-scale studies testing the hypothesis that diversity patterns across whole river systems are related to various local and spatial properties of the network structure are scarce (e.g., Astorga *et al.*, 2012). Thus, the nature of large-scale biological diversity in rivers is still a contentious topic (reviewed in Clarke *et al.*, 2008, Finn *et al.*, 2011).

Here we used data from an extensive monitoring program from Switzerland, Central Europe, that surveys the diversity of aquatic insects in rivers and streams across three major drainage basins covering an area of >40,000 km² (BDM Coordination Office, 2009). The monitoring program representatively covered 217 sites in catchment areas ranging in size over four orders of magnitude (0.1 to about 1000 km²) and >2500 m of elevation differences. The insects sampled belong to the orders of may-, stone- and caddisflies (EPT). These insects hold prominent roles in riverine food webs: they decompose organic matter, consume algae or predate on smaller invertebrates (Landolt & Sartori, 1997, Graf *et al.*, 2008), and are themselves an important food source of fish. Furthermore, they show high levels of diversity and are commonly used in biomonitoring programs (e.g., Sundermann *et al.*, 2011). EPT differ in their ecological niche preferences and exhibit different dispersal and population dynamics. As an order, mayflies are trophic generalists, and live in a wide range of habitats in the colline to montane zone, but are generally confined to well-oxygenated waters (Landolt & Sartori, 1997). Stoneflies are, compared to the other two orders, most-strongly confined to well-oxygenated, cool water (Landolt & Sartori, 1997). Caddisflies are covering a wider range of feeding guilds and also a generally wider range of habitats than may- and stoneflies (Graf *et al.*, 2008). The dispersal ability of species in the three orders is generally low and dispersal distances are mostly less than a few hundred meters (Macneale *et al.*, 2005,

Sundermann *et al.*, 2011), with the following dispersal hierarchy suggested: mayflies < caddisflies < stoneflies (Petersen *et al.*, 1999, Petersen *et al.*, 2004). These differences in ecological preferences and dispersal ability are suggesting that different factors are shaping diversity patterns of EPT, especially in a landscape highly structured in elevation such as the Alps.

We tested the effects of drainage basin (describing the regional species pool), network centrality (a major river network property), elevation, and catchment area size on α -diversity and community similarity of major groups of aquatic insects. Network centrality is an explanatory variable reflecting spatial connectivity and thus dispersal-limitation driven processes (Muneepeerakul *et al.*, 2008, Carrara *et al.*, 2012). Elevation is an explanatory variable reflecting local environmental conditions and thus affecting niche driven dynamics (Ward, 1994). Catchment area is an explanatory variable reflecting habitat capacity/size, which is affecting population size through extinction dynamics in a classic biogeography perspective (MacArthur & Wilson, 1967). All three variables are related to network position. The individual, isolated effect of these drivers on diversity has been shown in many studies (e.g., Ward, 1994, Heino *et al.*, 2003, Benda *et al.*, 2004, Clarke *et al.*, 2008, Muneepeerakul *et al.*, 2008, Carrara *et al.*, 2012), while large scale comparisons including all of them and their interactions are largely lacking. Furthermore, differences in the ecology of EPT, such as different habitat preference or dispersal ability, may generate unique responses to these explanatory variables. We addressed diversity patterns with hypotheses on the level of i) the regional species pool (biogeography, i.e., restriction to specific drainage basin), ii) within-network parameters describing local environmental or network properties and iii) the three insect orders and possible differences among them due to their specific ecology (Landolt & Sartori, 1997, Graf *et al.*, 2008). We first hypothesized that the regional species pool, given by the drainage basin, has a “top-down” control on α -diversity patterns. This hypothesis

suggests that the regionally present species pool is confining all lower-level interactions including both spatial as well as local environmental factors. Thus, we used drainage basin as a covariate reflecting biogeographic history. We secondly looked at diversity patterns in a multifactorial within-network perspective. We hypothesized that within-network parameters describing local environmental conditions and network properties such as connectivity have a “bottom-up” control on diversity. We especially hypothesized that local environmental conditions and network properties interact and thereby reflect the occurrence of ecological dynamics that are intrinsically linked in riverine networks. Thereby, models considering inherent river network-properties would allow explaining a large part of the variation in local species richness. Finally, knowing that the three insect orders differ in their ecological requirements, we hypothesized that a different set of variables explains local species richness between EPT-orders through species-sorting (Holyoak *et al.*, 2005). All EPT being generally poor dispersers, we hypothesized that network centrality is a major explanatory factor for all orders individually. However, we expected that diversity patterns of may- and stoneflies, which are more restricted to specific habitats (Landolt & Sartori, 1997), is better resolved than the diversity patterns of caddisflies, which are generally using a wider range of habitats (Graf *et al.*, 2008). This would indicate that factors affecting diversity in riverine systems depend on specific life histories and species traits of the organisms of interest.

MATERIAL AND METHODS

Background

Switzerland monitors its biological diversity in a large program, called “Biodiversity Monitoring in Switzerland” (BDM) (BDM Coordination Office, 2009). May-, stone-, and caddies-flies (Ephemeroptera, Plecoptera, Trichoptera; abbreviated as EPT) are monitored on a systematic sampling grid covering the whole of Switzerland. At each site, specifically

trained field biologists collect and identify the respective organisms to species level, using well-established and highly standardized methods (BDM Coordination Office, 2009).

Study area and sampling method

Switzerland lies in the centre of Europe (Fig. 1). It covers an area of 41,285 km², including different biogeographical units. Large parts of the country fall into the Alps (50% of the area) and the Jura mountains (10% of the area). There is a large Central Valley north of the Alps (30% of the area), which is the most densely human populated part of the study area, and finally there are a few valleys south of the Alps extending into sub-Mediterranean climates. Elevation in Switzerland ranges from 193 to 4,634 m.a.s.l. Several large European river systems have their source in Switzerland, extending from the krenal to the epipotamal zone. The country is drained by major drainage systems (Fig. 1): the river Rhine drainage basin (covers 71 % of the country, and drains into the North Sea), the river Rhone drainage basin (covers 20 % of the country, and drains into the Mediterranean Sea), the river Ticino drainage basin (covers 5 % of the country, and drains into the Po and then the Adriatic Sea), the river Inn drainage basin (covers 3.5 % of the country, and drains through the Danube into the Black Sea), and the river Etsch drainage basin (covers 0.5 % of the country, and drains into the Adriatic Sea). As the Inn and Etsch drainage basins cover only small areas they were combined with the Ticino basin and treated as “Ticino/Inn” drainage basin.

The EPT monitoring of the BDM currently comprises 217 investigated sampling sites (Fig. 1), chosen on a systematic sampling grid (BDM Coordination Office, 2009). Thereby, the distribution of chosen river sizes representatively reflects the total distribution of river sizes, avoiding that headwaters, which are much more numerous by definition, are under-represented. With this study design, all sites together representatively reflect the Swiss watercourses and the EPT species diversity therein. The sampling concept is based on watercourses from 2nd order streams up (Stucki, 2010). Standing waterbodies, 1st order

streams, and watercourses completely inaccessible by wading are not sampled for methodological reasons (Stucki, 2010). Each site was sampled once between 2009–2011. The seasonal timing of the sampling depended on the elevation, and took place between March and July. It had been optimised for the local phenology of EPT (Stucki, 2010). For each site, data on elevation (m.a.s.l.) and upstream catchment area (km²) are available.

The surveying method closely followed the “Macrozoobenthos Level I” module on benthic macroinvertebrates, described in detail in Koordinationsstelle Biodiversitätsmonitoring Schweiz (2010) and Stucki (2010). In short, all benthic macroinvertebrates were sampled with the kick-net method, using a standardized net with a 25 x 25 cm opening and 500 µm mesh size. At each site the sampling efforts (i.e., number of kick-net subsamples taken and time of “kick-netting”) were equal and not dependent on river size. Eight kick-net subsamples were taken to cover all major microhabitats within each site. The whole width of the stream/river at each site was sampled. To adjust for the inherently larger number of microhabitats in larger rivers, the area in which the eight subsamples were chosen from was proportionate to the river size: eight kick-net samples were taken to cover different habitat types and waterflow velocities in an area given by the river width x ten times the mean river width in length. In the following we use the term “site” to refer to these sampling sites in which we collected the community data. The sub-samples at a site were pooled and stored in 80% alcohol. EPT were identified by specialists. When possible, all EPT were identified to the species level, using predefined identification literature (Koordinationsstelle Biodiversitätsmonitoring Schweiz, 2010). While the identification to the species level was possible for most individuals, the larvae of a few EPT species are not identifiable to the species level or have not yet been described based on morphological characters. Such species were identified to the level of predefined species complexes only. In total, 61 mayfly species, 7 mayfly complexes, 47 stonefly species, 8 stonefly complexes, 116

caddisfly species and 30 caddisfly complexes were differentiated (for a list of the names of all these species see Koordinationsstelle Biodiversitätsmonitoring Schweiz, 2010). In the following, complexes are treated as species. The herein studied EPT species predominantly disperse along the waterlines and lateral dispersal of adults away from the river lines is limited (Petersen *et al.*, 2004).

Analysis

We analysed diversity patterns with generalized additive models (gam) with integrated smoothness estimation, using the R-package mgcv (Wood, 2011). Generally, local species richness (α -diversity) was the response variable, while the explanatory variables were drainage basin (levels: Rhine, Rhone or Ticino/Inn), catchment area ($\log_{10}$ -transformed), elevation, and network centrality of a site. The drainage basin gives major biogeographic areas in which all water drains through continental streams into the sea (Fig. 1). Catchment area is the total upstream area from a sampled site that drains into that site. Stream width, mean annual discharge or extension of riparian vegetation at a site directly scale with catchment area of that site (Leopold *et al.*, 1964). Thereby, catchment area is an approximation for local habitat capacity. We note, however, that catchment area as a property of the watershed has elements of a regional factor as well. Elevation is the elevation at the sampled site, reflecting local environmental conditions such as temperature or vegetation type, and can thus be seen as a variable reflecting local niche-conditions. The network centrality is defined as the mean distance of a site to all other sites. It measures how well a site is connected to all other sites in the network within a drainage basin, and is a proxy for dispersal limitation. Pairwise distances are measured along the river network, and averaged across all along-stream distances from any given site (Carrara *et al.*, 2012). We used a Pearson's correlation test to assure that the three continuous explanatory variables were not correlated with each other (see supporting information). For models on α -diversity (i.e.,

number of species, which are count-data) we used a poisson link function, and a χ^2 -significance test (Crawley, 2007). Models initially included all main factors and interactions. We hierarchically simplified four- and three-way interactions in the models based on the minimisation of the Akaike Information Criterion (AIC), until we had one best model explaining α -diversity of all EPT species, and one best model explaining α -diversity of may-, stone- and caddisflies separately. We used the fitted values of the gam to plot the predicted relationships of explanatory and response variables in all of our figures. Finally, we used a Pearson's correlation test to analyse pairwise comparisons of local species richness between may-, stone- and caddisflies.

We compared along-stream and Euclidian distance with different pairwise measures of among-community similarity (using the vegan-package, Oksanen *et al.*, 2009), namely the Jaccard index (based on presence-absence data only), the Bray-Curtis index (based on abundance data) and the Chao-corrected Jaccard index (taking into account the number of unseen species pairs, especially of rare species and putting weight on more common species). For all sites, we calculated the pairwise along-stream distance within the same drainage basin, the pairwise Euclidian distance and the absolute pairwise difference in elevation compared to all other sites. We used partial Mantel tests to compare among-community similarity matrices with among-community distance matrices. The partial correlation between these two matrices is conditioned on a third dissimilarity matrix that is describing the affiliation of sites to the three drainage basins. P-values are based on 999 permutations. We used a gam for significance testing and predicting community dissimilarity relative to along-stream distance, elevation distance and their interaction, using a binomial error distribution. All analyses were conducted in R Version 2.12.1 (R Development Core Team, 2010).

RESULTS

Local species richness (α -diversity) at a river or stream site ranged from 0 to 36 EPT species,

with a mean and median of 15.5 and 15 species respectively (Fig. 1). The highest α -diversity was found in the northern pre-alps and foothills as well as in some locations in the Jura mountains. Low levels of α -diversity were found in the Central Valley of Switzerland and at high elevations. At least six alpine-endemic species were found (see supporting information).

In the gam on diversity of all EPT, local species richness was significantly explained by the main effects of catchment area and elevation (Figs. 2 & 3; Table 1). Catchment area, elevation and their interaction also contributed significantly to the smooth terms. Adjusted R^2 of the gam is 0.33, with 50.1% deviance explained. Local species richness generally increased with increasing catchment area (Fig. 2A). Local species richness peaked at intermediate elevation between 700–1300 m.a.s.l. (Fig. 3), also supported by a highly significant smooth term of elevation (Table 1). There was no significant main effect of network centrality and drainage basin (differentiating among the three biogeographically separated drainage basin of the Rhine, Rhone and Ticino/Inn basin), but this factor was included in significant interactions. On average, local species richness decreased with increasing network centrality (Fig. 4), but there was a significant interaction between catchment area and network centrality. All further two-way interaction terms were non-significant but retained in the model based on AIC (Table 1). There was a significant three-way interaction between drainage basin, elevation and network centrality and a significant four-way interaction including also catchment area. The decrease in richness with increasing isolation within river networks (i.e., increasing network centrality) was consistent across the three drainage basins, but only evident in the river Rhine basin when excluding low elevation sites (<500 m; Fig. 4).

Overall, local species richness values of the three different insect orders of may- (E), stone- (P) and caddisflies (T) were similar, and significantly correlated with each other (E vs. P: $cor=0.5$, $t_{215}=8.5$, $p<0.0001$; E vs. T: $cor=0.54$, $t_{215}=9.4$, $p<0.0001$; P vs. T: $cor=0.29$, $t_{215}=4.4$, $p<0.0001$). Generally, local diversity in the three insect orders was explained by

different combinations of our explanatory variables drainage basin, catchment area, elevation, and network centrality in the gam (Fig. 5 and Table 2). Adjusted R^2 of the models and % deviance explained is 0.33 and 36.9% respectively for the mayfly model, 0.32 and 35.3% respectively for the stonefly model and 0.31 and 38.7% respectively for the caddisfly model. Local species richness of the three insect orders differently depended on the drainage basin (Fig. 2B), making drainage basin a highly significant term in all insect-order specific gams. Depending on the drainage basin, may-, stone- or caddisflies were on average the most diverse EPT species in a given site (Fig. 2B). Network centrality (for E) and elevation (for P) were the only other significant main-effects. Furthermore, local diversity was significantly explained in all insect orders by the two-way interactions of drainage basin x catchment area and drainage basin x network centrality.

Pairwise comparisons of among-community similarity revealed significant decays in community similarity with both increasing pairwise along-stream distance or Euclidian distance, conditioned on the drainage basin affiliation (Fig. A1). For all comparisons, the p -value was <0.001 , with the following partial Mantel- r values: Jaccard similarity versus pairwise along-stream distance ($r_{\text{partial Mantel}}=0.26$; Fig. A1a) and versus Euclidian distance ($r_{\text{partial Mantel}}=0.18$; Fig. A1b); Bray-Curtis similarity versus pairwise along-stream distance ($r_{\text{partial Mantel}}=0.17$; Fig. A1c) and versus Euclidian distance ($r_{\text{partial Mantel}}=0.15$; Fig. A1d); and finally, Chao similarity versus pairwise along-stream distance ($r_{\text{partial Mantel}}=0.24$; Fig. A1e) and versus Euclidian distance ($r_{\text{partial Mantel}}=0.18$; Fig. A1f). Decay in community similarity over distance was more pronounced for Euclidian distances than respective along-stream distances. Similarly, there was a significant decay in community similarity with increasing pairwise absolute elevation difference (Fig. A2; Jaccard similarity, $r_{\text{partial Mantel}}=0.48$; $p<0.001$). Predicted pairwise community similarity depended significantly on elevation difference (gam, $\text{Chi}^2=14.8$, $p=0.0001$, 26% deviance explained; Fig. A3), and an interaction

of elevation and along-stream difference (gam, $Chi^2=39.1$, $p<0.0001$), while along-stream difference was not significant as a main effect alone (gam, $Chi^2=8.8$, $p=0.13$).

DISCUSSION

The nature of large-scale biodiversity patterns in rivers is a contentious topic (reviewed in Vinson & Hawkins, 1998, Clarke *et al.*, 2008, Finn *et al.*, 2011). Here, we tested and confirmed hypotheses that α -diversity and community similarity patterns of aquatic insects are not only correlated to local environmental variables, but also to key network properties and large-scale spatial position in natural river systems (Fig. 1). Specifically, diversity depended on catchment area, elevation and an interaction with network centrality (Figs. 2–5). Our results support the hypothesis that geophysical characteristics of river network structure (Rodriguez-Iturbe and Rinaldo 1997) are complemented by characteristic patterns of diversity, and that the latter are likely driven by the river structure (Carrara *et al.*, 2012).

In the European Alps, topology and elevation differences of major river networks are prominent, and thus strongly affecting habitat size and position within the network. Small headwater streams (i.e., streams with a small catchment area) were found across an elevation range of >2000 m, and can be either highly connected within the network (small network centrality) or be highly isolated (high network centrality). These properties are inherent and comparable to other mountainous river systems (e.g., Himalaya, Caucasus, Rocky Mountains). Geomorphologists acknowledge that mean river-bed discharge or mean river-bed width at a site (both of which are proportionate to catchment area), connectivity and position within river systems are not independent (Leopold *et al.* 1964). There is an empirically observed relationship between landscape forming discharges and increasing width of the river cross-section in the downstream direction (Leopold *et al.* 1964), while the river network structure is also commonly defining dispersal pathways and connectivity among sites (Carrara

350 *et al.*, 2012). These inherent properties of river networks are closely reflecting two main
351 patterns affecting diversity within metacommunities, namely local habitat conditions and
352 connectivity (Gonzalez *et al.*, 1998, Mouquet & Loreau, 2003, Hanski & Gaggiotti, 2004),
353 and are thereby potential drivers of local community composition and diversity.

354 A main finding of our study is that local species richness within the metacommunity of
355 aquatic insects was not explained by single factors, but through their interactions (Table 1).
356 Thus, river network characteristics, local network properties and their interaction were
357 important individual contributors in explaining local EPT species richness. Sites with small
358 catchment area had significantly lower diversity, but even more so when they were also
359 highly isolated in the network or situated at high elevation (Table 1, Figs. 3–5). Local factors
360 or connectivity alone did not independently explain diversity pattern, rather we found support
361 for a combination of both. In our view, this reflects the intrinsic link of pure network
362 descriptors and environmental factors in rivers, such that no single local factor can be viewed
363 without considering the spatial connectivity, and that the spatial-explicit perspective cannot
364 be done without considering the possible influence of factors more related to local
365 environmental conditions. Experimental microcosm studies showed that dispersal along river-
366 like network structure can result in characteristic diversity patterns (Carrara *et al.*, 2012).
367 While our study is to our knowledge for macroinvertebrates unique in the large spatial extent
368 (for other taxonomic groups such as diatoms see Potapova & Charles, 2002), the interaction
369 of local environmental and regional factors has been observed in rivers at much smaller
370 spatial scales (Heino *et al.*, 2012), suggesting that it is true over a large range of scales.

371 A decreasing dependence of α -diversity on network centrality is predicted by dispersal
372 theory (Mouquet and Loreau 2003). At a first glance, one expects a decrease in richness with
373 increasing isolation (Fig. 4). However, we only observed this in two of the three drainage
374 basins, and the main effect of network centrality was non-significant. The significant three-

way interaction with drainage basin and elevation (Table 1) was due to a unimodal relationship in the river Rhine drainage basin. Network centrality, being a measure of connectivity, may closely reflect dispersal rates, and subsequently high and low dispersal (i.e., low and high network centrality) may decrease local diversity, but due to different reasons (dominance of a few superior species vs. lack of recolonization after local extinctions). Alternatively, the unimodal relationship could reflect anthropogenic activities that are most prominent at lower elevations. Excluding the low elevation sites in the river Rhine (with a threshold of 500 m) indeed makes the former unimodal relationship between network centrality and local species richness linear such that richness steadily decreases with higher isolation (Fig. 4).

While catchment area and elevation were good predictors of total EPT species richness, as also demonstrated for vertebrates (Muneepeerakul *et al.*, 2008), the set of factors correlating with local EPT species richness were different among the three orders of aquatic insects when looked at individually (Table 2). Furthermore, drainage basin became highly significant as a main factor, indicating that the pool of regionally available species within drainage basin is different across the three insect orders. Together, this indicates that we can not use the same set of parameters to equally describe the diversity and species richness patterns across orders of aquatic insect, as both the pool of regionally available species (Fig. 2B) and their dependence on local and spatial factors is different. Diversity of the ecologically most heterogeneous group of caddisflies was mostly explained drainage system as main effect and interactions therewith (Table 2b, Fig. 5b). This indicates that it is the regional species pool and subsequent differences in locally available species (Fig. 2b) that are driving diversity patterns. Local and spatial factors are less important to explain within-order local diversity, possibly due to the relative high variability in ecological requirements of different caddisfly species (Graf *et al.*, 2008). In may- and stoneflies, network centrality and elevation

respectively became significant as main effects and in interactions (Table 2a and c; Fig. 5). This corresponds well with the ecological requirements of these species groups (Landolt & Sartori, 1997): almost all stoneflies but also many mayflies are depending on cold, oxygen-rich water. Furthermore, stoneflies are generally highly sensitive to environmental pollution, which strongly confines them to mid and high elevations and smaller streams. Both may- and caddisflies are rather poor dispersers (Elliott, 2003, Petersen *et al.*, 2004). Species richness is significantly related to interactions of network centrality and other factors (catchment area and elevation), which is indicating that the (re)colonization of vacant sites is affected by the site's position within the network. However, this relationship is non-trivial, as network centrality was significant as a main factor only in the gam of mayflies (Table 2a). We suggest that peripheral sites may be beyond the dispersal abilities of some species (Sundermann *et al.*, 2011). Such patterns are consistent with the observation that dispersal is happening mostly along the rivers (Elliott, 2003), either in the aquatic larval stage, or as adults flying along the river and not over land (Petersen *et al.*, 2004).

For conservation biology it is of high relevance that a different set of explanatory variables explained diversity for each of the three different EPT orders. EPT have a long history of being used as indicator taxa, and many of them are threatened and listed in red lists. In our study area, there is not only a high total diversity of EPT (Lubini *et al.*, 2012), but also a high percentage of alpine-endemic EPT species. This indicates a high responsibility to protect these species in their natural environment, but different strategies may be needed for different orders: The composition and diversity of some species groups (especially E and P) are driven both by local, spatial and regional factors. These insect orders might not only be more affected by habitat change, but also by habitat fragmentation and subsequent dispersal limitation. Thus, only when the protection (or restoration) of local habitat conditions is seen in a network perspective, the species therein may profit. Recent studies on the success of river

restorations are indeed showing that the restoration of local conditions itself are not sufficient for the return of ecologically sensitive EPT species, but that a short, barrier-free distance to possible source populations is essential for successful (re)colonization (e.g., Sundermann *et al.*, 2011). Caddisflies (T), on the other hand, are ecologically more heterogeneous, and species-specific ecological requirements may blur overall effects of local and network parameters on their diversity, calling for an even more species-level focused conservation strategy.

The significance of multiple, interacting factors within river networks on diversity was also seen for our diversity measures describing among-community similarity. Pairwise among-community similarity patterns depended both on pairwise along-stream distance and elevation differences (Figs. A1 & A2). The more distant communities were, the more different they became. However, while overall highly significant, the dependence of community similarity on distance was associated with a high variability: communities could be relatively similar or dissimilar over both short or long distance (Fig. A1), suggesting that further mechanisms than dispersal limitation are affecting community compositions. Elevation is a likely factor affecting community similarity, as it is one of the strongest drivers of local environmental conditions (such as temperature, precipitation). Elevation not only affects α -diversity (as described above), but also strongly interacts with the effect of isolation on among-community similarity (Fig. A2). Large differences in elevation between two sites resulted in large differences in community composition even at relatively small along-stream distances (Fig. A3). This suggests that dispersal limitation is constraining among-community similarity, but mostly within the “elevation envelope” that is driving abiotic conditions.

We conclude that diversity of aquatic insect communities in river networks is correlated in intricate ways with an important network property, namely centrality within the network, and with elevation and catchment area. The latter are not only reflecting local conditions but

are related to river-network position. Drainage basin as a descriptor of the regional species pool seems to be less important when different orders of insects are addressed simultaneously, but becomes highly significant for each of them individually, indicating that they have regionally different, but complementing, species' pools in different drainage basins. The understanding of riverine diversity patterns is profiting through a network perspective and the linking of scales (Benda *et al.*, 2004, Lowe *et al.*, 2006), but manifold anthropogenic influences pose further challenges that need to be addressed, especially when we not only want to understand current diversity patterns, but also predict changes therein.

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SUPPORTING INFORMATION

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

Appendix S1 Additional results and further diversity measures.

Biosketch

Florian Altermatt is a senior scientist interested in metacommunity ecology, dispersal ecology and large-scale diversity patterns. He mainly studies invertebrates, combining comparative and experimental studies. Mathew Seymour is a PhD student under the supervision of F.A., studying diversity patterns in riverine systems. Nicolas Martinez is a project leader at the Biodiversity Monitoring Program Coordination Office, responsible for the EPT subproject.

Author contributions: F.A. conceived the ideas; F.A. and N.M. collected the data; F.A. and M.S. analysed the data; and F.A. led the writing.

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Tables

Table 1. Generalized additive model, explaining local species richness by drainage basin, catchment area, elevation and network centrality. Model estimates and significance of the smoothing terms are given. Adjusted R^2 of the model is 0.33, with 50.1% deviance explained.

Estimate	df	Chi ²	p-value
drainage basin	2	4.776	0.092
catchment area	1	6.500	0.011
elevation	1	7.683	0.005
network centrality	1	0.928	0.335
drainage basin x catchment area	2	5.141	0.076
drainage basin x elevation	2	4.846	0.088
drainage basin x network centrality	2	4.345	0.114
catchment area x network centrality	1	5.893	0.041
catchment area x elevation	1	0.003	0.955
elevation x network centrality	1	0.627	0.428
drainage basin x catchment area x elevation	2	5.048	0.080
drainage basin x catchment area x network centrality	2	4.287	0.117
drainage basin x elevation x network centrality	2	6.469	0.039
catchment area x elevation x network centrality	1	0.028	0.867
drainage basin x catchment area x elevation x network centrality	2	6.656	0.035
<i>Approximate significance of smooth terms (s)</i>			
s(network centrality)		6.033	0.323
s(catchment area)		21.01	<0.001
s(elevation)		23.19	0.003
s(network centrality x elevation)		65.76	<0.001
s(catchment area x elevation)		0.004	0.999

Table 2. Generalized additive models, explaining local species richness of mayflies (A), stoneflies (B) and caddisflies (C) by drainage basin, catchment area, elevation, network centrality and their interactions. Model estimates and significance of the smoothing terms are given. Adjusted R^2 of the models and % deviance explained is 0.33 and 36.9% respectively for the mayfly model, 0.32 and 35.3% respectively for the stonefly model and 0.31 and 38.7% respectively for the caddisfly model.

Estimate	df	Chi ²	p-value
A) Mayflies (Ephemeroptera)			
drainage basin	2	13.11	0.001
catchment area	1	0.181	0.671
elevation	1	0.672	0.412
network centrality	1	5.542	0.019
drainage basin x catchment area	2	12.53	0.002
drainage basin x elevation	2	2.972	0.226
drainage basin x network centrality	2	7.097	0.029
elevation x catchment area	1	0.149	0.699
elevation x network centrality	1	3.983	0.046
network centrality x catchment area	1	11.34	<0.001
<i>Approximate significance of smooth terms (s)</i>			
s(network centrality)		0	0.999
s(catchment area)		6.1	0.032
s(elevation)		0	0.999
s(network centrality x elevation)		29.2	0.066
s(catchment area x elevation)		0	0.999
B) Stoneflies (Plecoptera)			
drainage basin	2	10.14	0.006
catchment area	1	0.612	0.434
elevation	1	4.120	0.042
network centrality	1	0.124	0.725
drainage basin x catchment area	2	11.02	0.004
drainage basin x elevation	2	5.100	0.078
drainage basin x network centrality	2	8.199	0.017

elevation x catchment area	1	0.968	0.325
elevation x network centrality	1	0.727	0.394
network centrality x catchment area	1	5.163	0.023
<i>Approximate significance of smooth terms (s)</i>			
s(network centrality)		10.48	0.107
s(catchment area)		0.004	0.951
s(elevation)		0	0.999
s(network centrality x elevation)		48.17	<0.001
s(catchment area x elevation)		0	0.999
C) Caddisflies (Trichoptera)			
drainage basin	2	15.91	0.001
catchment area	1	0.395	0.530
elevation	1	3.809	0.051
network centrality	1	0.141	0.707
drainage basin x catchment area	2	13.53	0.001
drainage basin x elevation	2	4.323	0.115
drainage basin x network centrality	2	8.786	0.012
elevation x catchment area	1	1.437	0.231
elevation x network centrality	1	3.280	0.070
network centrality x catchment area	1	0.702	0.402
<i>Approximate significance of smooth terms (s)</i>			
s(network centrality)		23.12	0.002
s(catchment area)		12.54	0.021
s(elevation)		0	0.999
s(network centrality x elevation)		0.006	0.789
s(catchment area x elevation)		19.36	0.095

635 **Figure legends**

636 Fig. 1. Local species richness (α -diversity) of may-, stone- and caddisflies (EPT) in
 637 Switzerland, given for all 217 biodiversity monitoring sites. The main rivers and larger lakes
 638 are given for orientation (dark blue). The drainage basins are color-coded: Rhine drainage
 639 (light blue), Rhone drainage (violet), Ticino/Etsch/Inn drainage (green). Inset: Location of
 640 Switzerland (black) within Central Europe. The rivers draining Switzerland are schematically
 641 depicted.

Fig. 2. A) Boxplots of local species richness (α -diversity) of all may-, stone- and caddisflies (EPT) combined relative to catchment area (bins at $\log_{10}$ -scale) of a site. The data are shown separately for the three different drainage basins Rhine, Rhone and Ticino/Inn (colour coded; see Fig. 1). B) Mean ($\pm$ se) local species richness, separately given for may-, stone- and caddisflies in the three drainage basins.

Fig. 3. Bubble plot of local species richness of may-, stone- and caddisflies (EPT) relative to the elevation and the catchment area (size of circles, log₁₀-scale) of a site. The different colours refer to individual drainage basins (Fig. 1). The lines are predictions of a generalized additive model, predictions are given for each drainage basin.

Fig. 4. Local species richness of may-, stone- and caddisflies (EPT) relative to the network centrality of a site. Species richness decreases with increasing spatial isolation of a site, however the effect is only significant in the interaction with elevation and catchment area.

The lines are predictions of a generalized additive model, predictions given for each drainage basin. For the Rhine catchment, the model was done with all sites, but also for sites higher than 500 meters above sea level respectively only (>500). Sites at lower elevations are the most modified by humans. The different colours refer to individual drainage basins (Fig. 1).

Fig. 5. Local species richness of mayflies (a, d), stoneflies (b, e) and caddisflies (c, f) relative to the elevation (a–c) and the catchment area (d–f) of a site. The lines are predictions of generalized additive models done for each insect order separately.