



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 many decades, diversity patterns in riverine ecosystems were thought to be related to local environmental conditions. Recent theoretical work, however, 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. In this study we tested hypotheses on network position by relating river network geometry and connectivity to multi-level biodiversity patterns across large scales.

Location Three major alpine drainage basins in Switzerland were studied (Rhine, Rhone, Ticino), extending over an elevational gradient of > 2500 m and covering a total area of 41,285 km².

Methods We sampled all may-, stone- and caddisfly species at 217 sites which 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 to catchment area and elevation, which are related to network position.

Results Centrality within the river network, and catchment area and elevation had significant and interacting effects on α -diversity and community similarity. Alpha 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 than more peripheral communities did. Elevation was a strong predictor of α -diversity, with the most diverse communities found at mid-elevation sites. Community similarity decreased with increasing along-stream distance between sites.

Main conclusions Our results highlight the fact 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 indicate that riverine diversity should be addressed and protected taking the river network structure into account.

Keywords

Dendritic river network, dispersal, Ephemeroptera, macroinvertebrates, meta-community, Plecoptera, Switzerland, Trichoptera.

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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 meta-community theories provide a conceptual framework with which 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 can be complex (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 focused 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, 2008, 2010; Altermatt *et al.*, 2012). This approach, however, does not represent all natural systems, and in particular, patterns and processes may be very different 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 natural systems that have a dendritic structure (Rodríguez-Iturbe & Rinaldo, 1997; Benda *et al.*, 2004). These habitats not only are structured in a hierarchical way, but landscape structure and physical flows often dictate the distance and directionality of dispersal (Lancaster *et al.*, 1996; Elliott, 2003). It is important to understand diversity patterns in dendritic riverine habitats because, even though rivers and riparian areas cover a small proportion of the Earth (0.8%), they contain a disproportionately large number of species ($> 6\%$) (Vorosmarty *et al.*, 2010). In order to protect this diversity, an understanding of ecological processes in dendritic systems is crucial.

In the past, rivers were generally framed within a linear habitat (Vannote *et al.*, 1980; Benda *et al.*, 2004), even though their dendritic structure has long been recognized (Rodríguez-Iturbe & Rinaldo, 1997). Moreover, many local environmental factors were used to explain riverine diversity patterns from a niche-driven perspective (reviewed by Richards *et al.*, 1997; Vinson & Hawkins, 1998; Heino *et al.*, 2003). Recently, a paradigm shift in community ecology has led to an acknowledgement of the importance of spatial dynamics (Holyoak *et al.*, 2005). In the specific case of riverine ecosystems, a series of recent theoretical papers has addressed the origin of the characteristic diversity patterns (e.g. Labonne *et al.*, 2008; Muneeparakul *et al.*, 2008; Morrissey & de Kerckhove, 2009; Goldberg *et al.*, 2010; Lynch *et al.*, 2011). These theoretical studies explicitly considered the inherent hierarchical spatial structure of dendritic networks, and generally suggested that diversity patterns are strongly driven by limited dispersal along the network. In addition, individual drainage basins confine within them the pool of species that are potential dispersers.

The combination of these theoretical, empirical and experimental studies has increased our understanding of diversity patterns in river systems. However, previous empirical studies focused on diversity patterns either in small catchment

areas (e.g. Angermeier & Winston, 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 have indicated 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; Muneeparakul *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).

In this study we used data from an extensive monitoring programme in Switzerland, Central Europe, which surveys the diversity of aquatic insects in rivers and streams across three major drainage basins covering an area of $> 40,000 \text{ km}^2$ (BDM Coordination Office, 2009). The monitoring programme representatively covered 217 sites in catchment areas ranging in size over four orders of magnitude (0.1 to about 1000 km^2) and with elevational differences of $> 2500 \text{ m}$. The insects sampled belong to the orders of may-, stone- and caddisflies (Ephemeroptera, Plecoptera and Trichoptera, respectively; abbreviated as 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 for fish. Furthermore, they show high levels of diversity and are commonly used in biomonitoring programmes (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: they live in a wide range of habitats in the colline (hill) to montane zone, but are generally confined to well-oxygenated waters (Landolt & Sartori, 1997). Stoneflies are, compared with the other two orders, most strongly confined to well-oxygenated, cool water (Landolt & Sartori, 1997). Caddisflies cover 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 metres (Macneale *et al.*, 2005; Sundermann *et al.*, 2011), with the following dispersal hierarchy suggested: mayflies $<$ caddisflies $<$ stoneflies (Petersen *et al.*, 1999, 2004). These differences in ecological preferences and dispersal ability suggest that different factors shape the diversity patterns between these taxa, especially in a landscape highly structured in elevation such as the Alps.

We tested the effects of drainage basin (defining the regional species pool), network centrality (an important river network property), elevation and catchment area size on the α -diversity and community similarity of major groups of aquatic insects. Network centrality is an explanatory variable reflecting spatial connectivity and thus processes driven by

dispersal limitation (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 affects population size through extinction dynamics from a classical biogeographical perspective (MacArthur & Wilson, 1967). All three variables are related to network position. The individual, isolated effects of these drivers on diversity have been examined 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), but large-scale comparisons including all of them and their interactions are scarce. Furthermore, differences in the ecology of EPT, such as different habitat preferences or dispersal abilities, may generate unique responses to these explanatory variables. We addressed diversity patterns by evaluation of hypotheses at the following levels: (1) the regional species pool (i.e. restriction to a specific drainage basin); (2) within-network parameters describing local environmental or network properties; and (3) the three insect orders and possible differences among them owing to their specific ecology (Landolt & Sartori, 1997; Graf *et al.*, 2008). First, we 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 controls all lower-level interactions, including both spatial and local environmental factors, by the specific set of species found per drainage basin (due to the biogeographical history of the species). Thus, we used drainage basin as a covariate reflecting biogeographical history. Second, we looked at diversity patterns from a multi-factorial 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. In particular, we hypothesized that local environmental conditions and network properties interact and thereby reflect the occurrence of ecological dynamics, whereby environmental conditions and network properties are intrinsically linked in riverine networks. Hence, models considering inherent river network properties should be capable of explaining a large part of the variation in local species richness to be explained. Finally, knowing that the three insect orders differ in their ecological requirements, we hypothesized that different sets of variables explain local species richness between the three EPT orders through species-sorting (Holyoak *et al.*, 2005). Because all EPT are 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), are better resolved than the diversity patterns of caddisflies, which generally use a wider range of habitats (Graf *et al.*, 2008). This would indicate that factors affecting diversity in riverine systems depend on the specific life histories and species traits of the organisms of interest.

MATERIALS AND METHODS

Background

In Switzerland, biological diversity is monitored through the comprehensive programme 'Biodiversity Monitoring in Switzerland' (BDM) (BDM Coordination Office, 2009). May-, stone- and caddiesflies (EPT) are monitored on a systematic sampling grid covering the whole of Switzerland. At each site, specially 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, encompassing a number of 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 4634 m a.s.l. Several large European river systems have their source in Switzerland, with the rivers extending from the kernal to the epipotamal zone. The country is drained through major drainage systems (Fig. 1): the River Rhine drainage basin (covering 71% of the country and draining into the North Sea), the River Rhone drainage basin (covering 20% of the country and draining into the Mediterranean Sea), the River Ticino drainage basin (covering 5% of the country and draining into the Po and then the Adriatic Sea), the River Inn drainage basin (covering 3.5% of the country and draining through the Danube into the Black Sea) and the River Etsch drainage basin (covering 0.5% of the country and draining 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 the 'Ticino/Inn' drainage basin.

The EPT monitoring of the BDM currently covers the 217 investigated sampling sites (Fig. 1), which were 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. The sampling scheme ensures that headwaters, which are much more numerous by definition, are not 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 second-order streams upwards (Stucki, 2010). Standing waterbodies, first-order streams and watercourses that are completely inaccessible by wading were not sampled for methodological reasons (Stucki, 2010). Each site was sampled once between 2009 and 2011. The seasonal timing of the sampling depended on the elevation, and took place between March

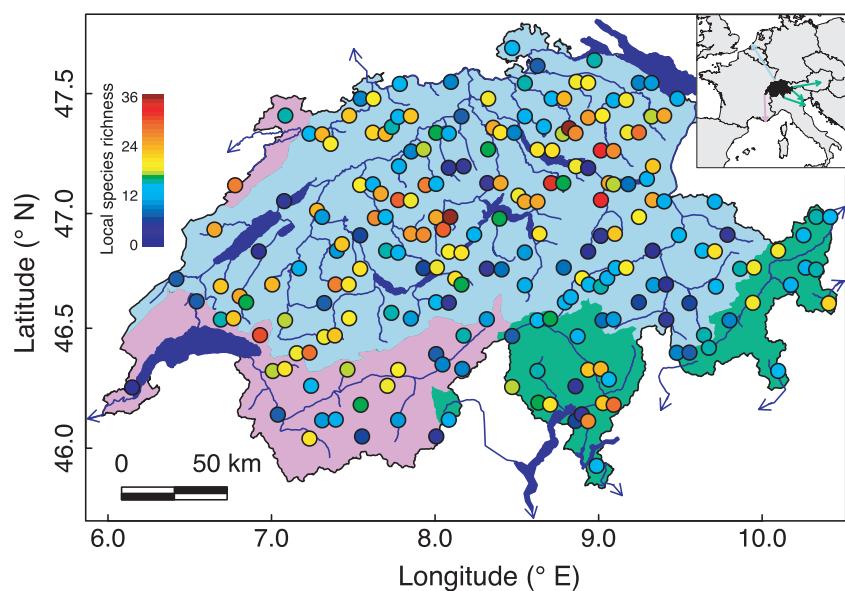


Figure 1 Local species richness (α -diversity) of may-, stone- and caddisflies (EPT) in Switzerland, for all 217 biodiversity monitoring sites. The main rivers and larger lakes are given for orientation purposes (dark blue). The drainage basins are colour-coded: Rhine drainage (light blue), Rhone drainage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

and July. It was optimized for the local phenology of EPT (Stucki, 2010). For each site, data on elevation (m a.s.l.) and upstream catchment area (km^2) 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 $25 \text{ cm} \times 25 \text{ cm}$ opening and $500\text{-}\mu\text{m}$ mesh size. All sites had equal sampling efforts (i.e. regarding the number of kick-net subsamples taken and duration of ‘kick-netting’), independent of the 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 from which the eight subsamples were chosen was proportional 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 \times (10 times the mean river width). In the following we use the term ‘site’ to refer to those sampling sites at which we collected the community data. The subsamples 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 identification to species level was possible for most individuals, the larvae of a few EPT species are not identifiable to species level, or have not yet been described based on morphological characters. Such species were identified to the level of predefined species complexes. 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 EPT species studied here disperse predominantly 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 (GAMs) with integrated smoothness estimation, using the R package MCV (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. Each drainage basin defines a major biogeographical area, in which all water drains through continental streams into the sea (Fig. 1). Catchment area is the total area upstream of a sampled site that drains into that site. Stream width, mean annual discharge and extent of riparian vegetation at a site scale directly with the catchment area of that site (Leopold *et al.*, 1964). Therefore, catchment area is an approximation for local habitat capacity. Elevation is the elevation at the sampled site, reflecting local environmental conditions such as temperature and 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 correlation test to ensure that the three continuous explanatory variables were not correlated with each other (see Appendix S1 in Supporting Information). For models on α -diversity (i.e. the numbers of species, which are count-data) we used a Poisson link function, and a chi-square 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 minimization of the Akaike information criterion (AIC), until we had one best model explaining the α -diversity of all EPT species, and one best model explaining the α -diversity of may-, stone- or 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 correlation test to analyse pairwise comparisons of local species richness between may-, stone- and caddisflies.

We compared along-stream and Euclidean distances with various pairwise measures of among-community similarity (using the R package VEGAN; 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 more weight on more common species). For all sites, we calculated the pairwise along-stream distance within the respective drainage basin, the pairwise Euclidean distance and the absolute pairwise difference in elevation compared with 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 describes the affiliation of sites to the three drainage basins. *P*-values are based on 999 permutations. We used a GAM for significance testing and for 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 a 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 species endemic to the Alps were found (see Appendix S1).

In the GAM on the 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

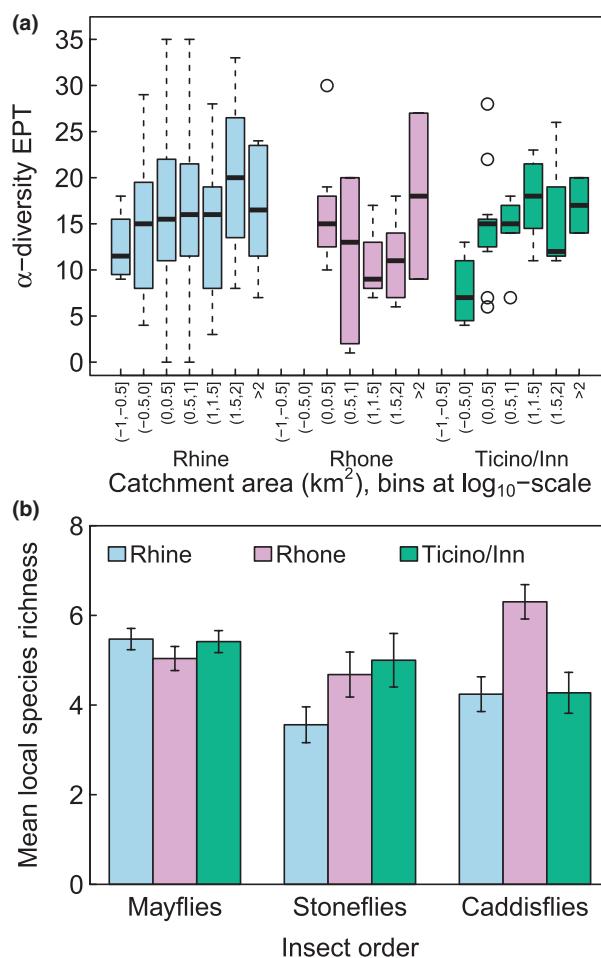


Figure 2 (a) Boxplots of local species richness (α -diversity) of all may-, stone- and caddisflies (EPT) combined relative to the catchment area (bins at \log_{10} -scale) of a site. The data are shown separately for the three drainage basins Rhine, Rhone and Ticino/Inn in Switzerland (colour-coded; see Fig. 1). The thick black line in the box is the median; the box extensions 25% and 75% quantiles, respectively. The whiskers (dashed lines) extend to the most extreme data point which is no more than 1.5 times the interquartile range from the box; outlier values more extreme than that are given as circles. (b) Mean (\pm SE) local species richness, given separately for may-, stone- and caddisflies in the three drainage basins.

area, elevation and their interaction also contributed significantly to the smooth terms. The 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 and 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 separate drainage basins of the Rhine, Rhone and Ticino/Inn), but these factors were 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

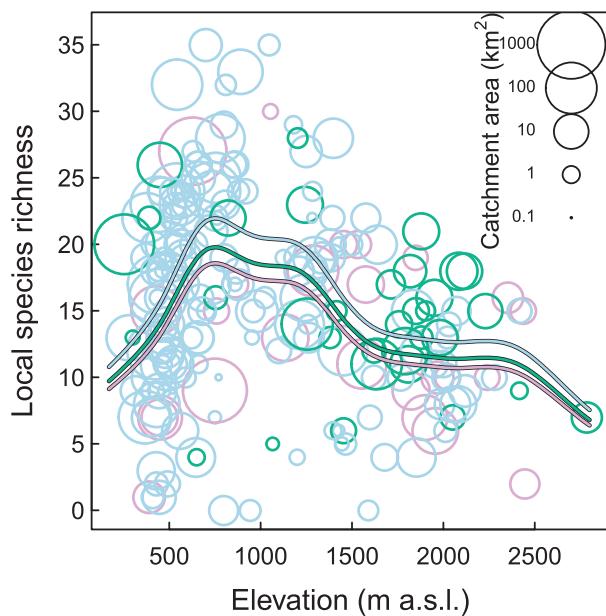


Figure 3 Bubble plot of local species richness of may-, stone- and caddisflies (EPT) in Switzerland relative to the elevation and the catchment area (size of circles, \log_{10} -scale) of a site. The different colours refer to individual drainage basins (see Fig. 1). The lines are predictions of a generalized additive model, with predictions given for each drainage basin.

centrality. All further two-way interaction terms were non-significant but were retained in the model based on the 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 insect orders of may- (E), stone- (P) and caddisflies (T) were similar, and significantly correlated with each other (E versus P: correlation coefficient (cor) = 0.5, $t_{215} = 8.5$, $P < 0.0001$; E versus T: $\text{cor} = 0.54$, $t_{215} = 9.4$, $P < 0.0001$; P versus T: $\text{cor} = 0.29$, $t_{215} = 4.4$, $P < 0.0001$). 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, Table 2). The adjusted R^2 of the models and percentage deviance explained are 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 and their relative proportion 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 mayflies) and elevation (for stoneflies)

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

Estimate	d.f.	χ^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 × catchment area	2	5.141	0.076
Drainage basin × elevation	2	4.846	0.088
Drainage basin × network centrality	2	4.345	0.114
Catchment area × network centrality	1	5.893	0.041
Catchment area × elevation	1	0.003	0.955
Elevation × network centrality	1	0.627	0.428
Drainage basin × catchment area × elevation	2	5.048	0.080
Drainage basin × catchment area × network centrality	2	4.287	0.117
Drainage basin × elevation × network centrality	2	6.469	0.039
Catchment area × elevation × network centrality	1	0.028	0.867
Drainage basin × catchment area × elevation × network centrality	2	6.656	0.035
Approximate significance of smoothing terms (s)			
s(network centrality)		6.033	0.323
s(catchment area)		21.01	< 0.001
s(elevation)		23.19	0.003
s(network centrality × elevation)		65.76	< 0.001
s(catchment area × elevation)		0.004	0.999

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 × catchment area and drainage basin × network centrality.

Pairwise comparisons of among-community similarity revealed significant decreases in community similarity with both increasing pairwise along-stream distance and increasing Euclidean distance, conditioned on the drainage basin affiliation (see Fig. S1 in Appendix S1). 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. S1a) and versus Euclidean distance ($r_{\text{partial Mantel}} = 0.18$; Fig. S1b); Bray-Curtis similarity versus pairwise along-stream distance ($r_{\text{partial Mantel}} = 0.17$; Fig. S1c) and versus Euclidean distance ($r_{\text{partial Mantel}} = 0.15$; Fig. S1d); and finally, Chao similarity versus pairwise along-stream distance ($r_{\text{partial Mantel}} = 0.24$; Fig. S1e) and versus Euclidean distance ($r_{\text{partial Mantel}} = 0.18$; Fig. S1f). The decrease in community similarity over distance was more pronounced for Euclidean distances than respective along-stream distances. Similarly, there was a significant decrease in community similarity with increasing pairwise absolute elevational difference (Fig. S2 in Appendix S1; Jaccard similarity, $r_{\text{partial Mantel}} = 0.48$; $P < 0.001$). Predicted pairwise

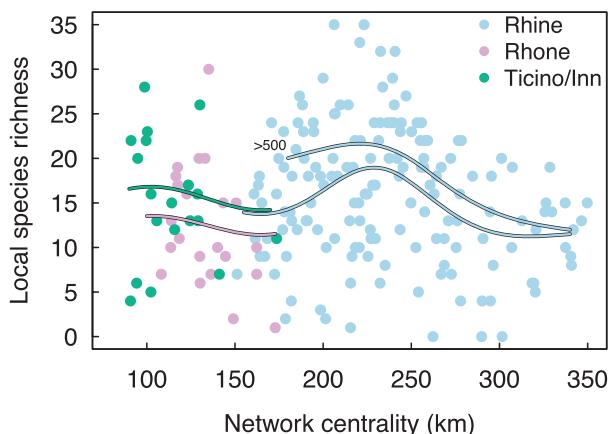


Figure 4 Local species richness of may-, stone- and caddisflies (EPT) in Switzerland relative to the network centrality of a site. Species richness decreases with increasing spatial isolation of a site; however, the effect is significant only in the interaction with elevation and catchment area. The lines are the predictions of a generalized additive model, with predictions given for each drainage basin. For the Rhine catchment, the model was run with all sites, but also only for sites higher than 500 m a.s.l. (> 500). Sites at lower elevations are the most strongly modified by humans. The different colours refer to individual drainage basins (see Fig. 1).

community similarity depended significantly on elevational difference (GAM, $\chi^2 = 14.8$, $P = 0.0001$, 26% deviance explained; Fig. S3 in Appendix S1), 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). In this study, we tested and confirmed hypotheses that α -diversity and community similarity patterns of aquatic insects are correlated not only with local environmental variables but also with 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 the geophysical characteristics of river network structure (Rodríguez-Iturbe & Rinaldo, 1997) are associated with characteristic patterns of diversity, and that the latter are probably driven by the river structure (Carrara *et al.*, 2012).

In the European Alps, there are large topological and elevational differences across major river networks, and strongly affecting habitat size and position within the network. Small headwater streams (i.e. streams with a small catchment area) were found across an elevational range of > 2000 m, and can either be highly connected within the network (low network centrality) or be highly isolated (high network centrality). These properties are inherent and comparable to those of

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 proportional 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 also commonly defines dispersal pathways and connectivity among sites (Carrara *et al.*, 2012). These dispersal pathways are also different to other aquatic systems, such as rock pools and ponds (Altermatt & Ebert, 2008, 2010). The inherent properties of river networks closely reflect the two main patterns affecting diversity within metacommunities, namely local habitat conditions and connectivity (Gonzalez *et al.*, 1998; Mouquet & Loreau, 2003; Hanski & Gaggiotti, 2004), and are thereby potential drivers of local community composition and diversity.

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

A decreasing dependence of α -diversity on network centrality is predicted by dispersal theory (Mouquet & Loreau, 2003). At first glance, a decrease in richness is expected with increasing isolation (Fig. 4). However, we observed this only in two of the three drainage basins, and the main effect of network centrality was non-significant. The significant three-way interaction with drainage basin and elevation (Table 1) was the result of a unimodal relationship in the River Rhine drainage basin. Network centrality, being a measure of connectivity, may closely reflect dispersal rates, and subsequently

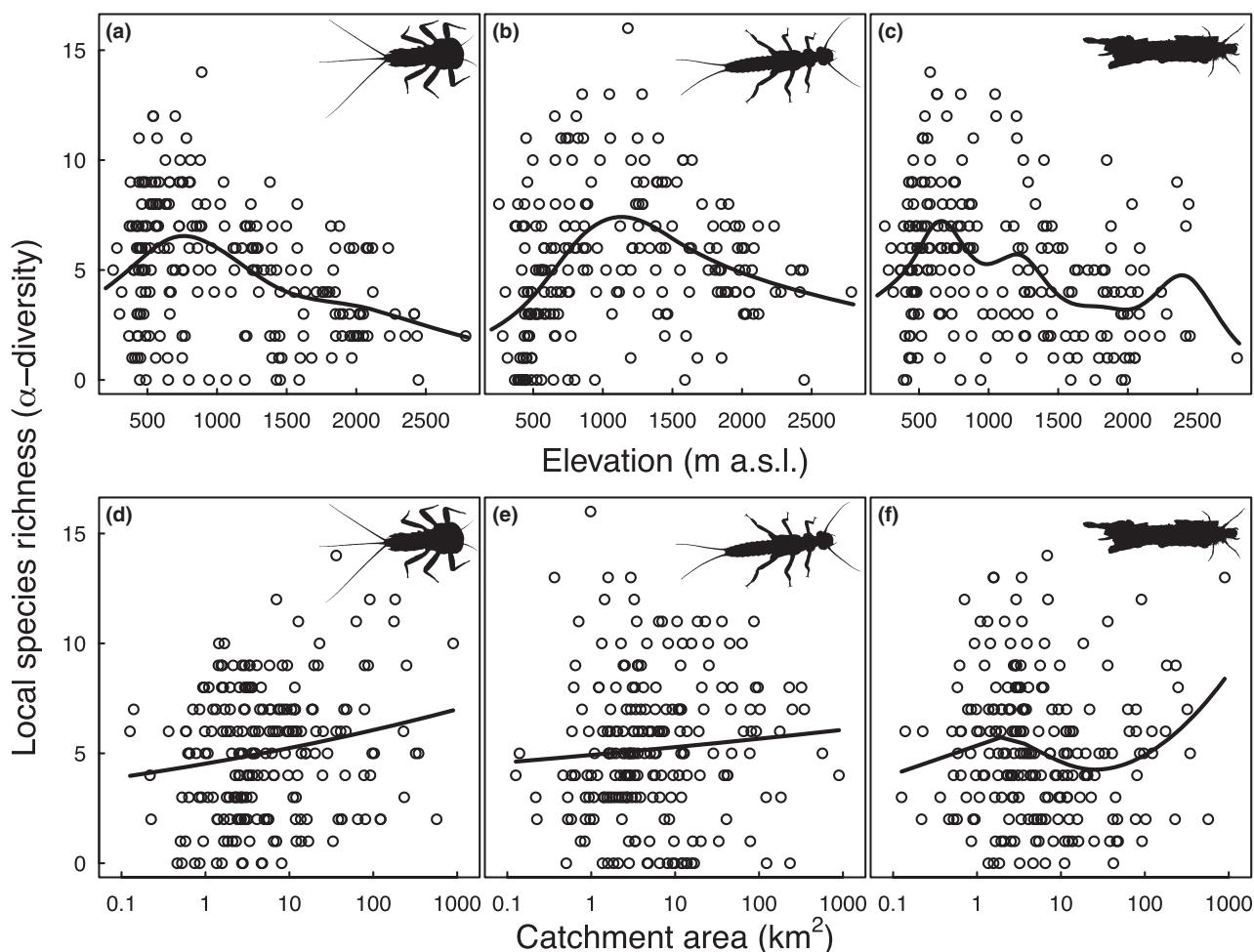


Figure 5 Local species richness of mayflies (a, d), stoneflies (b, e) and caddisflies (c, f) in Switzerland relative to the elevation (a–c) and the catchment area (d–f) of a site. The lines are predictions of generalized additive models, for each insect order separately.

both high and low dispersal rates (i.e. low and high network centrality) may decrease local diversity, but for different reasons (the dominance of a few superior species versus the lack of re-colonization after local extinctions). Alternatively, the unimodal relationship could reflect anthropogenic activities, which 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 levels of 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 sets of factors correlating with local EPT species richness were different among the three orders of aquatic insects considered individually (Table 2). Furthermore, drainage basin became highly significant as a main factor, indicating that the pool of regionally available species within a given drainage basin is different across the three insect orders. Together, this indicates that we cannot use the same set of parameters to equally describe

the diversity and species richness patterns across orders of aquatic insects, as both the pool of regionally available species (Fig. 2b) and their dependence on local and spatial factors are different. The diversity of the ecologically most heterogeneous group of caddisflies was best explained by drainage system as the 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 drive diversity patterns. Local and spatial factors are less important in explaining within-order local diversity, possibly because of the relatively 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,c, Fig. 5). This result corresponds well with the ecological requirements of these species groups (Landolt & Sartori, 1997): almost all stoneflies but also many mayflies depend 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

Table 2 Generalized additive models, explaining local species richness of (a) mayflies, (b) stoneflies, and (c) caddisflies by drainage basin, catchment area, elevation, network centrality and their interactions in the study area of Switzerland. Model estimates and significance of the smoothing terms are given. The adjusted R^2 of the models and percentage deviance explained are 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	d.f.	χ^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 × catchment area	2	12.53	0.002
Drainage basin × elevation	2	2.972	0.226
Drainage basin × network centrality	2	7.097	0.029
Elevation × catchment area	1	0.149	0.699
Elevation × network centrality	1	3.983	0.046
Network centrality × catchment area	1	11.34	<0.001
Approximate significance of smoothing terms (s)			
s(network centrality)	0	0.999	
s(catchment area)	6.1	0.032	
s(elevation)	0	0.999	
s(network centrality × elevation)	29.2	0.066	
s(catchment area × 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 × catchment area	2	11.02	0.004
Drainage basin × elevation	2	5.100	0.078
Drainage basin × network centrality	2	8.199	0.017
Elevation × catchment area	1	0.968	0.325
Elevation × network centrality	1	0.727	0.394
Network centrality × catchment area	1	5.163	0.023
Approximate significance of smooth terms (s)			
s(network centrality)	10.48	0.107	
s(catchment area)	0.004	0.951	
s(elevation)	0	0.999	
s(network centrality × elevation)	48.17	< 0.001	
s(catchment area × 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 × catchment area	2	13.53	0.001
Drainage basin × elevation	2	4.323	0.115
Drainage basin × network centrality	2	8.786	0.012
Elevation × catchment area	1	1.437	0.231
Elevation × network centrality	1	3.280	0.070
Network centrality × catchment area	1	0.702	0.402
Approximate significance of smooth terms (s)			
s(network centrality)	23.12	0.002	
s(catchment area)	12.54	0.021	
s(elevation)	0	0.999	
s(network centrality × elevation)	0.006	0.789	
s(catchment area × elevation)	19.36	0.095	

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 indicates 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 unreachable owing to the limited dispersal abilities of some species (Sundermann *et al.*, 2011). Such patterns are consistent with the observation that dispersal occurs mostly along rivers (Elliott, 2003), either during the aquatic larval stage, or because adults fly along the river but not over land (Petersen *et al.*, 2004).

For the purposes of conservation biology it is highly relevant that a different set of explanatory variables explained diversity for each of the three EPT orders. EPT have a long history of being used as indicator taxa, and many of them are threatened and appear on 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. It is thus very important 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 by local, spatial and regional factors. These insect orders might be more strongly affected not only by habitat change but also by habitat fragmentation and subsequent dispersal limitation. Thus, it might only be when the protection (or restoration) of local habitat conditions is seen from a network perspective that the species therein profit. Recent studies on the success of river restorations do indeed show that the restoration of local conditions is not in itself 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 the overall effects of local and network parameters on their diversity, calling for a conservation strategy focused even more strongly at the species level.

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 on elevational differences (Figs S1 & S2). 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 and long distance (Fig. S1), suggesting that mechanisms other than dispersal limitation affect community composition. Elevation is a factor likely to affect community similarity, as it is one of the strongest drivers of local environmental

conditions (for example temperature and precipitation). Elevation not only affects α -diversity (as described above), but also strongly interacts with the effect of isolation on among-community similarity (Fig. S2). Large differences in elevation between two sites were associated with large differences in community composition even at relatively small along-stream distances (Fig. S3). This suggests that dispersal limitation constrains among-community similarity, but mostly within the ‘elevational envelope’ that drives abiotic conditions.

We conclude that the diversity of aquatic insect communities in river networks is correlated in complex ways with an important network property, namely centrality within the network, and with elevation and catchment area. The latter not only reflect local conditions but also 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 profits from a network perspective and the linking of scales (Benda *et al.*, 2004; Lowe *et al.*, 2006), but manifold anthropogenic influences pose challenges that need to be addressed, especially when we want not only to understand current diversity patterns but also to 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.

BIOSKETCHES

Florian Altermatt is a senior scientist interested in meta-community ecology, dispersal ecology and large-scale diversity patterns. He studies mainly invertebrates, combining comparative and experimental studies.

Mathew Seymour is a PhD student under the supervision of Florian Altermatt, studying diversity patterns in riverine systems.

Nicolas Martinez is a project leader at the Biodiversity Monitoring in Switzerland (BDM) 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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