

# Fluvial network topology shapes communities of native and non-native amphipods

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**Abstract.** Habitat connectivity crucially influences dispersal of organisms. It is especially seen as an important driver of the spatial structuring of biological communities in ecosystems that have intrinsic and general connectivity patterns, such as the universal dendritic structure of fluvial networks. These networks not only define dispersal of native species, but also represent corridors of biological invasions, making understanding network topology effects on invasion dynamics and subsequent diversity patterns of high interest. We studied amphipod community diversity and structure in the upper 27,882-km<sup>2</sup> drainage basin of the river Rhine in Central Europe, focusing on differences between native and non-native species. Overall, species richness increased along the network from headwaters to the outlet nodes. We found, however, contrasting patterns of native and non-native amphipod richness along the network, with headwater nodes representing refugia for native species and more downstream nodes being hotspots of biological invasions. Importantly, while species turnover ( $\beta$ -diversity) of native species increased with distance between nodes in the network, this was not the case for non-native species, indicating a much lower dispersal limitation of the latter. Finally, the overall amphipod community structure closely mirrored the topological modularity of the network, highlighting the network's imprint on community structure. Our results underpin the importance of connectivity for community formation and the significance of rivers for biological invasions and suggest that empirically observed matches of diversity patterns in rivers predicted by null models are the long-term outcome of species invasions and species sorting.

**Key words:** biodiversity; community assembly; dendritic networks; habitat connectivity; invasion biology.

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## INTRODUCTION

Community ecologists have identified habitat connectivity as a fundamental factor influencing species distributions for a long time. Island biogeography (MacArthur and Wilson 1967) highlighted the role of dispersal for local species richness on top of the previously recognized role of single species' habitat requirements (ecological niche sensu Hutchinson 1957). More recently, metacommunity ecology shifted the focus from

mainly environmental conditions to dispersal dynamics of single species shaping the composition and diversity of ecological communities (Gilpin and Hanski 1991, Leibold et al. 2004). Thereby, spatial dynamics are on the one hand driven by the species-specific dispersal and invasion dynamics and on the other hand by the underlying landscape topology defining dispersal pathways.

In freshwater habitats, dispersal of aquatic organisms is mostly confined to well-defined and prevalent spatial networks shaped by the

fluvial processes (Rodríguez-Iturbe et al. 2009), compared to the spatially differently, and often less consistently, structured terrestrial habitats (blue vs. green networks, see Altermatt 2013). In fluvial networks, there is not only one universal topology defining dispersal pathways, but these networks are also directed by the flow of water. This has pronounced effects on dispersal of organisms (e.g., Seymour and Altermatt 2014), and many early studies focused on the effect of unbalanced dispersal and drift (Williams and Hynes 1976, Delucchi 1989, Van Riel et al. 2011). A series of recent theoretical studies on metapopulation and metacommunity models identified the general influence of the fluvial network topology on turnover dynamics and biodiversity within such networks (e.g., Fagan 2002, Munepeerakul et al. 2007, Carrara et al. 2012, Fronhofer and Altermatt 2017). Generally, all these models predict that species richness is highest in more central nodes of the network and that species richness increases along the network from headwater to downstream nodes, which, in turn, causes an increased species turnover ( $\beta$ -diversity) between headwater nodes. These theoretical predictions are supported by experimental studies, where dendritic connectivity drives microbial diversity patterns (Carrara et al. 2012, Seymour and Altermatt 2014). Finally, empirical data from riverine ecosystems worldwide are in consistent with these predictions and show that macroinvertebrate communities are shaped by network topology (e.g., Brown and Swan 2010, Altermatt et al. 2013, Grönroos et al. 2013, Fourtune et al. 2016). However, all these studies generally looked at homogenous groups of native species and were not considering effects of non-native species (but see Mari et al. 2011 for the example of a non-native species).

Recent anthropogenic influences increased the displacement of species beyond naturally occurring scales and rates (Mack et al. 2000). While non-native species are found in almost every ecosystem worldwide, riverine ecosystems are among the most heavily affected (Strayer 2010). As biological invasions often happen along corridors (e.g., Leuven et al. 2009, Mari et al. 2011), such as the fluvial network, a better understanding of the influence of connectivity on invasion dynamics and subsequent diversity patterns is needed (Campbell Grant et al. 2007, Panov et al.

2009). Past studies mostly looked at the spread of non-native species in fluvial networks (Leuven et al. 2009, Barták et al. 2013), while only few looked at how colonization in fluvial networks shapes  $\alpha$ - and  $\beta$ -diversity. Thus, we are lacking an understanding on the distribution and diversity patterns of native and non-native species within well-defined ecological guilds at the scale of whole fluvial networks. One could expect differences in the distribution pattern between native and non-native species due to differing dispersal capabilities (van Riel et al. 2009), due to a higher competitiveness (Grabowski et al. 2007) of the latter, for example, by additional functional groups, or due to differences in colonization time of the invaded habitats that presumably were in a steady state (Vellend 2010, Mari et al. 2014). Here, we studied diversity patterns of amphipod communities in the river Rhine drainage basin of Switzerland, with a special focus on native vs. non-native species. Amphipods are among the most common and widespread macroinvertebrates throughout freshwater habitats of the northern hemisphere (Väinölä et al. 2008). They provide important ecosystem functions and are key organisms of aquatic foodwebs. Multiple European freshwater ecosystems experienced many replicated cases of invasions by non-native amphipod species (Bij de Vaate et al. 2002, Hänfling et al. 2011), and many of these species are now present in the upper river Rhine (Altermatt et al. 2014). This allowed us to compare diversity patterns of native and non-native species along a fluvial network topology within the same taxonomic group. Focusing on a single group excludes potential effects of different dispersal modes (e.g., with flying adult stages of aquatic insect larvae) or life strategies (mode of reproduction, average lifespan, metabolic needs) while considering new functional groups (e.g., predatory behavior).

Specifically, we addressed the following hypotheses:

1. Catchment-level species richness ( $\alpha$ -diversity) increases within the fluvial network from headwater to downstream nodes as the former show a lower degree of connectivity.
2. Dispersal limitation leads to a distance decay relationship (DDR) of similarity (species turnover,  $\beta$ -diversity) with topological distance along the fluvial network.

3. Native and non-native amphipod species show different slopes of  $\alpha$ - and  $\beta$ -diversity patterns along the fluvial network due to differing dispersal limitation, species sorting, and temporal effects.
4. Community assembly and structure mirror the fluvial network topology (e.g., modularity).

These hypotheses are based on theoretical and verbal concepts of spatially explicit metacommunity theory in fluvial networks and invasion biology (e.g., Muneeppeerakul et al. 2007, Economo and Keitt 2008, Brown and Swan 2010, Carrara et al. 2012, Altermatt 2013). Finding these differences between native and non-native species would support differently partitioned ecological processes between those groups.

## METHODS

### Study area

The river Rhine is one of the largest European stream systems, draining an area of 185,300 km<sup>2</sup>. It originates in Switzerland and flows through Austria, Germany, France, and The Netherlands. Associated with recent environmental changes and the increasing connectivity to other ecosystems, the river Rhine has experienced a high number of invasions by non-native species over the last decades (e.g., Bij de Vaate et al. 2002).

We focused on the Rhine drainage basin of Switzerland (27,882 km<sup>2</sup>), which is the uppermost part of the network, and for which we had detailed data on amphipod occurrence at hand. This part of the network is also the only remaining part that has no artificial waterways connecting different drainage basins (Leuven et al. 2009). Hence, our focal network is a true dendritic network. In order to analyze the influence of network topology on amphipod communities, we constructed a digital representation of the fluvial network. Graph theory provides a suitable framework to study connectivity of habitats in a spatially explicit manner (Urban et al. 2009). We generated an adjacency matrix of catchments within Switzerland using geodata from swisstopo (Bern) and BAFU (2012). Based on this, we generated the graph representation of the network using the package igraph (Csárdi and Nepusz 2006). The resulting fluvial network representation assumes catchments being

nodes and stream flow direction being directed vertices. The Euclidean distances from one catchment outlet site to the next downstream catchment outlet site are included as weights of the vertices (the directed graph object is included in the Data S1). After construction of the fine-scale network representation, we collated the 2-km<sup>2</sup> catchments into combined larger catchments so that the network representation matches our sampling scheme and the available faunistic data. Hence, the analysis is based on a spatial resolution of 1000-km<sup>2</sup> catchments, represented by a total of 31 catchments referred to as nodes (see Appendix S1: Fig. S1 for an abstraction of the network figure). This allowed to study large-scale imprints of network topology and to deduce general implications.

### Study organisms

We focused on amphipods (Crustacea, Amphipoda) for which we assembled comprehensive data on all species found in surface waters of our study area. Data on subterranean species were excluded as their habitat connectivity relies on a different habitat network. Our data are based on previously published literature (see Altermatt et al. 2014), records from museum collections (natural history museums of Basel, Chur, Frauenfeld, Geneva, Lausanne, Zürich, the Canton of Ticino, and the Musée du Léman), reports by cantonal authorities and private companies (gray literature), governmental monitoring programs, and our own extensive sampling using a standardized kicknet approach (Altermatt et al. 2014, 2016, Alther et al. 2017). The most extensive part of our dataset was sampled between 2009 and 2016 in standardized governmental programs as well as our own semiquantitative samplings, which were done based on the same methodology. Given the somewhat heterogeneous and mostly semiquantitative data, we used presence/absence only and did all analyses on relatively large sub-catchments in order to even out any potential sampling bias. We only included records identified to the species level (identification after Eggers and Martens 2001). Species assignment followed the most recent taxonomy according to the World Amphipoda Database (<http://www.marinespecies.org/amphipoda/>). Since the most common amphipod species within Switzerland (*Gammarus fossarum* s.l.) is known to represent a cryptic species complex, we used a molecular identification procedure

(see *Molecular identification* section) with a representative and geographically well-spread subsample of these specimens (see Appendix S2: Fig. S1 for overview map). For two nodes, we only had information on the presence of *G. fossarum* s.l., and we thus assigned these *G. fossarum* s.l. specimens to any of the three types (A, B, or C) found at the closest downstream node.

The resulting database contained 150,087 amphipod specimens recorded from 1081 different sites within the river Rhine drainage. Species data from single sites then were aggregated to 1000-km<sup>2</sup> catchments, as done with the network representation. This led to the final 17 species × 31 node matrix used for the analysis. For additional analyses, we restricted the data to more recent and more consistently sampled data (after 2009), originating almost exclusively from official monitoring programs and our own sampling following the same protocol (Stucki 2010).

#### *Molecular identification*

A total of 6034 *G. fossarum* specimens from 283 sites were identified using molecular methods. Of these, 5819 specimens were based on the results from previous studies (Westram et al. 2011, Altermatt et al. 2014, 2016), some of which the identifications were based on microsatellite data, whereas other were based on 16S rRNA data. For an improved spatial coverage across Switzerland, we sequenced additional 215 specimens for the 16S region for this study specifically. For methodological details on the microsatellite identifications and previously published data, we refer to Westram et al. (2011) and Altermatt et al. (2014) and the references mentioned therein. For the detailed protocol of the 16S rRNA analyses, we refer to the Appendix S3.

#### *Statistical analysis*

All analyses are based on the above-described presence–absence matrix. This assures comparability of the results despite the various data sources. Whereas species richness was calculated as the number of species present for each node (catchment-level species richness), we calculated community similarity as 1 minus the Jaccard distance index using the `vegdist()` function in the package `vegan` (Oksanen et al. 2016). For partitioning the  $\beta$ -diversity into its turnover and nestedness component, we used the `beta.pair()`

function in the package `betapart` (Baselga and Orme 2012).

As we were interested in the form of the patterns of catchment-level species richness within the fluvial network but had no prior intuition on the mechanistic model, we analyzed catchment-level species richness using generalized additive models (GAMs) with implemented smoothness estimation from the package `mgcv` (Wood 2011). We ran separate models on distance to outlet and on betweenness centrality as explanatory variables. These were considered as the non-linear term in the model specification. Both measures repeatedly showed to be important and meaningful in ecology, with betweenness centrality depicting key nodes for connectivity of habitats (Urban et al. 2009, Jacoby and Freeman 2016). Catchment size and upstream distance were only weakly correlated (Spearman correlation coefficient,  $-0.48$ ), as there can be small catchments at both relatively small and large upstream distances. For fitting the model, we assumed the response variable to follow a Poisson distribution. Status (native or non-native) was included as a factorial explanatory variable, both in the smoothing parameter and in fixed factor. For the combined model using the total species richness, we ran separate models. For the significance test of the smoothing terms, we used a chi-square test. Differences between fitted GAMs were evaluated based on chi-square using an analysis of deviance table (`ANOVA.gam`) and checking the parametric term.

As a measure for node centrality of the catchments in the fluvial network, we used betweenness centrality defined as  $C_B(v) = \sum_{i \neq v \neq j} \frac{\sigma_{ij}(v)}{\sigma_{ij}}$  (Freeman 1977), where  $\sigma_{ij}$  denotes the number of geodesics (shortest paths) from node  $i$  to node  $j$ .  $\sigma_{ij}(v)$  are the geodesics from node  $i$  to node  $j$  that pass through node  $v$ . Hence,  $C_B$  translates to the proportion of geodesics connecting all possible pairs of nodes passing through a certain node. We calculated the normalized  $C_B(v)$  with the `betweenness()` function from the package `igraph` using weighted edges on the undirected graph representation of the network. We used the undirected network as calculating centrality based on the directed network would imply completely asymmetric dispersal which is biologically not sensible. As the fluvial network continues after the Rhine flows out of Switzerland, we added in

silico a dendritic network twice the size of the Rhine network within Switzerland to the outlet node to avoid artifacts with respect to network metrics due to the cut-off of the data/network in Basel. To ensure the appropriateness of this procedure, we conducted a sensitivity analysis by varying the size of the artificially added network and checking the outcomes.

To compare community similarity with topological distance, we used a Mantel test.  $P$ -values were based on 999 permutations. We calculated the topological distance between nodes along the network based on the graph within the package `igraph` and used the edge weights as distances between nodes. To include the flow direction as a biologically important property of the network, the pure topological distance is weighted by four times the product of the upstream-to-downstream ratio between nodes. The upstream-to-downstream ratio is maximized for two nodes that have identical distances of upstream and downstream reaches when moving from one to the other (upstream  $\times$  downstream distance proportion =  $0.5 \times 0.5 =$  ratio of 0.25). A comparison between nodes where one is located downstream of another results in a upstream-to-downstream ratio of 0 (upstream  $\times$  downstream distance proportion =  $0.0 \times 1.0$ ). With our correction of weighting the topological distance by four times the upstream-to-downstream ratio, a comparison of identical topological distances but between a headwater and a downstream node or two headwater nodes result in different values, with the latter resulting in a twofold distance compared to the first one. Furthermore, multiplication of the ratio assures a single value for a single comparison between nodes, irrespective of the node order of the comparison. For significance testing, we used three separate GAM models for native, non-native, and the total community data using a quasibinomial distribution.

Modularity of the network was determined based on edge betweenness of the graph using the `cluster_edge_betweenness()` function in the package `igraph`. Therefore, nodes within a module are more connected than between modules (less fragmented), and hence, ecological communities may be more similar within modules (Leibold et al. 2004). To compare the modularity with community structure, we relied on hierarchical clustering representation of both. We

therefore converted the modularity data into a dendrogram. We clustered community similarity hierarchically applying the complete linkage method in `hclust` using the Jaccard dissimilarity index. To then compare the spatial and biological clustering visually, we used tanglegrams using the package `dendextend` (Galili 2015). As a measure of similarity between these two clusterings, we used the entanglement value after applying a two-sided untangle algorithm. For significance testing, we bootstrapped the community data 10,000 times using the `cooc_null_model` from the package `EcoSimR` (Gotelli et al. 2015). This method randomized the community data matrix with fixed node and species sums, hence preserving the richness of nodes and total amphipod diversity within the Rhine drainage.

All analyses were performed in R 3.4.0 (R Core Team, 2017) using Rstudio ver. 1.0.143 (RStudio Team, 2016) and the packages `vegan` (Oksanen et al. 2016), `mgcv` (Wood 2011), `igraph` (Csárdi and Nepusz 2006), `dendextend` (Galili 2015), `EcoSimR` (Gotelli et al. 2015), `betapart` (Baselga and Orme 2012). Data and functions to reproduce results are included in Data S1. Maps were generated in ArcGIS 10.2.2 (ESRI Inc., Redlands, California, USA).

## RESULTS

Five native and twelve non-native species of surface amphipod species were present within the Rhine drainage basin of Switzerland (Appendix S4: Table S1). All native species belonged to the genus *Gammarus*, while the non-native amphipods additionally included species from the genera *Chelicorophium*, *Crangonyx*, *Dikerogammarus*, *Echinogammarus*, and *Synurella*. We found that catchment-level species richness ( $\alpha$ -diversity) significantly increased from headwater to downstream nodes along the fluvial network (Fig. 1). Communities of native species started at low (0–1) species richness at the furthest upstream nodes (large distance to outlet), then increased with decreasing distance to outlet, but quickly saturated at three species over the remaining, further downstream area (Fig. 2a, blue line). The fitted GAM had an adjusted  $R^2$  of 0.43 with 46.8% deviance explained. The smoothing term for native species was marginally significant ( $P = 0.0983$ ). Contrastingly, non-native species were absent over most of the larger distance to outlet sections,

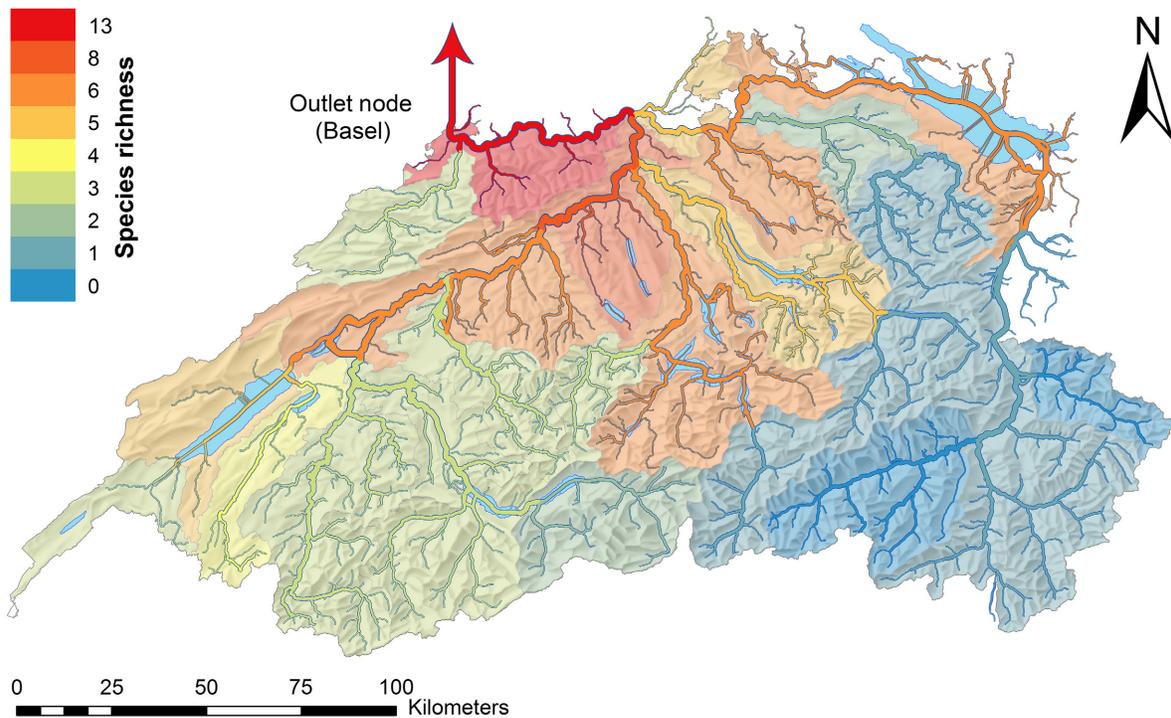


Fig. 1. Amphipod species richness in the river Rhine drainage basin of Switzerland. Local species richness along the fluvial network is depicted as a heatmap, with streams and underlying catchments colored with respect to the observed catchment-level species richness.

but showed a quasi-exponential increase in richness toward the outlet nodes (Fig. 2a, red line). The smoothing term was highly significant ( $P = 1.89e-07$ ). At the most downstream node, there were more non-native than native amphipod species (10 non-native species vs. three native species). Combining native and non-native species, amphipod richness increased steadily from upstream-to-downstream nodes (Fig. 2a, black line). The adjusted  $R^2$  of the GAM was 0.45, with 45.5% deviance explained. The respective smoothing term was highly significant ( $P = 8.16e-08$ ). There was a significant difference in amphipod richness in relation to upstream distance between native and non-native species (ANOVA, parametric term  $P = 4.15e-05$ ). An additional analysis using the restricted dataset of standardized samples from between 2010 and 2016 gave qualitatively consistent results, and results from the GAMs were still significant (see Appendix S5: Fig. S1).

As distance to outlet only captures a specific property of network topology, but ignores, for

example, node position in relation to the other nodes, we applied node centrality as additional measure of network topology commonly used in graph theory. Centrality of nodes (accounted as betweenness centrality) had a major and significant influence on amphipod richness. Catchment-level species richness increased with increasing betweenness centrality of nodes (Fig 2b). Again, this pattern was mostly driven by the non-native species (Fig. 2b, red line). The fitted GAM had an  $R^2$  of 0.65 with 50.7% deviance explained and a significant smoothing term ( $P = 7.5e-12$ ). The smoothing term for native species was not significant ( $P = 0.16$ ). As we considered the dendritic network extension below our furthest downstream node for which we had data, the most central node is correctly concordant with the most downstream node, where we also could observe the highest species richness. The general additive model fitted to the total species richness (Fig. 2b, black line) was highly significant (smoothing term  $P = 8.6e-09$ ), with an  $R^2$  of 0.61% and 48.1% deviance explained. Again, there was a

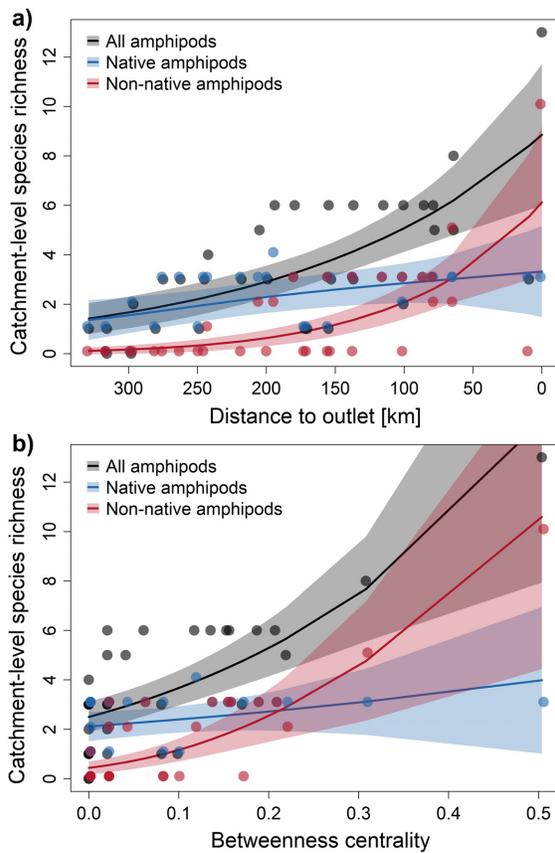


Fig. 2. (a) Catchment-level species richness ( $\alpha$ -diversity) relative to the distance to outlet along the fluvial network. (b) Catchment-level species richness ( $\alpha$ -diversity) relative to betweenness centrality of nodes within the fluvial network. In both panels, shading corresponds to the 95% confidence interval of the model predictions.

highly significant difference between native and non-native species (ANOVA, parametric term  $P = 2.40e-05$ ). The results from the restricted dataset were consistent with these results (see Appendix S5: Fig. S1).

Species turnover ( $\beta$ -diversity) of native species showed a DDR between nodes of the network (Fig. 3). The DDR was significant (Mantel tests with Kendall's rank correlation coefficient  $\tau$ ) when looking at the total amphipod community ( $\tau = -0.164, P = 0.002$ ). Also when looking at native species only, amphipod communities were less similar with increasing topological distance between nodes ( $\tau = -0.303, P = 0.001$ ). However, similarity between non-native species between

nodes in the network was not decreasing with topological distance ( $\tau = 0.048, P = 0.665$ ). The qualitative and quantitative same result was found when basing the analysis based on unweighted topological distances, so ignoring the flow direction. Overall, the quasibinomial GAM models to assess the change in community similarity as a function of the weighted topological distance did not fit well, with the model for the total community data showing an adjusted  $R^2$  of 0.07, only 6.6% deviance explained but a significant smoothing parameter ( $P = 1.6e-05$ ). The single model for native species had an adjusted  $R^2$  of 0.17% and 13.3% deviance explained and a highly significant smoothing parameter ( $P = <2.2-16$ ), whereas the model for non-native community data had an adjusted  $R^2$  of 0.13% and 14.3% deviance explained, and a just significant smoothing parameter ( $P = 0.0451$ ). Additional analyses with the subset of the data sampled in a standardized way between 2010 and 2016 gave qualitatively and quantitatively strongly consistent results (see Appendix S5: Fig. S1).

Amphipod communities in the Rhine drainage basin were organized according to the modularity of the network. There was a high consistency

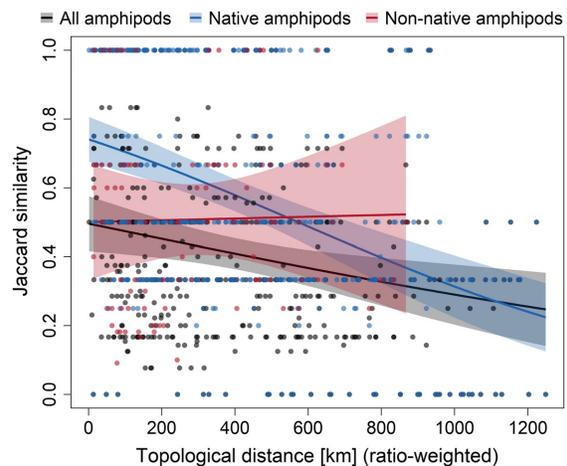


Fig. 3. Distance decay relationship of amphipod community similarity ( $\beta$ -diversity) with increasing topological distance between nodes. The decay is significant when looking at the total community (black) and pronounced in native amphipods (blue), but not in non-native amphipods (red). Lines are fits of binomial logistic GLMs, with shaded 95% confidence intervals.

between the hierarchical clustering of the nodes based on community similarity compared to the clustering based on network modularity. The observed entanglement (i.e., amount of crossing lines connecting the respective nodes of both clusterings: Fig 4a) was significantly lower compared to the entanglements resulting from 10,000 bootstrapped randomizations of amphipod communities (Appendix S6: Fig. S1;  $P = 0.0254$ ).

**DISCUSSION**

*Broad-scale pattern meets the theoretical expectations*

Connectivity of habitats and species dispersal have a major influence on community assembly

and biodiversity. In light of increased pressure on natural communities by non-native species, a detailed understanding of these processes is critical. In our study, we disentangled the imprint of fluvial network topology on various measures of community structure and diversity for native and non-native organisms within the same taxonomic group, namely freshwater amphipods, to test whether the underlying ecological mechanisms may differ.

Qualitative predictions of neutral models in dendritic networks can be used as a starting point/Null model to test our observations against (Muneepeerakul et al. 2007, Carrara et al. 2012, Fronhofer and Altermatt 2017). Those general models project a constant increase in catchment-level richness

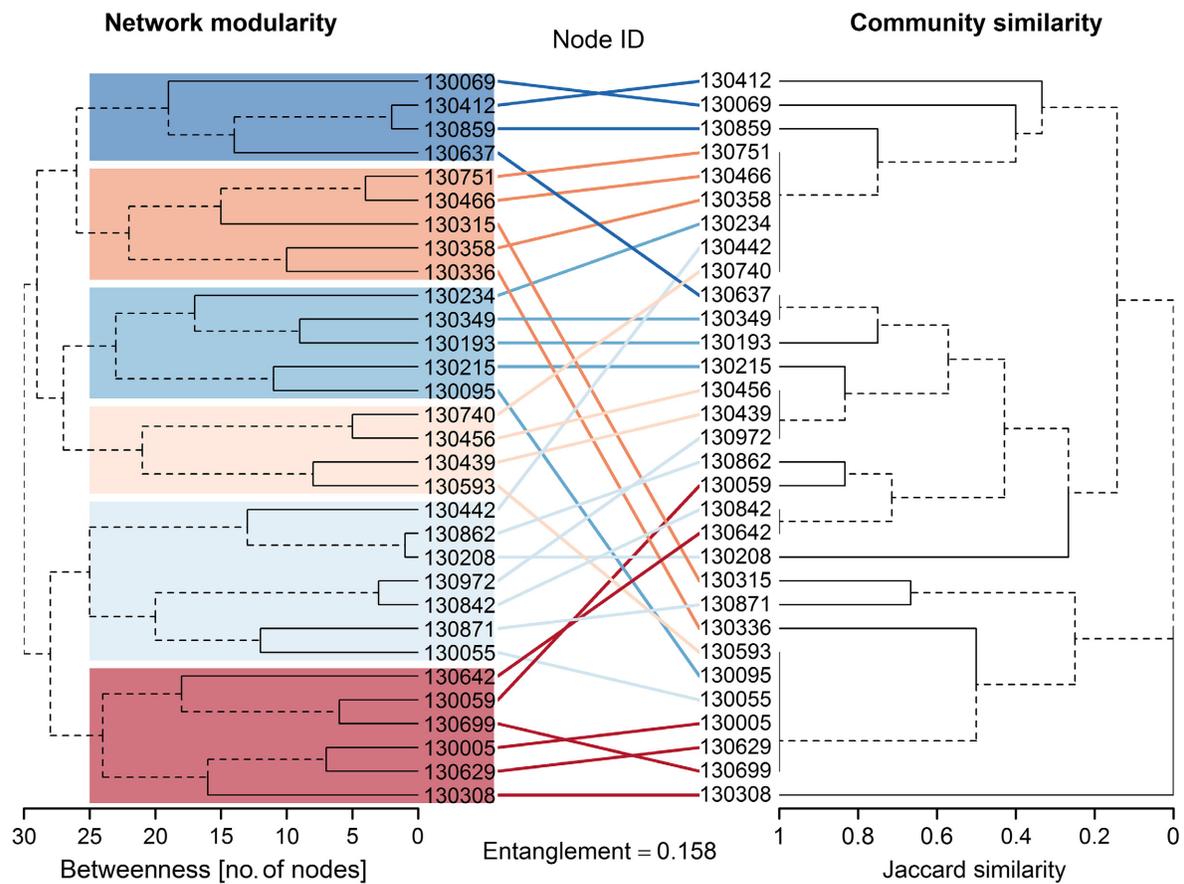


Fig. 4. Comparison of the fluvial network clustering based on modularity (left) and the amphipod community clustering based on community similarity (right). The node-based congruence (entanglement) between these two clusterings is 0.158. Color shading corresponds to larger subcatchments within the Rhine drainage area (dark blue: Drei-Seen-Land; orange: Upper Aare; blue: Lower Aare & Limmat; light orange: Reuss; light blue: Lower Rhine & Thur; red: Upper Rhine).

( $\alpha$ -diversity) along the fluvial network due to differing levels of node connectivity. In fact, we found this pattern in the Rhine drainage basin of Switzerland (Figs. 1 and 2), however, only when considering both native and non-native species combined. Thus, while non-native species are ecologically and demographically clearly different to native species (Grabowski et al. 2007), the large-scale diversity patterns can still be explained by dispersal limitation alone. This suggests that dispersal limitation as a main driver of this predicted pattern may be overwhelming ecological differences.

#### *Non-exclusive explanations for the richness pattern*

On contrary, the  $\alpha$ -diversity patterns of the native species alone did not follow the predicted pattern. However, as there were rarely more than three native species found in the same catchment (out of the five possible native species), the lack of this pattern may also be due to the small numbers only. There are several non-exclusive explanations for the observed pattern of an increasing diversity along the network:

First, strong dispersal limitation in native species restricts different species to different nodes (causing a high  $\beta$ -diversity) or parts of the network (Shurin et al. 2009) due to community structuring and species divergence over extended timescales, but simultaneously results in similar species richness ( $\alpha$ -diversity) given homogeneous speciation rates across space. Previous studies confirm low dispersal rates in native *Gammarus* species (Westram et al. 2013, Weiss et al. 2014). For non-native species, previous studies found an increased role of dispersal (Hänfling et al. 2011, Van Riel et al. 2011) combined with higher competitiveness (Grabowski et al. 2007). These findings support the first interpretation.

Second, pronounced species sorting by habitat filtering in dendritic networks due to confined dispersal leads to steady states of community composition over extended timescales (Brown and Swan 2010, Vitorino Júnior et al. 2016). In fact, there are only five native amphipod species, all being member of the genus *Gammarus* and belonging to the same ecological guild. This indicates a saturation of native amphipod communities (Loreau 2000, Pinto-Sánchez et al. 2014) that reached a steady state. Only speciation or

ecologically different immigrant species would then add diversity on top of the existing steady state. Indeed, non-native species recorded so far exceed the number of native species and are also ecologically distinct (Grabowski et al. 2007), including previously absent functional groups. Examples of this were predatory amphipods such as *Dikerogammarus haemobaphes* or *Dikerogammarus villosus*, filter-feeding species such as *Chelicorophium curvoispinum*, or groundwater-associated species such as *Synurella ambulans*. Hence, we hypothesize an intraguild saturation by habitat filtering, only allowing new guilds to establish. This is supported by the notion that newly arriving species were often partially replacing previously arrived non-native species of the same guild (as, e.g., with *D. haemobaphes* and the later arriving *D. villosus*, replacing the first; personal observation, Kley and Maier 2003). This replacement would be particularly pronounced in the lower parts of the network where most of the non-native species arrive, whereas headwaters should consistently exhibit species sorting and saturation. In this scenario, sympatric speciation would also allow for more species, but would be expected to be more pronounced in less connected nodes of the network due to increased admixture in more central nodes (Fourtune et al. 2016).

Third, temporal effects could have led to the observed realization of species richness across the fluvial network either by a replacement of native by non-native species or by the different timescales of network colonization (Mari et al. 2014, Seymour and Altermatt 2014). As outlined in the previous section, the native species probably reached a steady state and potential replacement by non-native species only took place during the past decades. The non-native species hence are still in a transient state. However, we are not aware of any native species that actually went extinct and there is no historical report mentioning amphipod species that are no longer present in the Rhine drainage basin. The latter process of different timescales for network colonization and community formation by native and non-native amphipods is somewhat a combination of various explanations mentioned above. Dispersal and colonization in the focal fluvial network happened on a fixed connectivity for all aquatic organisms, while the timescales

differed for native and non-native species. Whereas the influence of the first condition was studied (Lynch et al. 2011), the effect of different timescales remains unexplored. While the native species colonized habitats after the last glacial maximum (Hewitt 1999), the non-native species only arrived recently. Thus, we can compare the species distribution resulting from at least 15,000 yr of colonization relative to the distribution of non-native species that colonized habitats throughout the fluvial network within the last 100 yr (Bij de Vaate et al. 2002, Altermatt et al. 2014). After thousands of years, the native amphipods adapted to the different environments present throughout the network, subsequently colonized it, and reached all nodes. In contrast, the non-natives only had a few decades and did not reach all the nodes so far. The observed pattern therefore would be a mixture of adapted and well-spread native species that colonized the network after deglaciation but did not diverge so far, mixed with very recently arriving non-native species that could neither adapt nor reach all the nodes of the network so far. As non-native species still were absent in headwater nodes, they represented ecological refugia for native species, despite the ongoing invasion. Hence, they play an important role in sustaining diversity and assuring native species persistence, especially given the general downstream drift of individuals. In a conservation biology's view, headwater nodes should be seen as important refugia and source populations to sustain native species.

While we found a strong indication of network structure shaping community patterns of amphipods, and pronounced differences between native and non-native species, we acknowledge that network structure, and spatial components in general, is not the sole driver of community composition (Vellend 2010). It has been shown in various studies of aquatic invertebrates, including amphipods, that specific environmental factors are also important drivers of community structure (e.g., Eisenring et al. 2016, Kaelin and Altermatt 2016). However, the past focus on environmental factors has only led to a partially satisfying explanation of community dynamics, and the inclusion of network components has been acknowledged more recently (Tonkin et al. 2018).

### *Species turnover pattern*

When focusing on species turnover ( $\beta$ -diversity) within the fluvial network, we found the predicted DDR (Nekola and White 1999, Soininen et al. 2007) within amphipod communities of the Rhine drainage basin of Switzerland (Fig. 3). Again, we checked this relationship for native and non-native species separately. We observed a DDR in native species which suggests that native species are dispersal-limited (Brown and Swan 2010). This interpretation supports possible dispersal limitation as suggested by the richness pattern along the fluvial network (see *Non-exclusive explanations for the richness pattern* section). Distance decay relationships have been shown in other systems as well (e.g., Cañedo-Argüelles et al. 2015) and are a well-known phenomenon. On the contrary, we did not observe a DDR in non-native species. This was rather surprising given the general prevalence of DDRs (Soininen et al. 2007) and suggests either minor dispersal limitation or a potentially increased influence of species sorting on non-native amphipod diversity (Heino 2011). As the similarity between non-native communities stays intermediate independent of distance to outlet, species sorting seems to be a driving force (Brown and Swan 2010). Constant and ongoing turnover seems to be more prevalent in non-native species, whereas native species seemed to have reached some sort of steady state regarding their distribution throughout the network. This is again in concordance with the results from species richness patterns. Because the theoretical expectation of an increasing diversity along the network only holds with sufficient levels of dispersal (Economato and Keitt 2008), we conclude that non-native species show this elevated level of dispersal, whereas native species reached some sort of equilibrium and are dispersal-limited. Finding both in non-native species, a decreasing species richness along the network and no DDR suggests that these non-native communities are nested, with communities representing conglomerates of others. Partitioning the  $\beta$ -diversity into separate turnover and nestedness components (sensu Baselga 2010) shows that the observed pattern is mainly due to turnover effects (Appendix S7: Fig. S1). It seems that native communities are more nested the closer they are, whereas non-native communities are more nested the further apart they are (Appendix S7: Fig. S1).

This in turn indicates an ongoing invasion process and that once established non-native species do not disappear again.

#### *Network topology influences amphipod communities*

Fluvial network topology had a significant imprint on amphipod community assembly (Fig. 4). Our bootstrapping approach showed that community assembly is clustered within modules of the network. This mirroring is significant despite the rather unrestricted randomization of the communities. We randomized species presence of nodes but kept the total frequency of single species and species richness of nodes constant (Gotelli et al. 2015). Hence, the chosen Null model kept recently colonizing non-native species rare and preserved the pattern of increasing richness along the network as well. The communities of the upper parts of the network closely reflected the spatial network topology, whereas the downstream communities were less consistently mirroring network topology. This again highlights the disruptive effect of non-native species on native communities, but also shows the dampening effect of network length.

We showed that network topology has a significant influence on diversity and community assembly on amphipods within a large fluvial network. The effects differed between native and non-native species, indicating different significance of ecological processes, such as dispersal, selection, and drift, acting at different timescales. The influence of network topology on invasion processes of fluvial networks has to be taken into account for conservation approaches of such ecological networks (Lynch et al. 2011) and highlights the importance of habitat connectivity and dispersal for community assembly and biodiversity (Mari et al. 2014). Our study is the first comparison within a single taxonomic group but encompassing several species. We highlight the general ecological differences between native and non-native species and its consequences on spatial arrangement of species within invaded communities. General expectations from meta-community theory apply, but further studies are needed to understand the interplay of connectivity and network position with environmental drivers.

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