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Lessons from the macroinvertebrates: species-genetic diversity correlations highlight important dissimilar relationships

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SUMMARY

1. Species and genetic diversity patterns are predicted to co-vary due to similar mechanistic processes. Previous studies assessing species and genetic diversity correlations (SGDCs) have focused primarily on local diversity patterns or island-like systems and ignore the underlying dispersal network. Here we assessed local and regional SGDCs using freshwater macroinvertebrates sampled across the Rhine river network, a spatially large and highly connected system, in Switzerland.

2. We utilised a set of polymorphic microsatellite markers to assess the genetic diversity of two amphipod species of the *Gammarus fossarum* complex, which were compared to species level diversities of Amphipoda, Ephemeroptera, Plecoptera, Trichoptera and family level macroinvertebrate diversity across 217 randomly selected sites. All sites were selected based on a representative and standardised species-sampling scheme. We analysed within site (α-SGDC) and between-site SGDC (β-SGDC).

3. Against our expectation, we generally found negative or null α-SGDCs and β-SGDCs. However, we did find genetic diversity to be spatially structured, whereas species richness was related to local environmental factors.

4. These findings suggest that the genetic and species levels of diversity observed are driven by different mechanisms (e.g., environment versus demography), or operate across different temporal or spatial scales (e.g., colonisation history or dendritic river network structure), and may be attributed to differences in the species' ecology or life history. Overall, conservation measures in riverine systems aiming at only one level of diversity may not necessarily benefit other levels of diversity.

Keywords: amphipods, dendritic networks, dispersal, *Gammarus fossarum*, river Rhine

Introduction

From a theoretical understanding, a parallelism between ecological and evolutionary patterns and processes is generally recognised (e.g., Antonovics, 1976; Vellend, 2010). However, empirically they have been rarely studied simultaneously. This long-standing separation is partly due to original expectations that ecological processes occur much more rapidly compared to evolutionary processes (Thompson, 1998). However, several recent studies have shown that evolutionary processes do occur rapidly, allowing ecological and evolutionary timescales to overlap and subsequently influence each other simultaneously (e.g., Hairston *et al.*, 2005). This has resulted in recent conceptual studies (e.g., Vellend & Geber, 2005; Vellend, 2010; Laroche *et al.*, 2015) assessing whether species and genetic diversity patterns should correlate in nature, and whether these diversity

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measures can be used interchangeably as measures of biodiversity. We are currently facing major diversity losses at local, regional and global scales (e.g., Cardinale *et al.*, 2012). An understanding of the relationship between species and genetic diversity is thus greatly needed, because the resilience of biological systems is often linked to either or both of these diversity levels. Understanding the interchangeability between species and genetic diversity is also paramount with the general decline in taxonomic expertise and rise in environmental DNA (eDNA) based measures of biodiversity (Ficetola *et al.*, 2008; Mächler *et al.*, 2014; Deiner *et al.*, 2015).

Species and genetic diversity correlations (SGDCs) are expected to be positive under various scenarios (Vellend & Geber, 2005), whereby environmental factors, life history traits and spatial dynamics have all been shown to independently affect the genetic structure as well as the species composition of communities. Simultaneous or parallel influences of environmental factors on both levels of diversity may occur, suggesting similar rates of random extinction and drift (Vellend, 2010). Species diversity may also increase with increased genetic diversity since more genotypes may allow and maintain interactions with more species (Booth & Grime, 2003). A large body of literature also exists on the effect of life history on the genetic structure, for example how different life histories with respect to dispersal stage and strategy make populations more or less genetically connected, and how life history traits correlate with species richness (Lande, 1988; Hughes, Huey & Schmidt, 2013; Seymour, Deiner & Altermatt, 2016).

Empirical evidence for SGDC is mixed. On the one hand, empirical studies have repeatedly found positive SGDCs, suggesting that local environmental characteristics influence species diversity through natural selection, which subsequently alters genetic diversity (e.g., He *et al.*, 2008; Lamy *et al.*, 2013). On the other hand, there are numerous empirical studies that found negative or null SGDCs, suggesting separate evolutionary processes acting on species and genetic diversity (He & Lamont, 2010; Taberlet *et al.*, 2012). Negative or null SGDCs are especially found in spatially structured communities (e.g., metacommunities), suggesting local environmental selection and dispersal limitation may interact to influence species and genetic diversity (e.g., (Derry *et al.*, 2009). Subsequently, there is no consensus on whether the positive co-variation in species and genetic diversity is a consistent pattern across systems or different spatial and temporal scales.

Previous species-genetic correlation studies have focused primarily on the local scale or across communities without an explicit linkage through dispersal (Silvertown, Biss & Freeland, 2009; Taberlet *et al.*, 2012; Lamy *et al.*, 2013). However, this neglects the spatial effects of migration and dispersal, which are key processes involved in diversity dynamics (Vellend & Geber, 2005), especially in systems where the movement of individuals is restricted due to natural network structure, such as for example in dendritic river-like networks (Altermatt, 2013). Such complex system networks have been empirically shown to influence species (Carrara *et al.*, 2014; Seymour & Altermatt, 2014; Seymour, Fronhofer & Altermatt, 2015) and genetic diversity patterns (Finn *et al.*, 2011; Hughes *et al.*, 2013; Seymour *et al.*, 2013; Paz-Vinas *et al.* 2015). Species and genetic diversity are directly influenced by the unique hierarchical structure of river networks, whereby confluences and lower reaches of the river network often promote migration and dispersal (Altermatt, 2013), which leads to an increased local diversity. In contrast, upper reaches and headwaters are expected to harbour comparably lower diversity and rare species due to isolation (increased dispersal limitation) and the effects of drift (Finn *et al.*, 2011).

We utilised a set of polymorphic microsatellite markers to assess the genetic diversity of two amphipod species of the *Gammarus fossarum* complex (*G. fossarum* A and *G. fossarum* B; Altermatt *et al.*, 2014), which were compared to species level diversities of Amphipoda, Ephemeroptera, Plecoptera, Trichoptera and family level macroinvertebrate diversity sampled across the Rhine river network within Switzerland (Altermatt, Seymour & Martinez, 2013; Kaelin & Altermatt, 2016), which is a large and highly connected network. All of these species have similar dispersal behaviour during their aquatic stages, while EPT may disperse overland during their winged adult stages (Elliott, 2003; Alp *et al.*, 2012).

We asked three main questions regarding species-genetic diversity correlation in large continuous and complex networks (e.g., river networks). First, do we find similar species and genetic patterns (i.e. SGDCs) for our set of taxa studied across the Rhine network, which would suggest that similar diversity mechanisms are occurring across this system? Second, for these taxa, are species or genetic diversity patterns spatially or environmentally structured? Third, what are the possible mechanisms driving SGDCs within our study system based on these findings? In addition, we put our results and conclusions in context of a companion study (Fourtune *et al.*, 2016), which addresses SGDCs in fish communities across a whole river drainage basin of comparable size.

Methods

Study system/organisms

Data on the distribution and diversity of freshwater macroinvertebrates were sampled across 217 sites within the Rhine drainage (covering 28 054 km^2) in Switzerland, Central Europe. The data were systematically collected within the Swiss Biodiversity Monitoring Program, with sampling having occurred once for each site between 2009 and 2012 (BDM Coordination Office, 2009, Altermatt *et al*., 2013; Kaelin & Altermatt, 2016).

General standardised sampling methods were used to collect macroinvertebrates (for details see Altermatt *et al*., 2013). In short, sampling sites were randomly selected on a systematic grid across Switzerland, which takes into account the natural distribution of river sizes (Stucki, 2010). The sampling occurred between March and July, depending on the elevation, and local macroinvertebrate development cycles (BDM Coordination Office, 2009; Stucki, 2010). All macroinvertebrates were sampled, using a standardised kick-net method following the methods described in Altermatt *et al.* (2013). Trained field biologists collected and preserved individuals from all sites, and taxonomic specialists subsequently identified them, using established standardised methods and identification keys (BDM Coordination Office, 2009). All individuals were identified to the family level (for a list of all families, see supplement). Mayflies, stoneflies and caddisflies (Ephemeroptera, Plecoptera and Trichoptera) as well as amphipods (Amphipoda) were identified to the species level by taxonomic specialists using previously established nomenclature and identification keys and checklists from Switzerland (BDM Coordination Office, 2009, Stucki, 2010; Altermatt *et al*., 2014). Elevation and stream width were measured as environmental variables for all BDM sites at the time macroinvertebrate samples were taken (BDM Coordination Office, 2009 and Kaelin & Altermatt, 2016). We subsequently used taxa diversity at the family level diversity for all aquatic macroinvertebrates, and at the species level for highly diverse groups of Ephemeroptera, Plecoptera and Trichoptera (EPT) and the less diverse, but widely distributed, Amphipoda. Family level data are commonly used for overall assessments of water quality in river ecosystems (e.g., Tachet, Bournaud & Richoux 1991). EPT data are commonly used for assessments and conservation of aquatic biodiversity with more than 500 species occurring in Switzerland (Lenat, 1988).

In parallel, we measured within-species genetic diversity for two distinct amphipod species of the *G. fossarum* complex (*G.* A and *G. fossarum* B) (Müller, 2000), using allelic richness as a proxy of genetic richness. *Gammarus fossarum* is an ecologically important amphipod complex that has colonised the Rhine drainage since the Pleistocene (Müller, 2000). We chose to measure genetic diversity (using microsatellites) of these two species (Altermatt, Alther & Mächler, 2016; Eisenring *et al*., 2016), as they are important for ecotoxicology, biodiversity and are relatively widely distributed, which is a precondition for obtaining genetic data from many populations in a given study. In contrast, many EPT species are only found at a few sites (1 to 10 sites), which limits large-scale genetic studies across many populations and across environmentally diverse systems, including the Rhine river network, which is the focus of this study.

Microsatellites

We genotyped *G. fossarum* samples from all sites where they were present (112 of 217 sites), using 10 previously developed microsatellite markers (gf08, gf10, gf13, gf18, gf19, gf21, gf22, gf24, gf27 and gf28) (Westram, Jokela & Keller, 2010). Based on the genotype data, we identified two previously recognised cryptic species of *G. fossarum* (referred to as *G. fossarum* A and *G. fossarum* B (Müller, 2000; Altermatt *et al*., 2014). In total we found *G. fossarum* A at 96 sites and *G. fossarum* B at 38 sites, including 22 sites where *G. fossarum* A and *G. fossarum* B co-occurred (Fig. 1). DNA was extracted using the HotSHOT method, following Montero-Pau, Gomez & Munoz (2008). PCR reactions were conducted using multiplex amplifications, following Westram *et al.* (2010). PCR products were diluted 1 : 10 in Milli-Q water (Millipore, Billerica, MA) before we mixed them with GeneScan LIZ 500 (Applied Biosystems, Forster City, CA) and HiDi™ formamide (Applied Biosystems, Woolston, Warrington). These samples were subsequently run on an ABI 3730xl DNA Analyser (Applied Biosystems). We scored peaks in the program GeneMarker® Version 2.4.0 (Softgenetics, LC State Collage, PA). Genotype sample sizes depended on the local abundance, and ranged from 1 to 61 (mean 26 ± 17 SD) for *G. fossarum* A and 2 to 71 for *G. fossarum* B (mean 25 ± 18 SD). Genotypes were analysed and manually edited using GeneMarker® software (v. 2.4.0). Individuals missing three or more loci were removed from the analysis. All loci were checked for null alleles and allelic drop out using MICROCHECKER 2.2.3 (van Oosterhout *et al*., 2004). Linkage disequilibrium and deviations from

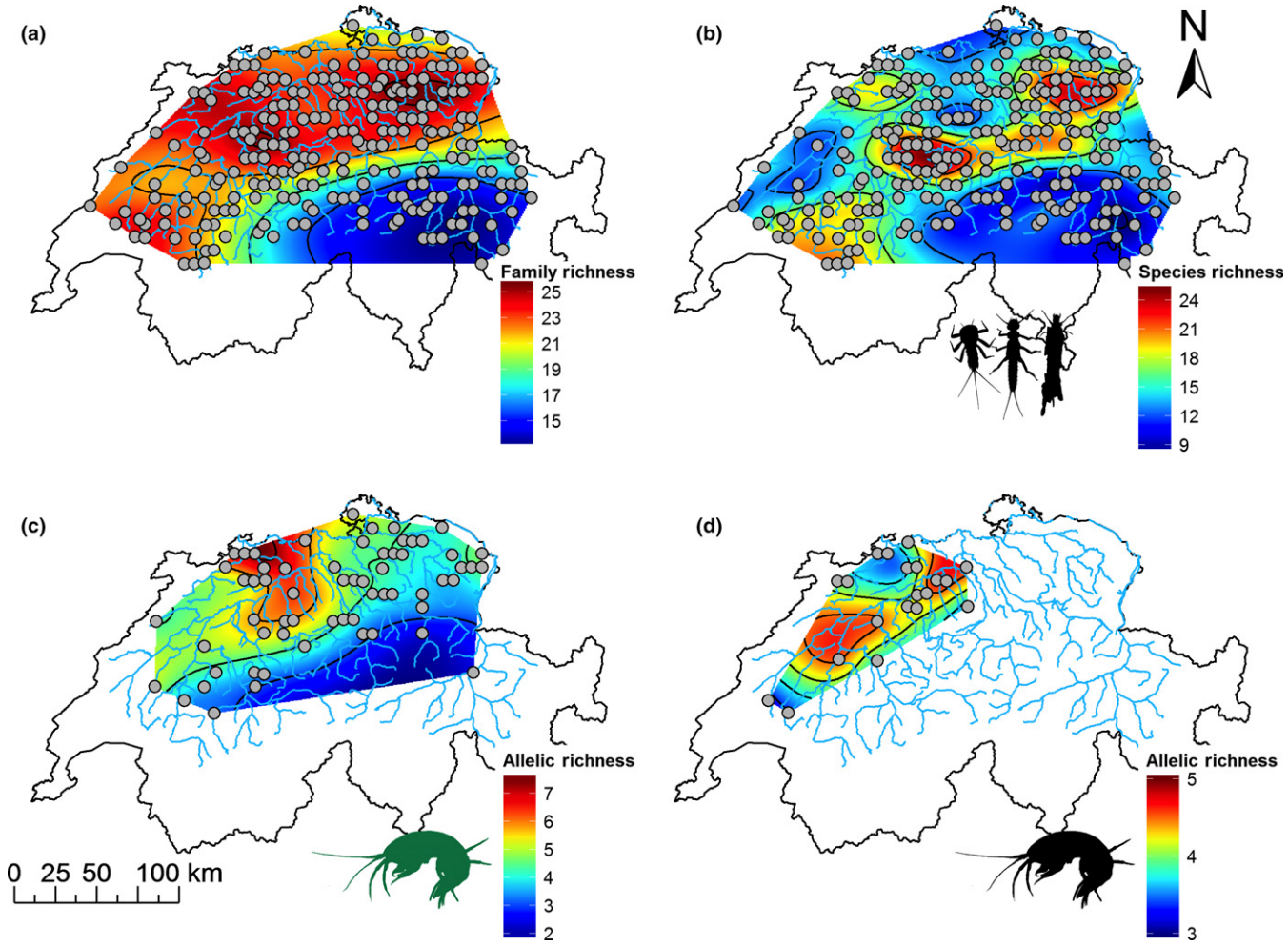

Fig. 1 Interpolated local family richness of freshwater macroinvertebrates (a). Interpolated local species richness of Ephemeroptera, Plecoptera and Trichoptera (b). Interpolated local allelic richness (i.e. genetic diversity) of *G. fossarum* A (c) and *G. fossarum* B (d). Richness values are depicted, using a colour gradient, with red colours representing high richness and blue colours representing low richness. Interpolations were made across the range of each taxon within the River Rhine catchment area in Switzerland, defined by the convex polygon including all sites in which the respective macroinvertebrates were found (grey dots). Colour figure can be viewed at wileyonlinelibrary.com.

Hardy–Weinberg equilibrium, using the exact test, were assessed using GENEPOP 4.5.1 (Rousset 2008).

Species and genetic diversity measures

We calculated the sample size needed to adequately measure the local genetic (i.e. allelic) diversity by calculating saturation curves using all sites with 50 or more individuals genotyped. Our simulation results show allelic richness saturated at 15 to 20 individuals for most populations (Fig. S1). Thus, we subsequently rarified the number of individuals to calculate allelic richness at each site to 20 individuals, to ensure only populations with adequate sampling were included and that differences in sample size would not influence the results of our analyses, following the rarefaction method of Petit, El Mousadik & Pons (1998). Sites for which we had genotyped less than 20 individuals were excluded. Our final analyses thus included 62 sites with *G. fossarum* A and 21 sites with *G. fossarum* B (including three sites where both *G. fossarum* A and *G. fossarum* B occurred). Importantly, the spatial congruence of these two species is naturally only relatively small, which limits an analysis that considers only co-occurrences or sites that overlap in range. Such an analyses would be of additional value, but is prohibited by the naturally small overlap of the species' ranges.

For all levels of diversity (genetic and species), we calculated within site (α-diversity) and among site (β-diversity) values. We spatially interpolated each measure of α-diversity, across the study sites, using the *fields*-package in R (Nychka *et al.*, 2016). We calculated α-genetic

diversity of *G. fossarum* A and *G. fossarum* B as allelic richness (Petit *et al*., 1998) and β-genetic diversity as Jost's D genetic distance (Jost, 2008). Likewise, we used local species/family richness to calculate species α-diversity and true β-diversity following the terminology of Jost (Jost, 2006) using the R package samba (Jurasinski & Retzer, 2012). Jost's D and true β-diversity are derived from the same true diversity relationship, whereby the differences among species communities or genetic groups is related to the multiplicative relationship between α-diversity and β-diversity (Jost, 2008). Thus, β-diversities at the genetic and the species level can be directly compared.

Statistics

We compared α-SGDC for each pairwise comparison of *G. fossarum* A and *G. fossarum* B allelic richness against each community diversity measure for Ephemeroptera, Plecoptera, Trichoptera, Amphipoda species richness and family level macroinvertebrate richness using generalised linear models (GLM) with a Poisson error distribution (Zuur *et al*., 2009). We assessed the relationship between local species richness (Ephemeroptera, Plecoptera, Trichoptera, and Amphipod species richness) and local site characteristics, including elevation (metres above sea-level) and stream-width (metres), using linear regression models (Zuur *et al*., 2009).

We assessed the relationship between distance among sites and genetic/species level diversity using linear regression models with the β-diversity measure (i.e. beta-diversity or Jost's D), averaged per site, against the pair-wise among-site distance (Euclidean or Topological). We used the arithmetic mean of all values per site in the analysis, instead of using all individual values and controlling for multiple comparisons with Mantel tests, as the latter has been discouraged recently (Guillot & Rousset, 2013). Topological distance was calculated using the network analyst toolkit in ArcGIS version 10 (ESRI 2011) and was found to be a better spatial distance measure for comparing differences among communities compared to Euclidean distance (Seymour *et al*., 2016). We found indications of spatial population structure in *G. fossarum* A and *G. fossarum* B, so we investigated the possibility of population structure using a discriminant analysis of principal components (DAPCs) (Jombart, Devillard & Balloux, 2010) using the R-package adegenet (Jombart, 2008). DAPC does not rely on a population genetics model and it is not constrained by Hardy–Weinberg or linkage equilibrium assumptions; making it a robust method to test for genetic differentiation. We evaluated the numbers of clusters (K) between 2 and 30 for *G. fossarum* A and between 2 and 10 for *G. fossarum* B. The Bayesian information criterion (BIC) was then used to evaluate the relevance of different K values to population structure. Assignment values for the selected number of clusters were then generated for each individual, using DAPC. All statistical analyses were performed using the program R version 3.2.1 (R Development Core Team 2015).

Results

Microsatellite analysis

There was no evidence of linkage disequilibrium among loci for *G. fossarum* A or *G. fossarum* B. Across the 62 sample localities, for *G. fossarum* A, 142 of 621 tests suggested deviations from HWE, however, there was no consistent pattern of HWE deviations across populations for individual loci. Null allele observations per loci for *G. fossarum* A were inconsistent across populations, suggesting the absence of null alleles. Across the 21 sampling localities for *G. fossarum* B, 75 of 211 tests suggested deviations from HWE, with locus gf10 deviating for 16 out of 21 sampling sites. Null alleles were present in half of the sampling sites for loci gf10 and gf21, so they were removed from subsequent analyses. This, however, did not qualitatively change the results of our analyses. Importantly, all our analyses of differentiation are based on the DAPC method, which is not constrained by Hardy–Weinberg or linkage equilibrium assumptions.

Within-site relationships

Mean local allelic richness (across all 10 loci) of *G. fossarum* A ranged from 1.90 to 8.84 (mean across sites 4.63 ± 1.33 SD). Mean local allelic richness of *G. fossarum* B ranged from 3.15 to 5.12 (mean across sites 4.03 ± 0.57 SD). Amphipoda species richness was 1 to 3 species (mean across sites 1.28 ± 0.50 SD), with *G. fossarum* A sites having 1 to 3 (1.19 ± 0.44 SD) and *G. fossarum* B sites having 1–3 (mean across sites 1.54 ± 0.59 SD) amphipod species. Ephemeroptera species richness ranged from 1 to 12 (mean across sites 6.46 ± 2.61 SD). Plecoptera species richness ranged from 0 to 16 (mean across sites 6.51 ± 2.93 SD). Trichoptera species richness ranged from 0 to 13 (mean across sites 4.41 ± 2.86 SD). Family level richness of macroinvertebrates ranged from 11 to 34 (mean across sites 24.18 ± 5.28 SD) (Fig. 1).

We found a significant positive α-SGDC between *G. fossarum* A allelic richness and Amphipoda species richness (Fig. 2, Table S1). We found significant negative α-SGDCs between *G. fossarum* A allelic richness and species richness of Ephemeroptera and Trichoptera and family level macroinvertebrate richness. We found a non-significant (null) α-SGDC between *G. fossarum* A allelic richness and Plecoptera species richness. We found non-significant α-SGDCs between *G. fossarum* B and all richness measures (Fig. 3, Table S2).

We found significant positive correlations between Plecoptera and Trichoptera species richness and elevation ($P < 0.001$, d.f. = 78 and $P = 0.008$, d.f. = 78 respectively) (Fig. S3 & Table S2). Amphipoda species richness was significantly negatively correlated with elevation ($P = 0.020$, d.f. = 78) (Fig. S3 & Table S2). Ephemeroptera species richness was significantly positively correlated with river width ($P = 0.004$, d.f. = 78) (Fig. S4 & Table S2).

Among-site relationships

Gammarus fossarum A mean β-genetic diversity (Jost's D) was 0.50–0.76 (0.60 ± 0.07 SD). *G. fossarum* B was 0.15–0.33 (0.21 ± 0.05 SD). Ephemeroptera mean β-diversity (true beta-diversity) was 1.15–1.61 (1.37 ± 0.08 SD). Plecoptera mean β-diversity was 1–1.50 (1.27 ± 0.11 SD). Trichoptera mean β-diversity was 1–1.69 (1.46 ± 0.10 SD). Macroinvertebrate family mean β-diversity was 1.25–1.52 (1.32 ± 0.05 SD) (Fig. 4). We found a significant ($P < 0.01$) linear relationship between *G. fossarum* A and *G. fossarum* B genetic β-diversity and pairwise topological distance (Fig. 4). However, we did not find a significant relationship between measures of species β-diversity and topological pairwise distance. We found a positive β-SGDC between *G. fossarum* A and Plecoptera and a negative β-SGDC between *G. fossarum* A and Trichoptera (Fig. S4). We found a negative β-SGDC between *G. fossarum* B and Plecoptera (Fig. S5). We found non-significant β-SGDCs between all other pairs of species and genetic β-diversity (supplementary material Figs S4 & S5).

For all tested K's, with 5–24 clusters suggested for *G. fossarum* A and 2–8 suggested for *G. fossarum* B, we selected $K = 5$ for *G. fossarum* A and $K = 2$ for *G. fossarum* B as the most parsimonious clustering. Results of the DAPC suggest genetic geographic differentiation for *G. fossarum* A and *G. fossarum* B (Fig. 5). Clustering occurred primarily within the distinct subdrainages of the river Rhine (Alpine Rhine, Aare, Reuss, Limmat).

Discussion

While Amphipoda species diversity positively correlated with *G. fossarum* A genetic diversity, all other α-SGDCs were negatively correlated or uncorrelated (null-relationship), suggesting that local factors influencing macroinvertebrate diversity differed. Genetic β-diversities were spatially correlated, while species β-diversities were not spatially correlated, suggesting differing influences of migration/dispersal on riverine macroinvertebrates at the species versus the genetic level (e.g., Sei, Lang & Berg, 2009), prohibiting positive β-SGDC. The relationship and significance between local environmental factors and species α-diversity varied among orders, suggesting ecological dissimilarity (reflected in life history or functional traits) among macroinvertebrate groups, which supports previous findings of mechanisms for null or negative α-SGDCs (He & Lamont, 2010).

Previous studies that found positive SGDC between local species and genetic diversity showed that local

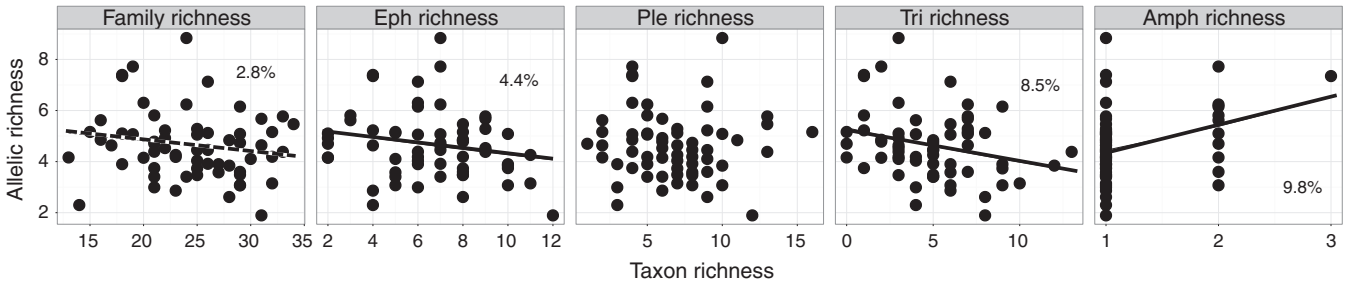

Fig. 2 Correlation between allelic richness of *G. fossarum* A (*y*-axis) and family richness of Amphipoda, and species richness of Ephemeroptera (Eph), Plecoptera (Ple), Trichoptera (Tri), and Amphipoda (Amph; all *x*-axis), respectively. Dotted lines are given when a correlation was significant ($P < 0.05$) and solid lines are given when a correlation was highly significant ($P < 0.01$). Explained deviance for the corresponding significant correlations is provided in each panel. Response variables (allelic richness, our proxy for genetic richness) used in all individual GLM analyses are given on the *y*-axis and explanatory variables (taxa richness) are labelled on the *x*-axis.

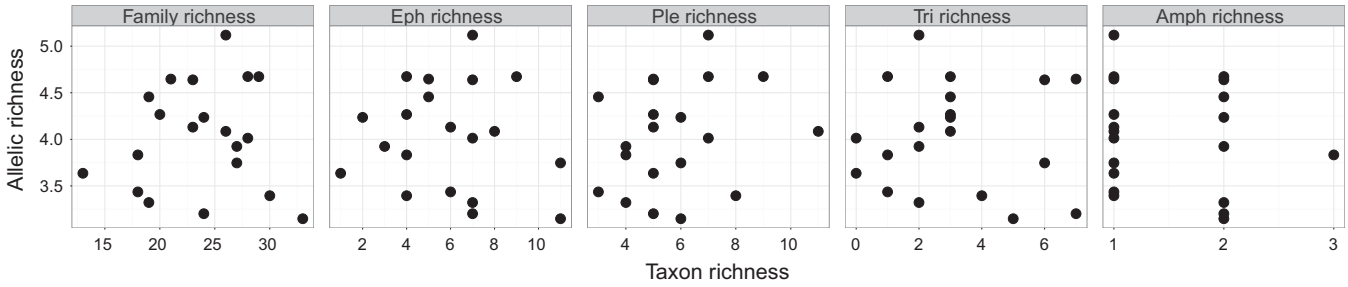

Fig. 3 Correlation between allelic richness of *G. fossarum* B (*y*-axis) and family richness of Amphipoda, and species richness of Ephemeroptera (Eph), Plecoptera (Ple), Trichoptera (Tri), and Amphipoda (Amph, all *x*-axis) respectively. Response variables (allelic richness, our proxy for genetic richness) used in all individual GLM analyses are given on the *y*-axis and explanatory variables (taxa richness) are labelled on the *x*-axis.

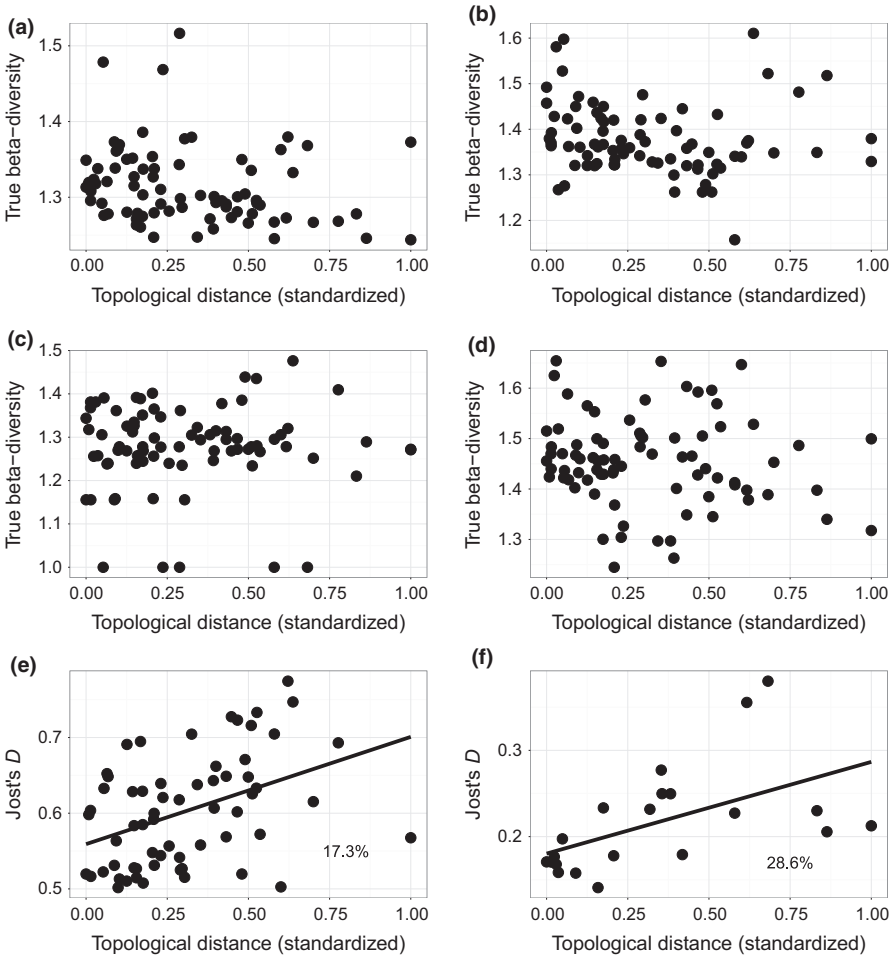

Fig. 4 True beta-diversity (among-community diversity) relative to standardised pairwise topological distance for macroinvertebrate family level diversity (a), Ephemeroptera species diversity (b), Plecoptera species diversity (c) and Trichoptera species diversity (d) respectively. Jost's D genetic among-community diversity relative to standardised pairwise topological distance for *G. fossarum* A (e) and *G. fossarum* B (f). Each point is the mean of all pairwise comparisons for a unique sampling site. Solid lines are shown where there are significant ($P < 0.01$) linear relationships. Explained deviance for the corresponding significant correlations is provided in each panel.

environmental and physical variation significantly correlates with species richness (He *et al.*, 2008; Lamy *et al.*, 2013), suggesting that species richness may be locally selected, which then influences genetic diversity. While we also found local environmental factors to positively correlate with species richness across the river network, the factors varied by species group, suggesting different local selective pressures for different species groups. Plecoptera and Trichoptera species richness were highly related to elevation (Fig. S2), while Ephemeroptera were associated with stream width (Fig. S3). This is consistent to previous findings which demonstrated that local environmental factors, such as agricultural land use, coarse woody debris, oxygen concentration and temperature,

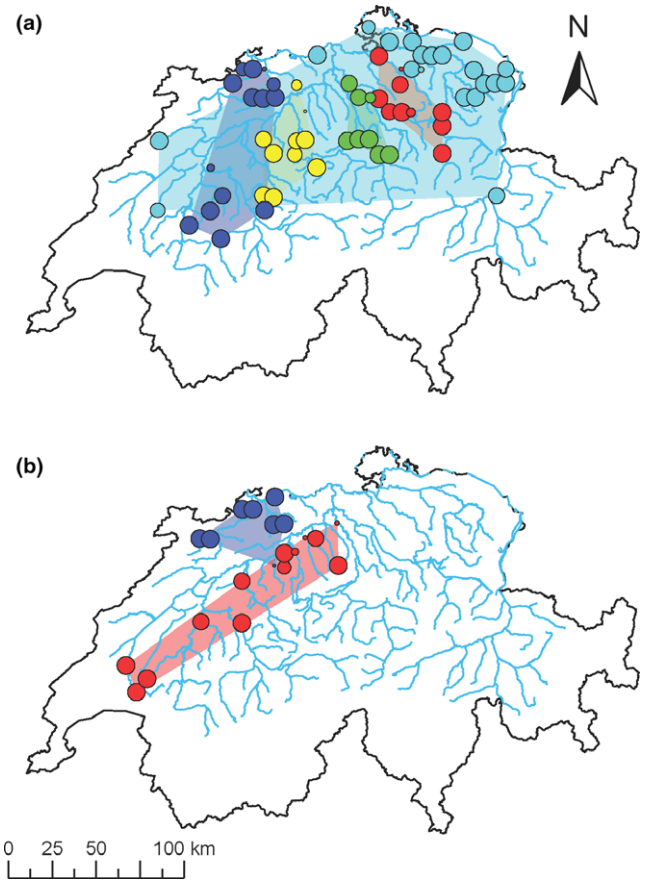

Fig. 5 Discriminant analysis of principal components (DAPC) results for *G. fossarum* A (a) and *G. fossarum* B (b). Each colour represents a unique cluster with the corresponding coloured convex hull showing the spatial extent of each cluster. Points show unique sampling locations. The size of the point corresponds to the assignment score of the corresponding site to the displayed cluster. Colour figure can be viewed at wileyonlinelibrary.com.

which are known to co-vary with elevation in Switzerland, influence Plecoptera and Trichoptera species diversity patterns through local selection (Harding *et al.*, 1998; Clapcott *et al.*, 2012). Amphipoda species richness negatively correlated with elevation (Fig. S2), which likely reflects colonisation history (dispersal), or natural selection due to limiting environmental factors upstream. These findings suggest that *G. fossarum* and other Amphipoda species may be affected by different local selective pressures compared to EPT species, either through differences in niche occupancy (e.g., Eisenring *et al.*, 2016) or strong competitive exclusion. This may account for our positive α-SGDC between Amphipoda species and *G. fossarum* A and null or negative α-SGDCs for all other comparisons.

The observed spatial structure based on the pairwise distance and DAPC analyses, of *G. fossarum* A and B genetic diversity is likely due to dispersal limitation acting on both diversity patterns, as Amphipoda (including *Gammarus* spp.) are generally highly restricted to the river network for their movement and dispersal (Elliott, 2003). Conversely, the EPT community similarities show no spatial structure, which may be due to a greater influence of local selection compared to dispersal limitation. The null spatial relationship may also imply that EPT species are not as restricted to the river network for dispersal as previously suggested (Clarke *et al.*, 2008) and at least some species may disperse frequently between catchments (Miller, Blinn & Keim, 2002), potentially aided by the effects of passive wind dispersal. Such differences in demographic dispersal ability between Amphipoda and EPT species might also suggest different colonisation histories, which have been proposed as an explanation for a lack of covariance in species-genetic diversity patterns (e.g., Taberlet *et al.*, 2012). Many species in this study either expanded their range from refugium populations following the glacial maximum or newly colonised the Rhine network at about the same time (last glacial maximum ~20 000 years ago). Possibly, the winged adult stages of EPT species could colonise sites that were blocked to Amphipoda for example by natural large waterfalls. Likewise any successful colonisation of Amphipoda above such dispersal barriers may have resulted in founder effects due to small initial population sizes compared to EPT founding populations. This, for example, may be reflected in the lower genetic diversity of *G. fossarum* A in the eastern part of Switzerland, which is upstream of the Rhine Falls.

The combined effects of differing local limitation factors on species diversity and differing species and genetic spatial signals suggest that functional and life history traits (He & Lamont, 2010) or demographic differences (Taberlet *et al.*, 2012) between riverine macroinvertebrate groups, likely account for the non-positive SGDCs in this and other studies. This is, for example, in contrast with a recent study of SGDCs in freshwater systems by Múrria *et al.* (2015), which found a positive SGDC between species and haplotype diversity across 8 sites in Central America. A positive SGDC is thought to be due to close ecological similarity (e.g., species with similar life histories), and thereby parallel eco-evolutionary dynamics occurring at both levels of diversity. Subsequently our null and negative SGDC findings may indicate differences in ecological similarity and functionality, and subsequently different selective processes, between the species-genetic groups being compared. Specifically, the consistent negative α- and β-SGDC between *G. fossarum* and Trichoptera suggest these two diversity levels are not only under different local

pressure but also driven by different spatial network structures. This suggests that SGDC between these two levels cannot be used interchangeably, and, perhaps more importantly, suggests a strong dissimilarity in ecology between these two levels of diversity. Consequently, different areas/strategies may be needed for conservation focus and biodiversity preservation across these levels of diversity and taxa (Eldon *et al*., 2013).

Our findings, and those of Fourtune *et al.* (2016), highlight the importance of local and spatial processes influencing SGDCs, especially in complex systems such as river networks. While we found mostly non-positive SGDCs, Fourtune *et al.* (2016) identified positive SGDC relationships, utilising a similar methodology approach and geographic area as this study, but focusing on different organisms, namely fish species, inhabiting the Garonne-Dordogne river network in France. Fourtune *et al.* (2016) found positive α-SGDCs for all fish species, which were in turn related to two local environmental factors, but also different dispersal dynamics of fish versus invertebrates. In the analogy to our study, Fourtune *et al.* (2016) did not find consistent or strong positive β-SGDCs. Together, we conclude that the processes underlying SGDCs are greatly dependent on specific influences of local and spatial factors, especially in structured landscapes including dendritic networks and the respective dispersal properties of the species of interest. As such, SGDC may not be common or a general finding when comparing groups of species that lack ecological similarity, thereby limiting the usage of SGDCs in conservation.

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Supporting Information

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

Figure S1. Results of the saturation simulation curves for the *G. fossarum* A and *G. fossarum* B allelic richness.

Figure S2. Elevation (m) versus species richness (Eph = Ephemeroptera, Ple = Plecoptera, Tri = Trichoptera, Amph = Amphipoda).

Figure S3. Stream width (m) versus species richness (Eph = Ephemeroptera, Ple = Plecoptera, Tri = Trichoptera, Amph = Amphipoda).

Figure S4. Beta-diversity correlations between FosA genetic diversity (Jost's D) and Eph (A) Ple (B) Tri (C) and Family (D) level True beta-diversity.

Figure S5. Beta-diversity correlations between FosB genetic diversity (Jost's D) and Eph (A) Ple (B) Tri (C) and Family (D) level True beta-diversity. Each point shows a unique sampling site mean.

Table S1. Statistical summary of the species-genetic comparisons.

Table S2. Summary statistics of the species richness versus local elevation and width.

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