



ARTICLE

Freshwater Ecology

Spatiotemporal dynamics in freshwater amphipod assemblages are associated with surrounding terrestrial land use type

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Bundesamt für Umwelt; Schweizerischer Nationalfonds zur Förderung der Wissenschaftlichen Forschung, Grant/Award Numbers: 310030_197410, PP00P3_179089; University of Zurich Research Priority Programme Global Change and Biodiversity

Handling Editor: Bryan Brown**Abstract**

Biological assemblages are the result of dynamic processes that have explicit temporal and spatial dimensions. Although biodiversity patterns can be directly inferred from the structure of these assemblages, an assessment of changes through time and space is needed to understand how organisms initially assembled and how they are responding to local environmental and biotic factors. Small freshwater streams are particularly affected by contemporary anthropogenic activities and biological invasions, yet they are commonly less studied, as studies often focus on lakes and large streams. Here, we conducted a spatially explicit analysis of keystone shredder assemblages across eight years in 12 replicated small tributary streams. In each stream, we monitored multiple sites per kilometer of stream length. By assessing temporal beta diversity dynamics, defined by the gain or loss of species or abundance per species at individual sites, we show that changes in amphipod assemblages occur within the context of the surrounding terrestrial matrix and reflect recent amphipod colonization history. While amphipod composition was mostly constant in streams located in forested catchments, streams embedded in catchments with more extensive agricultural land use displayed more pronounced temporal changes, either driven by colonization of unoccupied upstream locations or by more pronounced but undirected fluctuations in gains and losses of species or abundance per species. Our study thus suggests that agricultural landscapes might destabilize aquatic amphipod assemblages, causing higher temporal changes in community structures and highlighting the vulnerability of aquatic ecosystems to terrestrial land use drivers.

KEYWORDSagriculture, Amphipoda, community, *Dikerogammarus*, *Gammarus*, land use, macroinvertebrates, temporal beta-diversity, tipping point

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INTRODUCTION

Understanding the patterns of species communities and assemblages and the processes that create them has been for many decades at the core of ecological research. The observation that taxa occur (and co-occur) at some locations but not at others is not only fascinating for scientists but also has far-reaching implications for biodiversity conservation and the maintenance of ecosystem services and functions (Cardinale et al., 2006; Clare et al., 2022). Although snapshot studies can relay critical information about the current structure of species assemblages (“assemblage” sensu Fauth et al., 1996) and their relative characteristics, they do not cover the often highly dynamic assembly processes, which possess explicit spatial and temporal dimensions.

Riverine systems offer a unique setting for investigating species assemblages through space and time and are especially relevant because of the strong anthropogenic changes to rivers and their surrounding terrestrial catchments. Composed of linear habitat elements embedded in a terrestrial matrix with a directional flow, the distinctive riverine networks provide well-delimited and hierarchical spatial extents within which species can disperse and interact (Altermatt, 2013; Tonkin et al., 2018). Due to these spatial constraints, temporally resolved data facilitate interpretation of observed changes in assemblage composition. For example, movement of individuals or populations can be temporally tracked along linear river reaches, allowing us to infer colonization and extinction patterns (Giometto et al., 2014; Leuven et al., 2009). Additionally, freshwater taxa are subjected to multiple threats, including anthropogenic activities, biological invasions, and climate change (Reid et al., 2019). Assessing temporal changes of species assemblages in freshwater could thus inform us on how assemblages are responding to such stressors and current environmental conditions and provide more insight than if assemblages were considered static units only (Cook et al., 2018; Hillebrand et al., 2018).

Hitherto, spatiotemporal resolved data on species assemblages have been widely available for larger waterbodies, such as lakes or rivers (e.g., Leuven et al., 2009; Nalepa et al., 2009). On the contrary, small streams have generally received much less attention (but see, e.g., Bêche et al., 2006; Durance & Ormerod, 2007), yet their underrepresentation in long-term research is unwarranted given their essential characteristics. First, they are an integral part of the freshwater network, both with respect to contributing more than 50% of the total global stream length (Downing et al., 2012) and exerting significant influence on downstream reaches (Mooney et al., 2020). Second, they are a critical interface between terrestrial and aquatic systems, where fundamental

cross-ecosystem processes such as the decomposition of terrestrial detritus or insect emergence take place (Biggs et al., 2017; Fisher & Likens, 1973; Gounand et al., 2018). Finally, small streams harbor enigmatic organismal biodiversity and can act as refugia for sensitive species (Biggs et al., 2017; Finn et al., 2011).

A fitting example of such species are amphipods (Crustacea: Amphipoda), which are predominant freshwater macroinvertebrates distributed across temperate Palaearctic aquatic systems (Väinölä et al., 2008) and iconic inhabitants of small streams. These small crustaceans often numerically dominate macroinvertebrate communities, occupy a central position in both freshwater and marine aquatic food webs as both predator and prey, and are particularly recognized for their key role as shredders of organic detritus (Best & Stachowicz, 2014; Macneil et al., 1997; Woodward et al., 2008). Despite their relative abundance, amphipods are sensitive to the negative effects of environmental changes, such as the anthropogenic land uses, drying of streams or increased water temperatures (Eisenring et al., 2016; Elbrecht et al., 2016; Vadher et al., 2018), contamination by pollutants (Burdon et al., 2019; Zubrod et al., 2014), invasions by competitor taxa (Macneil et al., 2013), or cascading effects by changes in the riparian vegetation (Little & Altermatt, 2018b). Given the widespread presence of these threats, understanding changes in amphipod assemblages in small streams is needed, as these could have strong and possibly cascading effects on the nutrient cycling process and aquatic food webs (Cardinale et al., 2006; Creed et al., 2009; Huston, 1997).

We investigated the structure of amphipod assemblages through time and space in replicated small tributary streams, covering catchments of different land use types and intensities. We used amphipod abundance data collected across eight years at 12 small tributaries of Lake Constance, in northeastern Switzerland. We predicted temporal beta diversity to display spatial patterns at both (1) the stream level and (2) the landscape level. At the stream level, we expected sites closer to stream outlets to display higher turnover rates and changes in abundances per species. Priority effects occurring at the interface between lake and stream are thought to determine colonization patterns in upstream reaches (Little & Altermatt, 2018a); consequently, we believed competition to be strongest at this interface, from where competitors from the regional species pool (i.e., the lake) colonize towards upstream sites. At the landscape level, we predicted land use in the stream catchments would affect frequency of observed changes. Specifically, we expected amphipod assemblages in streams predominantly embedded in forested areas to display only minor temporal beta diversity fluctuations. In contrast, in less forested streams,

disturbances caused by agricultural or urban land use could result in either the loss of species or individuals or in the recolonization of unoccupied sites, depending on the intensity and persistence of the disturbances and on the amphipods' occurrence in time in relation to our observations. Thanks to our knowledge of amphipod distribution within and between replicated tributaries over time, our study allowed us to resolve the spatial structure of temporal beta-diversity dynamics of key invertebrates in stream ecosystems.

METHODS

Study area and sampling design

We investigated up to eight years of temporal changes in amphipod communities at 12 naturally replicated headwater streams, in which assemblage structure was sampled in longitudinal transects. The streams, located in the north-eastern part of Switzerland, are up to 2.5–6.7 km long

tributaries of Lake Constance, a large freshwater lake of 536-km² surface area (Figure 1; Appendix S1: Figure S1). Five of the studied streams drain in the Untersee, the smaller basin of the lake that lays at the forested western region of the lake. The seven other streams drain in the Obersee, the larger basin to the east that is mostly surrounded by agricultural fields and urban areas. Streams were sampled up to five times between 2012 and 2020, with sampling in 2012 and 2013 (data from Altermatt et al., 2016), 2015 (data from Little & Altermatt, 2018a), and 2019 and 2020. Streams were sampled during the vegetative season, with some streams/years being sampled at a higher spatial or temporal resolution (here down-sampled to allow comparison across years). In general, sampling was longitudinally stratified along the streams, with spatially denser sampling at stream outlets, and less dense coverage at upstream localities. The sampling in 2019 and 2020 was conducted such that the highest spatial and temporal overlap of sampling sites (see previous studies by Altermatt et al., 2016 and Little & Altermatt, 2018a) across the 12 streams gave up to 8-year long time series.

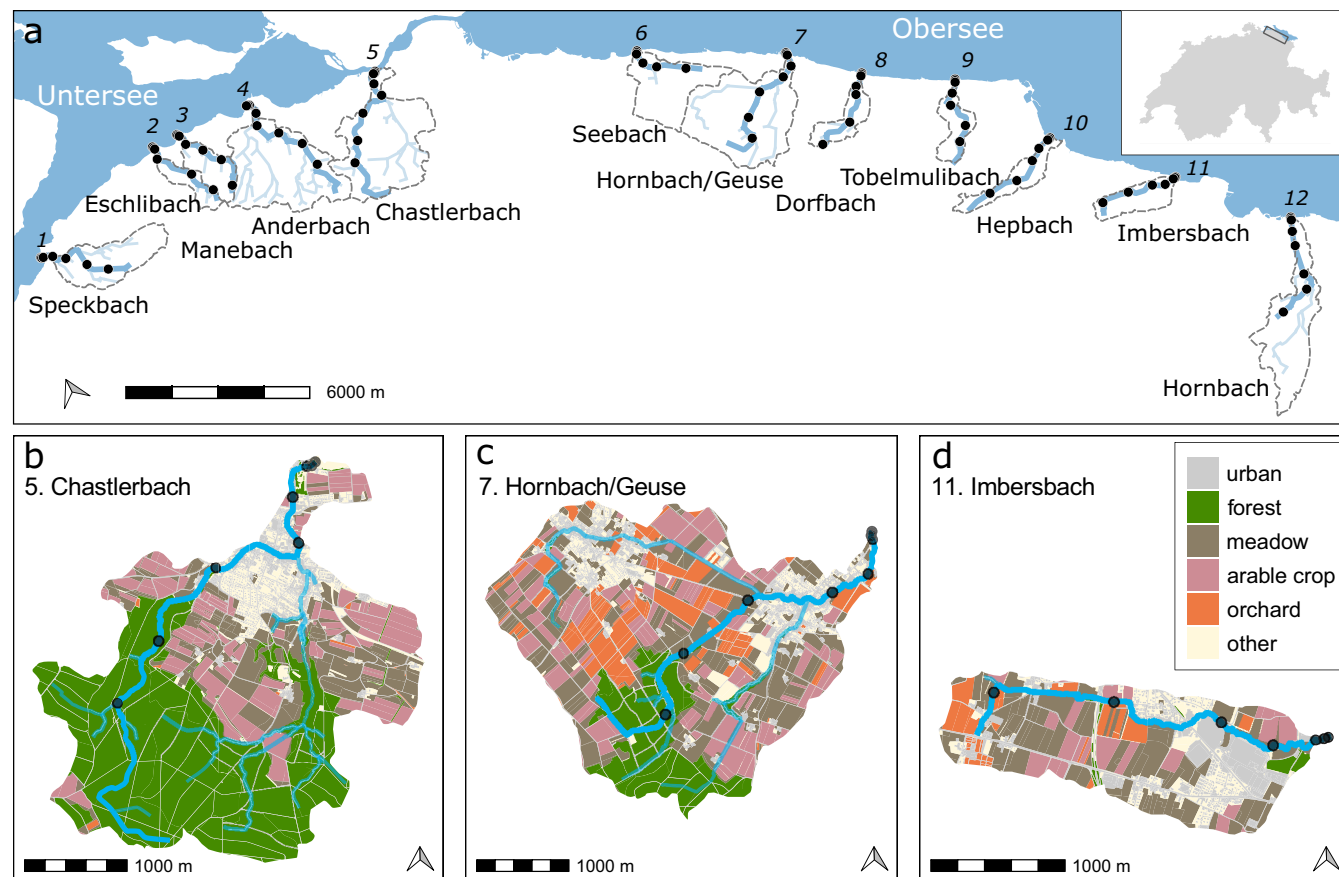


FIGURE 1 Overview of the study area and stream topology. (a) Distribution of the 12 tributaries along Lake Constance (northeast Switzerland), with streams 1–5 draining in the Untersee and streams 6–12 draining in the Obersee. Points represent the individual sampling sites. (b–d) Land use cover within three selected catchments. The whole stream is shown in light blue, with the sampled stem indicated by a thicker line. Points along the latter indicate sampling sites. Panels showing all 12 streams individually are given in Appendix S1: Figure S1.

We investigated a total of 86 sites across 12 streams, each surveyed 2–5 times between 2012 and 2020 (Appendix S1: Table S1), for a total of 295 independent replicates (over time and space). Two sites were not sampled in autumn 2015 but were sampled in both April 2015 and January 2016, respectively. Given the general low inter-seasonal changes in amphipod assemblages within a year (Little & Altermatt, 2018a), mean values across these two samples were used to infer the missing data for these two sites/time points. All sampling sites were located at fixed distances from the outlet along the main stem, starting at the stream outlet (0 m) and moving upstream to 50, 100, 500, 1000, 2000, 3000, and 4000 m, with the two furthest sites only sampled if the total stream length allowed for it. We used the kick-net method (Barbour et al., 1999) to take several quantitative subsamples at each site, adequately covering the local microhabitats. Samples were sieved (500- μ m mesh size) to exclude the smallest juveniles. Subsamples were pooled, and a semi-quantitative portion of amphipods was stored in ethanol for later identification (pooled sample per site, such that the number of amphipods per area could be calculated). For all analyses, we standardized abundances as the mean number of amphipods sampled per kick-net at a site (i.e., the sampled area reflected 0.25×0.25 m of the streambed). Overall, methods used for sampling and identifying amphipods were in concordance across the whole study period.

All individuals collected were identified to species level using a stereomicroscope and cataloging specific traits according to an identification key covering all Swiss amphipods (Altermatt et al., 2019). Previous genetic analyses showed that only one type (type A) of the *Gammarus fossarum* complex is found in the larger study area, and thus subsequently all members of that complex can be treated as one species of *G. fossarum* (Altermatt et al., 2016; Alther et al., 2021). The two species, *G. fossarum* and *G. pulex*, are morphologically highly similar, and small individuals or females with uropods broken off—for example, following sampling and handling—can sometimes not be reliably told apart. If a clear morphological assignment was not possible, these individuals were assigned to one of the two species, maintaining the identified ratio of *G. fossarum* to *G. pulex* present at the site. We also repeated the analyses in which those unidentified individuals were removed (overall, these were less than 14% of all amphipod individuals sampled).

Landscape variables

We extracted information about stream and catchment topologies from the Swiss national 1:25,000 scale digital

map. We located sampling sites at the desired distance from stream outlets and calculated stream length and draining areas of major stream stems. We then obtained land use data from a 25-m buffer corridor along the sampled stem draining areas from the Swiss agricultural land use map and the official cadastral survey. We then calculated the relative (%) cover area for the predominant land use types within this buffer, separating urban, forest, meadow, arable crop, and orchard land use types. Spatial analyses were performed with the software QGIS ver. 3.16 and R ver. 4.0.5 (QGIS Development Team, 2022; R Core Team, 2021).

Data analysis

Species richness

All statistical analyses were performed with the software R ver. 4.0.5 (R Core Team, 2021). We analyzed amphipod species richness at individual sites using generalized mixed-effect models (GLMMs) with the R package “lme4” (Bates et al., 2015). To test for species richness gradients within streams, we included distance from the outlet as a fixed effect, while stream identity was included as a random effect to account for the variance in species richness across streams. To control for repeated samplings, we included year as a fixed effect. *p* values were obtained by performing likelihood ratio tests.

Temporal beta-diversity index

Temporal changes in amphipod assemblages at individual sites were assessed using temporal beta-diversity indices (TBIs), which measure how the community composition at one site changes between two time points (Legendre, 2019). These indices can be further decomposed into gains or losses of species or abundances per species (Legendre, 2019). For each site, we computed TBI between sampled sequential surveys. Sequential survey pairs were as follows: 2012 and 2013, 2013 and 2015, 2013 and 2019 (if 2015 was missing), 2015 and 2019, and 2019 and 2020. This method measures dissimilarities and thus cannot be calculated between survey pairs where no amphipods were found at either time points. We calculated the indices with the TBI function in the R package “adespatial” (Dray et al., 2021), using the percentage difference method ($D_{\%diff}$) to account for changes in both richness and abundances per species. The function further allows to decompose $D_{\%diff}$ into gains or losses of species or abundances per species, respectively, so that $D_{\%diff} = D_{gain} + D_{loss}$. Abundance data were log-transformed ($\log_e(10y + 1)$) to

account for overdispersion and precision of abundance estimates. Differences in amphipod assemblages between sequential surveys were tested with paired t tests, and p values were obtained based on 9999 random permutations. Though we acknowledge sequential survey pairs present different temporal gaps, we are interested in the overall magnitude and directions of assemblage changes only, and consequently, we do not adjust TBI by the time interval between their two surveys.

Temporal beta-diversity along stream length and across land use types

To investigate the effect of distance from the outlet on the rates of change in amphipod assemblage composition ($D_{\%diff}$), we needed to account for the replicated nature in time of our response variable, that is, for having a nested structure of multiple temporal comparisons for individual sites. Since we have no a priori knowledge of the error distribution of our data, we opted for a conservative approach. We collapsed temporal replication by extracting one $D_{\%diff}$ index per site from the mean of all temporal comparisons available at that site. We then applied an arcsine transformation to the site-specific $D_{\%diff}$ and used this parameter as our response variable in a linear mixed-effect model (R package “lme4”; Bates et al., 2015), with distance from the outlet as explanatory variable and stream identity as random effect. To test for the effects of land use types on assemblage changes, we first ran a principal components analysis (PCA) at the stream level that included catchment drainage area (in square kilometers), lake system (binary value), and relative cover of the predominant land use types (urban, forest, meadow, arable crop, and orchard) within a 25-m buffer of the sampled stem. We then used the first principal component (PC1) as explanatory variable in our model. Second, since our predictors worked at the stream level, we not only accounted for temporal, but also for spatial replication. Again, we opted for a conservative approach and collapsed spatial replication by averaging the previously obtained site-specific $D_{\%diff}$ within each stream. We applied an arcsine transformation to the stream-specific $D_{\%diff}$ and used this parameter as our response variable in a linear regression. We excluded outlet sites from these two analyses because they are predominantly influenced by the assemblage of lake-inhabiting amphipods and vary strongly due to inherent fluctuations in the water level of the lake and thus are not indicative of assemblage turnover. In the last step, we compared the stream-level regression model with a site-level analog to verify whether comparable results would be obtained with an analysis that investigates the same dynamics at a smaller scale. We used the same PCA

procedure and variables as above to extract landscape descriptors at the site level within a 25-m circular buffer of the sampling points. We again used PC1 as explanatory variable and arcsine-transformed site-specific $D_{\%diff}$ in our model. To account for within-stream similarities, we used a mixed-effect model and included stream identity as a random effect.

In all of our results, we use the “evidence-based” language suggested by Muff et al. (2022), which highlights effect sizes and directions instead of p values only.

RESULTS

Species richness

Across all 12 streams and eight years, in total five amphipod species were found, namely, *Dikerogammarus villosus*, *G. fossarum* (type A), *G. lacustris*, *G. pulex*, and *G. roeselii*. Overall, species displayed consistent occupation patterns; the native *G. fossarum* was often the dominant species at upstream (>50 m) sites, especially in the streams at the Untersee. Individuals of *G. pulex* were only recurrently found at three streams draining at Obersee. *Gammarus lacustris* was only found at two outlet sites in 2012. The highly invasive *D. villosus* was mostly found in low densities at outlet sites, whereas *G. roeselii* was similarly frequently present at outlet sites but also colonized upstream sites in two streams. Species richness declined with upstream distance from the outlet ($\chi^2 = 9.40$, $p = 0.002$; Figure 2; Appendix S1: Figure S2). Barring one exception at a 1000-m site, the highest number of co-existing species ($n = 3$) was found only at 0- and 50-m sites, and co-occurrence of amphipod species at more than 50 m from the outlet was uncommon (>1 species was found in only 13% of samples at 100–4000 m sites). Average richness across all sites and years was 1 ± 0.72 (\pm SD). Species richness patterns across whole streams, that is, γ -diversity, did not change over time (i.e., no significant year-effect; $\chi^2 = 0.01$, $p = 0.907$).

Temporal beta-diversity index

TBI analyses showed that overall, across the 12 streams, sites were on average subject to only minor assemblage changes, and none of the sites presented evidence of different assemblages between survey pairs (all paired t tests had $p > 0.1$). However, we observed three pronounced qualitatively and quantitatively different patterns of spatiotemporal changes within individual streams, which we could further distinguish by looking at the decomposed gains (D_{gain}) and losses (D_{loss}). The first was

for streams draining into the Untersee (stream IDs 1–5), where assemblage change was generally low (mean $D_{\%diff}$ [SD] = 0.28 [0.29]). There we observed both D_{gain} and D_{loss} of low magnitude along the whole stream length, so that net directional change ($D_{gain} - D_{loss}$) across all years remained close to zero (Figures 3a and 4; Appendix S1: Figure S3). Secondly, we saw two streams (stream IDs 6 and 7) displaying higher temporal assemblage heterogeneity (mean $D_{\%diff}$ [SD] = 0.51 [0.34]). Net directional change was once again close to zero, but the amplitude in the fluctuation of D_{gain} and D_{loss} was higher (Figures 3b and 4; Appendix S1: Figure S3). Gains or

losses in these streams were not associated with specific survey pairs or sites along the stream length, and they were caused not only by abundance changes but also by changes in species richness (i.e., local species extinctions and recolonizations; Appendix S1: Figure S4). The third pattern was observed in three streams (stream IDs 9, 11, and 12). There, overall assemblage change was intermediate (mean $D_{\%diff}$ [SD] = 0.39 [0.37]), but decomposed TBI revealed a positive directional change not present in other streams (Figures 3c and 4; Appendix S1: Figure S3). Colonization of unoccupied sites—and in part, gains in amphipod abundance—drove the positive pattern, resulting in the

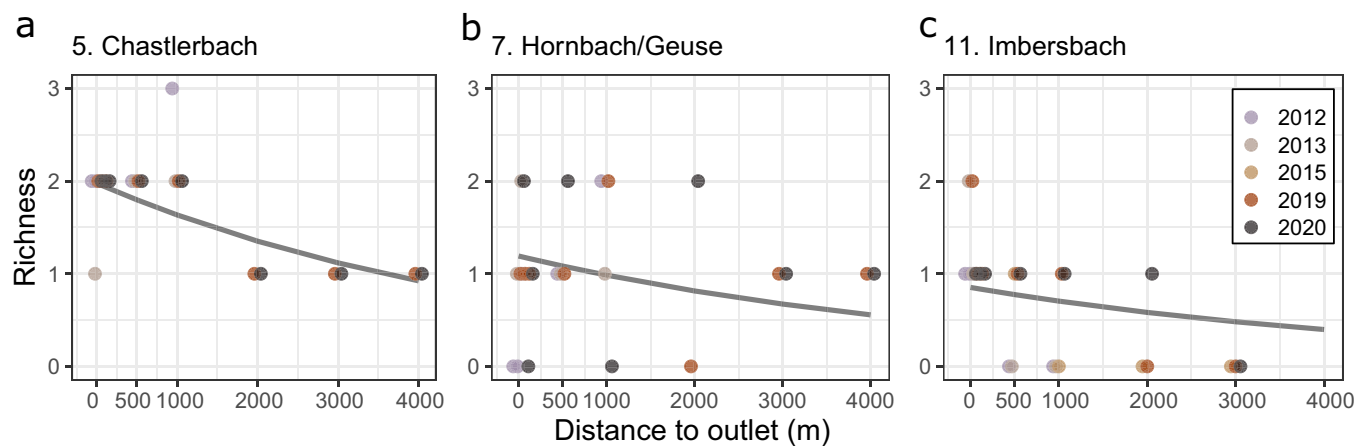


FIGURE 2 Spatial patterns of amphipod species richness for three representative streams studied. We found species richness to decrease with increasing distance to the outlet. Points represent empirically assessed number of amphipod species present at the site, whereas lines indicate predicted values derived from the statistical model. Sites are identified by their distance to the stream outlet, represented on the x-axis. Panels showing all 12 streams individually are given in Appendix S1: Figure S2.

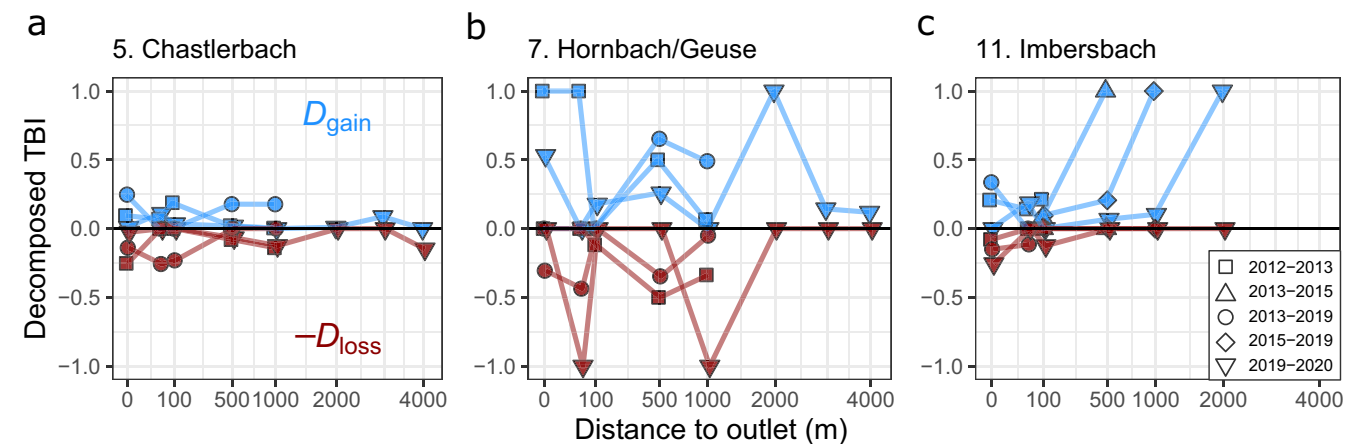


FIGURE 3 Temporal beta-diversity indices (TBIs) in three representative streams studied. The y-axis gives the total change ($D_{\%diff}$) decomposed into its components (positive D_{gain} and negative D_{loss}). Positive TBI values denote gains in abundance per species and/or species richness in the paired years, while negative values denote losses. Each paired year thus presents both D_{gain} and D_{loss} , whose sum is bound to [0, 1]. The three streams displayed represent three different patterns observed in the data: (a) amphipod assemblages undergo small positive and negative changes both along the stream length and across years. (b) Assemblage changes are again bi-directional, but their variance is greater. (c) Changes in the assemblage composition are directional, exhibiting in this case a clear positive TBI trend. Panels showing all 12 streams individually are given in Appendix S1: Figure S3.

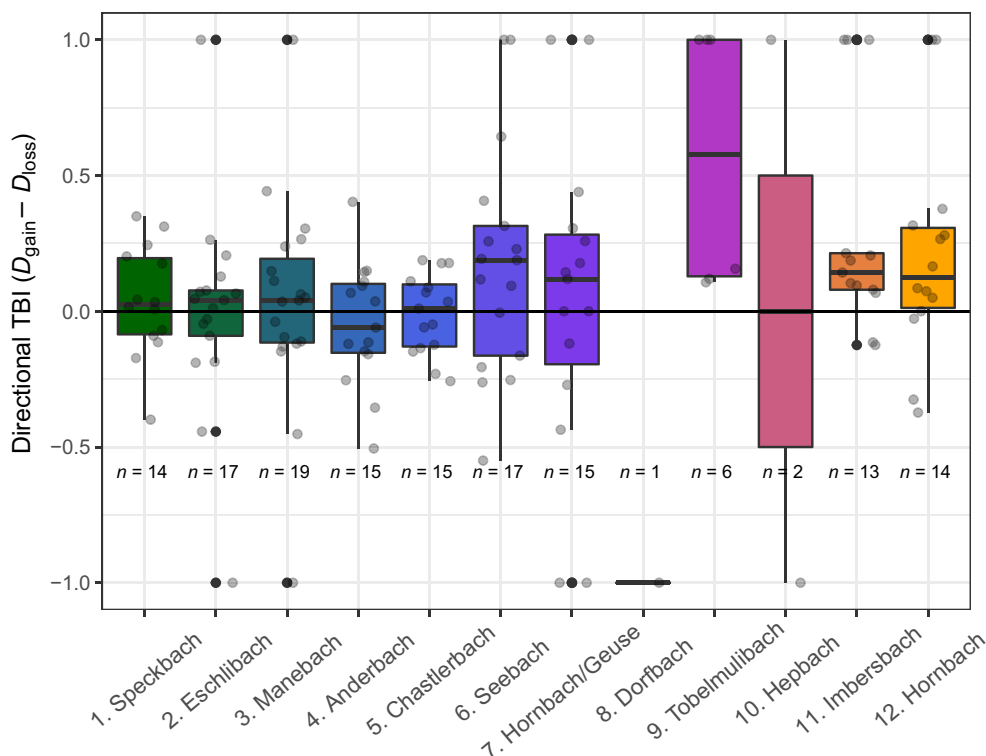


FIGURE 4 Within stream variability and directionality of temporal beta-diversity indices (TBIs). Temporal changes at individual sites were aggregated at the stream level, giving an overview of the direction of assemblage composition changes that occurred between 2012 and 2020 at the 12 studied streams. Gray points represent $D_{\text{gain}} - D_{\text{loss}}$ values of each TBI computed. Positive directional TBI values indicate that assemblage changes were mainly driven by gains in abundance per species and/or diversity of amphipods in the paired years, while negative values denote that losses were predominant. Outlet (0 m) sites were excluded due to their strong influence by the lake amphipod community. Streams are ordered according to their geographic location, from the westernmost stream (Speckbach, ID 1) to the easternmost stream (Hornbach, ID 12). Box limits indicate the first and third quartiles, midlines indicate the median, whiskers indicate the 1.5 interquartile ranges, and black points are the outliers beyond the 1.5 interquartile ranges.

overall D_{gain} exceeding D_{loss} (Appendix S1: Figure S4). Two streams (stream IDs 8 and 10) remained largely unoccupied for the duration of the study, only allowing the computing of two TBI for each stream (Figure 4; Appendix S1: Figure S3).

Temporal beta-diversity along stream length and across land use types

Distance to the stream outlet had no effect on amphipod assemblage changes (D_{diff} ; $\chi^2 = 0.52$, $p = 0.471$), and we observed no consistent patterns along the stream length when all streams were considered together (Appendix S1: Figure S5). To investigate land use type effects on D_{diff} , we first used a PCA to partition streams into different land use and abiotic factors found in their respective catchments. This PCA corroborated the opposing forces of agricultural land use and forest cover across the different catchments: The first component (PC1) explained 47.4% of the variance and was mainly related to the land use types forest,

meadow, arable crop, and orchard (Figure 5a). Lake system Obersee and its streams were associated with the more agricultural landscape, while the lake system Untersee and its streams were associated with greater forest cover and had generally larger drainage areas. A linear regression showed moderate evidence of PC1 having a positive effect on stream-specific D_{diff} ($t_{10} = 2.321$, $p = 0.043$). Streams that were more extensively surrounded by agricultural land thus tended to display, on average, larger amphipod assemblage composition changes. Importantly, this moderate evidence was strongly affected by two streams that had only one and two data points, respectively (and otherwise had all unoccupied sites, for which TBI cannot be calculated), compared to an average of 14.5 (ranging from 6 to 19) TBI values for the other streams. When excluding these two streams with minimal TBI values, we could show more robust evidence of an effect of larger amphipod assemblage composition turnover with increasing surrounding agricultural land use ($t_8 = 3.185$, $p = 0.013$; Figure 5b). We also observed a clear separation between streams located at the Untersee and the ones located at the Obersee.

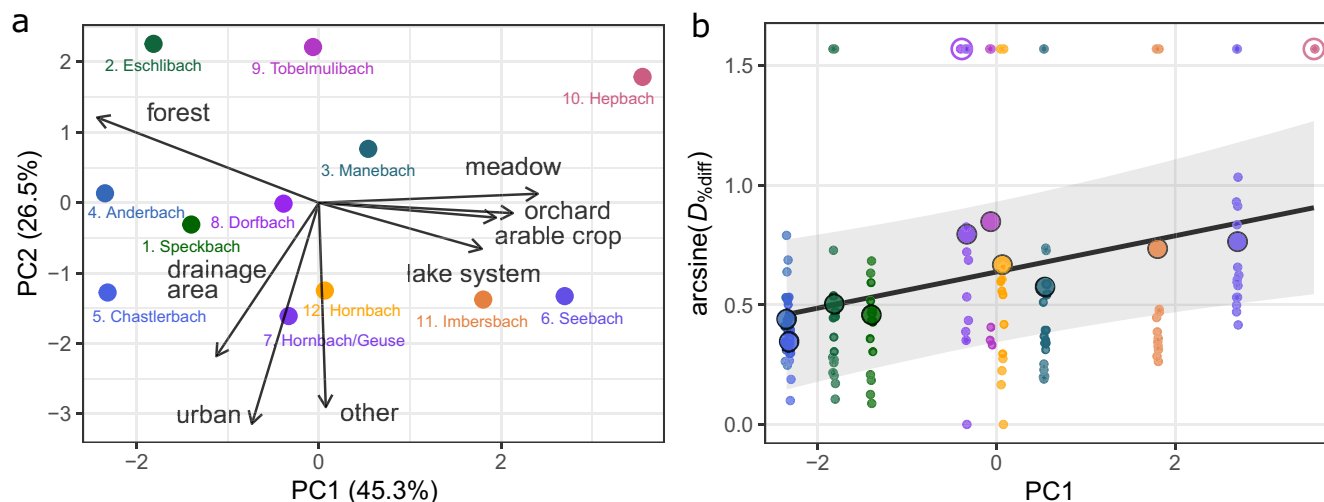


FIGURE 5 Stream environmental similarities and their effect on amphipod assemblage changes. (a) Results of principal components analysis (PCA) used to compute environmental similarities of the 12 studied streams. We included in the analysis the six main land use types, whole catchment drainage area, and lake system at which the streams drain. (b) Correlation between PC1 and the temporal beta-diversity (arcsine transformed $D_{\%diff}$) at the stream level. Smaller points, slightly jittered to improve their visibility, represent all the computed $D_{\%diff}$ values, whereas the larger points represent the mean $D_{\%diff}$ value of each stream. This differs from the mean of all computed $D_{\%diff}$ values (small points), because it was obtained by first averaging values within sites, then within streams. The two empty circles show mean $D_{\%diff}$ values of the two streams excluded from the analysis due to insufficient data on community turnover (streams mostly unoccupied; see [Methods](#)). The line indicates predicted values derived from the model with prediction interval area in light gray.

When collapsing $D_{\%diff}$ at the stream level, streams draining at the Untersee exhibited on average smaller composition changes than streams draining at the Obersee (Untersee: mean $D_{\%diff}$ [SD] = 0.19 [0.03]; Obersee: mean $D_{\%diff}$ [SD] = 0.63 [0.29]; Mann–Whitney U , $p = 0.006$; Appendix S1: Figure S6a). This clear difference was still present when again excluding the two streams at the Obersee with only one and two data points, respectively, each with maximum value (i.e., $D_{\%diff} = 1$; Mann–Whitney U , $p = 0.008$; Appendix S1: Figure S6b). Finally, our analog site-level model performed similarly to the stream-level model. Also at site level, the first component (PC1) described the opposing forces of agriculture and forest land cover, although here it only accounted for 26.8% of the variation (Appendix S1: Figure S7a). A linear regression showed very strong evidence of PC1 having a positive effect on stream-specific $D_{\%diff}$, ($\chi^2 = 14.135$, $p < 0.001$), meaning that amphipod assemblages tended to change more in sites with more predominant agricultural land (Appendix S1: Figure S7b).

DISCUSSION

Species assemblages are dynamic entities that change across time and space. Failing to address this fundamental characteristic limits our understanding of how current and future environmental conditions are affecting the process

and outcome of species and community assembly (Cook et al., 2018; Hillebrand et al., 2018), which is especially important to understand in the context of global anthropogenic changes (IPBES, 2019). By studying temporal beta-diversity patterns of amphipod assemblages in replicated small tributaries, we could show that assemblage changes are associated with the surrounding terrestrial matrix and recent amphipod colonization history. Amphipod composition was largely constant in streams located in forested catchments, whereas streams more extensively embedded in agricultural landscapes displayed more pronounced temporal changes, driven either by colonization of unoccupied upstream locations or by more pronounced but undirected fluctuations in gains and losses of species or abundance per species.

Our results suggest that anthropogenic disturbances and intense terrestrial land use play a direct role in destabilizing amphipod assemblages. It is well recognized that agricultural landscapes and their associated human activities can modify freshwater ecosystems and promote changes in aquatic communities (Cook et al., 2018; Petsch et al., 2021). On the one hand, increased amplitudes of fluctuations, as observed in some streams, can be an early warning that precedes the sudden transition of a community to a new state (Carpenter et al., 2011; Scheffer et al., 2009), or they could be the manifestation of continuous but stochastic recolonization from forested sites. However, our data do not allow a direct assessment

of such transitions or stochastic colonizations. The observed fluctuations are mostly driven by abundance changes in *G. fossarum*, while *G. roeslii* and *G. pulex* sometimes co-occur and sometimes do not. Thus, they might either co-occur but in fluctuating abundances, or they might exclude each other at the river scale, but not at small spatial scales.

On the other hand, the observed colonization of upstream sites supports our initial prediction that habitats previously unsuitable became suitable over time, promoting recolonization by dispersing individuals from the closest downstream population (Tonkin et al., 2014). Although the causes for the previous unsuitability of these sites are unknown, the absence of these otherwise vastly widespread shredders would suggest localized factors affecting the quality of individual streams. It is unlikely for other events, such as drying or flooding, to be responsible for this absence, as nearby streams, which share similar morphologies and flow regimes, would have been likewise affected. Importantly, unoccupied sites were almost exclusively reported in streams in the more agricultural eastern part of the study area, which is also known to be more heavily affected by pesticide run-offs, which can be detrimental to stream amphipod communities (Burdon et al., 2019; Zubrod et al., 2014). There, we also observed two streams that were almost completely unoccupied throughout the whole study, strongly suggesting more intense or persistent anthropogenic disturbances preventing colonization efforts (Petsch et al., 2021). Though we speculate unfavorable water conditions to at least partially explain the observed patterns, we acknowledge that more targeted studies would be required to understand the mechanisms behind the absence of these shredders.

We observed more species-rich amphipod assemblages at outlet sites and a decrease in species richness with increasing upstream distance. Coexistence of multiple species at upstream reaches (100–4000 m) was uncommon, supporting previous findings of priority effects determining the predominant colonization by one of the species present in the regional species pool (Drake, 1991; Little & Altermatt, 2018a). Contrary to our initial prediction, however, we did not find evidence of species turnovers or shifts in species dominance occurring more frequently at the more species-rich downstream sites. Rather, coexistence seemed to be maintained with some fluctuations throughout the duration of the study, possibly pointing to mechanisms allowing these species to co-exist despite fulfilling the same functional role. One possible explanation is given by the linear structure and position within the riverine network of these tributaries. On the one hand, the lake system acts as the regional species pool from where species can colonize the tributaries, in analogy to a sink-source

metacommunity (Leibold et al., 2004). On the other hand, species that have successfully colonized the upstream reaches of a tributary can have individuals disperse to downstream sites through drift (Elliott, 2002). These sites of coexistence—not necessarily at the outlet—might represent the interface between these two population sources and thus be maintained even in the presence of intraguild competition. From an island biogeography perspective (MacArthur & Wilson, 1967), the lake system and the tributaries can be seen as mainland and islands, respectively, with the tributaries islands being located at equal distances from the lake mainland. This would differentiate the small tributaries studied from other small streams investigated in the literature, which often consider small streams as being much more isolated within riverine networks (Altermatt, 2013; Tonkin et al., 2018).

While several amphipod species have been found across the larger regional scale (Altermatt et al., 2019), the studied tributary streams remain relatively species poor, constraining the efficacy of the TBI analyses performed. Applying this method to more species-rich assemblages could improve the understanding of ongoing temporal changes and possibly offer insight into the mechanisms that drive them (Lindholm et al., 2021; Tatsumi et al., 2021). Nevertheless, the amphipod assemblages studied here are characteristic of relatively species-poor yet numerically dominant freshwater invertebrates, occupying a central ecological niche within these small streams and providing fundamental ecosystem services (Woodward et al., 2008). Gaining a more comprehensive knowledge of temporal beta-diversity and its components for such key-stone species should be a priority because these could have cascading consequences not only within, but also across ecosystems (Cardinale et al., 2006; Gounand et al., 2018). We are also aware that we may not be able to tease apart agriculture from forest effects that go beyond their overall difference. Mechanisms such as pesticide inflows, leaf litter abundance, or composition could have interacting effects, but they are also likely to act at different spatial and temporal scales. Little and Altermatt (2018b) found that benthic leaf litter diversity in tributaries of Lake Constance was generally lower in forested streams, but benthic litter biomass was not always related to the degree of catchment forestation. Even though our data were collected with high spatiotemporal resolution, we cannot fully disentangle the multitude of these effects.

In conclusion, we show pronounced differences in spatiotemporal dynamics in community assembly in key freshwater invertebrates depending on the terrestrial land use type surrounding replicated and otherwise directly comparable small tributary streams. Our study stresses the importance of computing TBI in such replicated systems to understand trajectories of species assemblages.

By observing 12 streams and yet taking into account the individuality of each one, we were able to reveal patterns that might otherwise not have emerged from overall trends. With all streams being equally connected to a regional species pool (Lake Constance, into which all tributary streams drain), the difference in community structure and temporal beta-diversity changes can be mostly associated with different extents of agricultural land use. Where agricultural land use was intense, aquatic communities showed particular increases in the temporal variability in community assembly, indicating the possibility of alternating states driven by terrestrial land uses. Our work highlights that anthropogenic change in terrestrial systems not only affects richness and composition of aquatic communities but also has pronounced effects on their temporal stability and assembly. A higher amplitude in community assembly in more agriculturally affected systems makes these communities overall less resilient and increases the risk of overall community collapses, especially in situations where land use drivers are synchronized across different catchments.

ACKNOWLEDGMENTS

We thank Roman Alther, Elvira Mächler, Chelsea Little, Sarah Bollina, Raphaël Bossart, Jeanine Brantschen, Teo Cereghetti, Francesca Cerroti, Samuel Hürlemann, Géraldine Keat, Mara Knüsel, Andrin Krähenbühl, and Rebecca Oester for data contribution and fieldwork. We thank Roman Alther and François Keck for their comments on the manuscript and support during the project. We also thank two anonymous reviewers for their comments on our manuscript. Funding is from the Swiss Federal Office for Environment (FOEN/BAFU), the University of Zurich Research Priority Programme Global Change and Biodiversity, and the Swiss National Science Foundation (grants No. PP00P3_179089 and 310030_197410) to FA.



CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data (Cereghetti & Altermatt, 2023) are available from Zenodo <https://doi.org/10.5281/zenodo.7620983>. These data include data from Altermatt et al. (2016), available from Figshare: https://doi.org/10.6084/m9.figshare.c.3626972_D1.v1, and data from Little and Altermatt (2018), available from Dryad: <https://doi.org/10.5061/dryad.75jq1>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Cereghetti, Eva, and Florian Altermatt. 2023. “Spatiotemporal Dynamics in Freshwater Amphipod Assemblages are Associated with Surrounding Terrestrial Land Use Type.” *Ecosphere* 14(3): e4469. <https://doi.org/10.1002/ecs2.4469>