

Original research article

Elements of metacommunity structure of river and riparian assemblages: Communities, taxonomic groups and deconstructed trait groups

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ARTICLE INFO

Article history:

Received 15 May 2015

Received in revised form 18 November 2015

Accepted 18 December 2015

Available online

Keywords:

Context dependency

Metacommunity types

Floodplain

LTER

Stream macroinvertebrates

Traits

ABSTRACT

The elements of metacommunity structure (EMS) framework gives rise to important ecological insights through the distinction of metacommunities into several different idealised structures. We examined the EMS in assemblages occupying a low-mountain river system in central Germany, sampled over three consecutive years. We compared the idealised distributions of assemblages in both the riparian floodplain zone (carabid beetles and spiders) and the benthic instream environment (benthic invertebrates). We further deconstructed instream organisms into taxonomic and trait groups to examine whether greater signal emerges in more similar species groups. We found little evidence of strong competition, even for trait-modality groups, and nestedness was almost non-existent. In addition to random distributions, Gleasonian distributions (indicating clear, but individualistic turnover between sites) were the most commonly identified structure. Clear differences were apparent between different trait groups, particularly between within-trait modalities. These were most evident for different dispersal modes and life cycle durations, with strong dispersers showing possible signs of mass effects. While random distributions may have partly reflected small sample sizes, clearly coherent patterns were evident for many groups, indicating a sufficient gradient in environmental conditions. The prevalence of random distributions suggests many species are responding to a variety of environmental filters in these river-floodplain metacommunities in an anthropogenically-dominated landscape, whereas Gleasonian distributions indicate species are responding idiosyncratically to a primary environmental gradient. Our findings further emphasise the prevalence of context dependency (spatio-temporal variability) in metacommunity studies, thus we stress the need to further disentangle the causes of such variation.

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1. Introduction

Understanding metacommunity patterns and processes is fundamental not only to enhance our basic ecological understanding but also for developing strategies for effective restoration and bioassessment programmes (Heino, 2013b; Tonkin et al., 2014). A common approach has been to disentangle the relative roles of environmental and spatial variables (Cottenie et al., 2003), but this approach is not without its problems, as outlined in Anderson et al. (2011). Alternative means are available to examine metacommunity

structure, such as examining the emergent properties of a metacommunity matrix through the elements of metacommunity structure (EMS) framework (Leibold and Mikkelsen, 2002; Presley et al., 2010). This framework allows for the differentiation of metacommunities into a suite of different idealised structures simultaneously, rather than individually, based on the structure of the species-by-site matrix in relation to a null distribution. These include random distributions, checkerboards (i.e. species pairs occur together less than expected by chance) (Diamond, 1975), nested subsets (i.e. species poor communities form a subset of species rich communities) (Patterson and Atmar, 1986), Clementsian (i.e. species respond to environmental gradients in groups or discrete communities) (Clements, 1916), Gleasonian (i.e. species respond individually to environmental gradients) (Gleason, 1926), and evenly-spaced (i.e. species ranges are arranged evenly along environmental gradients) (Tilman, 1982) gradients.

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Disentangling these distributional patterns stems from long-standing and intense debates in ecology. For instance, species poor communities may be nested subsets of more complete assemblages (Patterson and Atmar, 1986; Ulrich et al., 2009); species may assemble in an idiosyncratic manner (i.e. Gleasonian) (Gleason, 1926) or form compartments with distinct range boundaries in response to similar environmental conditions (i.e. Clementsian) (Clements, 1916); or species sets may form into checkerboard distributions potentially arising through intense interspecific competition (Diamond, 1975) or other factors such as environmental heterogeneity (Heino, 2013a). Differences in species ranges may reflect differences in habitat or environmental conditions, functional traits and levels of biotic interactions, among other factors.

One particular location acting as a biodiversity hotspot with a variety of habitat conditions, functional linkages, and reciprocal metaecosystem flows of nutrients, matter and organisms (Polis et al., 1997) is the aquatic-terrestrial ecotone. Soininen et al. (2015) recently called for a more holistic approach to research linking aquatic and terrestrial environments. The isolated approach to studying these systems is surprising given how strongly coupled they are in reality (e.g. Baxter et al., 2005). The linkage between rivers and their riparian zone is particularly strong in light of their greater edge ratio than many other aquatic systems (Baxter et al., 2005; Richardson et al., 2010). This raises interesting questions as to the structure of metacommunities across this interface. For instance, whether different patterns emerge when comparing complete between-habitat assemblages, spanning the aquatic-terrestrial ecotone, or individually in their respective habitat zones. One might expect a weaker competition signal, or assemblage turnover between locations, when considering assemblages holistically, than within the more tightly competing groups in their respective habitats, including those with similar traits.

Common ancestry (i.e. taxonomic groups), is a limited approach to grouping species assemblages, as trait-based groups likely represent more interactive species subsets. Functional traits relate to the ecological functioning of ecosystems and thus represent a process-focused view on ecosystems, beneficial for disentangling ecological processes (McGill et al., 2006). Traits, moreover, likely overcome some issues relating to spatial and temporal variability (Poff, 1997; Menezes et al., 2010). Focusing on traits rather than taxonomically-derived groups may be a more effective approach to identify stressors (Gayraud et al., 2003; Lange et al., 2014) and examine climate change influences (Poff et al., 2010). However, it is likely more informative to study traits in concert with more traditional taxonomic measures when examining species distributions and environmental associations (e.g. Bonada et al., 2007). Given the central role of dispersal shaping metacommunities (Leibold et al., 2004; Holyoak et al., 2005), traits reflecting dispersal ability and other factors controlling species' specialisation should be particularly important in shaping metacommunity structure (Thompson and Townsend, 2006; Heino, 2013c).

We examined patterns in metacommunity structure in a low-mountain river systems in central Germany over three consecutive years, by applying the EMS framework. We compared idealised range distributional patterns between instream benthic invertebrates, riparian spiders (Order: Araneae) and riparian carabid beetles (Order: Coleoptera; Family: Carabidae). Based on three statistics, coherence, turnover and boundary clumping, this approach enables the differentiation of metacommunities into several distinct metacommunity types based on their species-by-site matrices (Leibold and Mikkelsen, 2002; Presley et al., 2010), and can identify important changes in the makeup of assemblages. For instance, Fernandes et al. (2014) found that metacommunity structure changed from nested subsets through to quasi-Clementsian from the beginning to end of the flood season for floodplain fish communities in the Pantanal Wetland, South America. Given the

potential differences in distributions of groups of species with different functional traits, we compared the structure of different deconstructed trait groups for benthic invertebrate communities. In total we used 26 individual groupings, including seven traits and sixteen trait modalities, making 78 species-by-site matrices in total.

We asked the following questions: Q1. Does metacommunity structure differ between aquatic invertebrates and riparian carabids and spiders? Q2. Do different functional trait groups produce different metacommunity structure, and do within-trait modalities differ? For instance, (Q2a) does a greater level of competition for resources and space emerge within trait groups than taxonomic groups, resulting in more checkerboarding patterns? (Q2b) Do stronger dispersers have weak structuring resulting from mass effects at these small spatial scales? Q3. Do these patterns vary temporally?

2. Methods

2.1. Study site

The Rhine-Main-Observatory (RMO) is a long-term ecosystem research (LTER) site that comprises the entire Kinzig catchment (1060 km²) in the central German state of Hesse. The Kinzig River is a low-mountain river system draining a range of land use types, ranging from natural and managed forest, agriculture, horticulture and urban areas.

2.2. Sampling

We used data collected from 15 sites in the RMO as part of the annual LTER site monitoring (Fig. 1). These 15 sites were situated along the Kinzig River in the active floodplain area, including both aquatic and terrestrial/floodplain (riparian) zones (Fig. 1). This section harbours a gradient of environmental conditions based on land use, including forest, pasture and urban zones. These were each sampled once per year in summer for three years, between 2010 and 2012. The sampling regime of these 15 sites began in 2010, thus we focused on the full suite of available data from the RMO LTER site. Each site consists of a 100-m length of river and a 30-m lateral stretch from the river's centre point (60-m cross section; 6000 m² area).

2.2.1. Instream

We employed the official EU Water Framework Directive (WFD) multi-habitat sampling protocols (Haase et al., 2004) to sample benthic invertebrates. This method enables coverage of the range of microhabitat conditions present at a site, by taking 20 subsamples representative of their coverage. Samples were subsequently stored in 70% ethanol for laboratory processing and identification. Taxonomic identification followed the EU-WFD-compliant operational taxon list (Haase et al., 2006).

2.2.2. Riparian

We sampled riparian spiders (Order: Araneae) and carabid beetles (Order: Coleoptera; Family: Carabidae) using eight 5.5-cm diameter pitfall traps in the riparian zone at each location. Traps were distributed to cover the range of microhabitat environments available at each location. Traps were deployed in August each year and remained in place for two weeks. We used Renner solution to kill and preserve organisms, and traps were re-deployed in the same locations annually. Juvenile spiders were excluded from the analyses.

2.3. Data preparation

We examined patterns in metacommunity structure between a range of different assemblage groups for a variety of purposes,

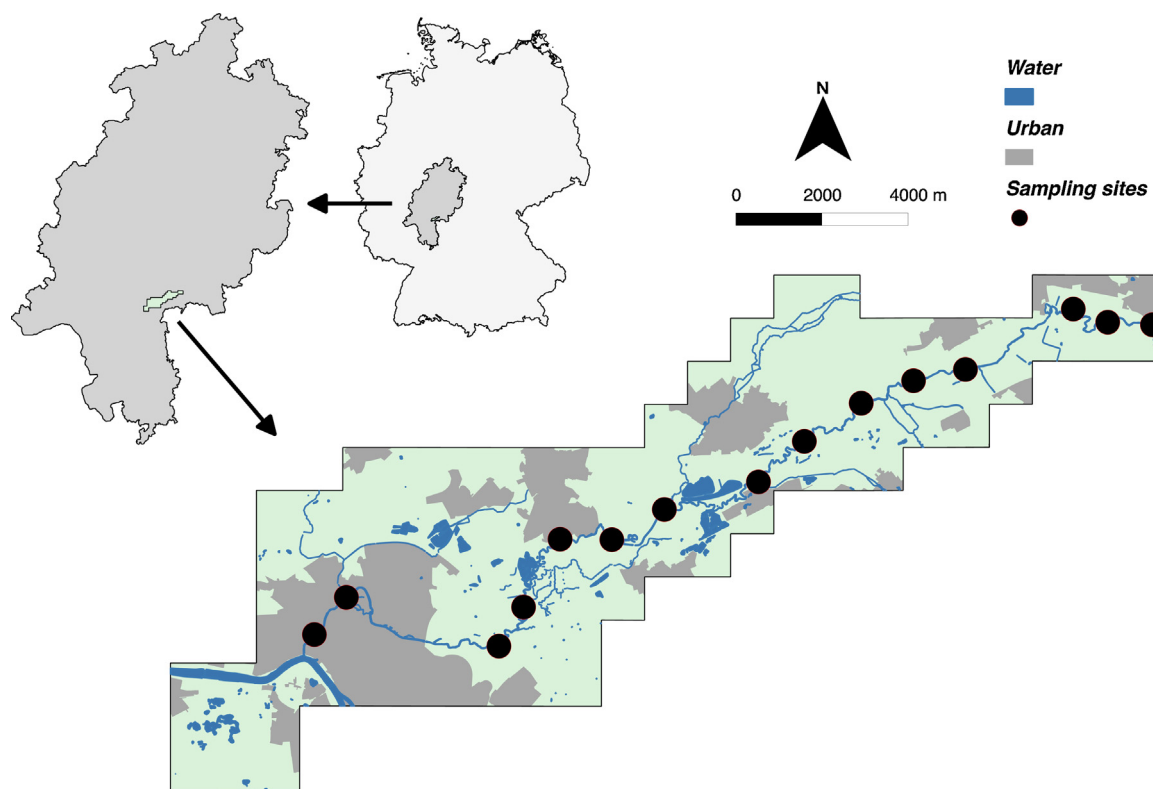


Fig. 1. Map showing the location of the 15 sites along the Rhine-Main-Observatory LTER site situated on the Kinzig River, Hessen, Germany.

including competition or simply that they are often treated as units for applied or basic ecological purposes (e.g. EPT are used for biomonitoring and reflect environmental gradients well; Tonkin, 2014). Some groups were intended to represent varying levels of potential competitive interactions. For instance, we might expect a greater amount of competitive interactions in trait groups than taxonomic orders (similar functions rather than common ancestry

Table 1
Codes and abbreviations of data used in the study to examine elements of metacommunity structure.

Code	Classification	Explanation
all	All	All organisms
riparian	Community	Riparian spiders and beetles
inverts	Community	Benthic invertebrates
beetles	Community	Riparian beetles (family: Carabiidae)
spiders	Community	Riparian spiders (order: Araneae)
ephemeroptera	Taxonomic	Ephemeroptera
trichoptera	Taxonomic	Trichoptera
diptera	Taxonomic	Diptera
ept	Taxonomic	Ephemeroptera, Plecoptera and Trichoptera
non_ept	Taxonomic	non Ephemeroptera, Plecoptera and Trichoptera
adult_naqua	Trait	Non-aquatic adult stage
adult_aqua	Trait	Aquatic adult stage
ae_ac_disp	Trait	Aerial active dispersal mode
aq_disp	Trait	Aquatic dispersal mode
dc_high	Trait	High dispersal capacity
dc_low	Trait	Low dispersal capacity
mps_l	Trait	Large maximum potential size (>2cm)
mps_s	Trait	Small maximum potential size (<2cm)
lcd_l1	Trait	Life cycle duration <1 year
lcd_g1	Trait	Life cycle duration >1 year
univoltine	Trait	One life cycle per year
multivoltine	Trait	Multiple life cycles per year
shredder	Trait	Shredder feeding mode
scraper	Trait	Scraper feeding mode
filter_feeder	Trait	Filter feeder feeding mode
predator	Trait	Predator feeding mode

should lead to more competition). Nevertheless, it is important to note here that our approach, based on presence-absence data, is not the most direct way to measure this, but we focus on differentiating metacommunities into different types, where such processes that may be operating extremely clearly can be inferred. We thus grouped organisms into a variety of matrices for use in our metacommunity analyses (Table 1). First, we combined all organisms, both instream and terrestrial (Classification: All); second, we grouped the riparian spiders and beetles into a combined riparian group, and also kept each of the three organism groups separate (Classification: Community); third, we split benthic invertebrates into orders, but only kept groups with enough species (Ephemeroptera, Trichoptera and Diptera; Classification: Taxonomic); fourth, we split EPT (Ephemeroptera, Plecoptera and Trichoptera) and non-EPT organisms (all non-EPT groups; Classification: Taxonomic); and finally, we deconstructed communities into several trait-based groups of benthic invertebrates (Classification: Trait).

Deconstructed trait groups were created using data compiled as part of the STAR project (Bis and Usseglio-Polatera, 2004; Furse et al., 2006). In this database, trait modalities (e.g. trait = dispersal mode; modality = aquatic active disperser) are assigned scores on a scale of 0–3 (some are 0–5), with low representing no affinity and high representing high affinity of a particular species for the particular trait modality. All of the traits used in the present paper are scaled from 0 to 3. Species can be assigned affinities for several trait modalities for the same trait. For instance, a species can be both an active aquatic and active aerial disperser. In this case it would have non-zero scores for each of these two trait modalities. We also used an additional dispersal capacity metric, created from the STAR trait database (Li et al., 2015).

We deconstructed communities into the following different trait modality groups using these fuzzy coding values: adult stage (aquatic vs. non-aquatic), dispersal mode, dispersal capacity, maximum potential size, life cycle duration, voltinism, and feeding

mode. These groups represent a ‘community’ of individuals with similar trait modalities (e.g. a ‘community’ of aerial active dispersers) allowing a deeper understanding of underlying mechanisms shaping overall metacommunity structure (Heino, 2013c). With the exception of feeding modes, we split invertebrates into two relatively evenly-sized groups in terms of species number in each group to ensure adequate sample size. We considered a species to have a particular modality if its affinity value for a particular modality was two or three. With the exception of a feeding mode, we ensured species were assigned to only one group and thus groups were independent. For instance, for the maximum potential size trait, we ensured large taxa were those with a score of two or greater for modalities 2–4 cm, 4–8 cm and >8 cm; whereas small taxa had to exclusively have values in the remaining categories (all <2 cm). For feeding modes, we allowed species to be a member of any of the four groups (i.e. a species could be in both the shredder and predator groups if assigned a value of two or greater), thus groups were not independent. For dispersal mode, we first assigned a species as an aerial active disperser if it had a modality affinity of two or three. All remaining species were assigned as aquatic dispersers as, if a species had an affinity for aerial passive dispersal in the database, it always also had an affinity for either active or passive aquatic dispersal. For dispersal capacity, we split species into high and low capacities (greater vs. less than or equal to 7).

2.4. Statistical analyses

The elements of metacommunity structure (EMS) framework enables differentiation of metacommunities into several different best-fit idealised structures, examining patterns in species range distributions in three consecutive stages: coherence, species turnover and range boundary clumping (Leibold and Mikkelsen, 2002; Presley et al., 2010). Originally, Leibold and Mikkelsen (2002) outlined six different idealised structures: random distributions, checkerboards, nested subsets, Clementsian, Gleasonian and evenly-spaced gradients. Presley et al. (2010) expanded on these to include the examination of range boundary clumping for nested subsets (i.e. random, clumped or hyperdispersed species loss), as well as placing communities into six quasi-structures where non-significant turnover is evident. We followed the approach of Presley et al. (2010) to classify metacommunities into one of fourteen different idealised structures. Detailed explanations of the approach can be found in Leibold and Mikkelsen (2002) and Presley et al. (2010) and a summary table of the main structures is available in Heino et al. (2015d). Moreover, Tonkin et al. (2015d) details the full procedure including the workflow in R, but we will briefly summarise the main details in the following section.

We used the R package *Metacom* (Dallas, 2014) to examine EMS. This approach relies on null models to compare observed distributions (using a presence-absence species-by-site matrix) with those expected by chance. Patterns are tested on a presence-absence site-by-species matrix ordinated through reciprocal averaging (RA) (Gauch et al., 1977), to maximise correspondence within the matrix. Ordination axes are then representative of a latent environmental gradient structuring the metacommunity (Leibold and Mikkelsen, 2002). As the first two RA axes can potentially represent important information about the assemblages (Presley et al., 2009), we focus on both axes in our assessment. However, given the mostly random structures on the secondary axis, we restrict these results to the Supplementary material (Table S1). We used the “R0” (“fixed-equiprobable”) method to constrain our null matrices, running 1000 simulations of these null models to compare with our observed matrix. As rare species are known to disproportionately effect the outcome of EMS

results, particularly coherence and range boundary clumping (Presley et al., 2009), we excluded species with less than two occurrences in each year.

The first stage of the EMS approach is to check for coherence in species distributions, indicative of species responding to a similar environmental gradient. A coherent metacommunity is one with significantly fewer embedded absences (a gap in species ranges) in the observed matrix than in the simulated null matrices, examined using a z-test. A metacommunity with more embedded absences than expected by chance (negative coherence) is deemed to have a checkerboard distribution (Diamond, 1975), and the alternative distribution is random (but see, Dallas and Drake, 2014 for concerns about interpreting random and Gleasonian patterns). Rather than representing random species occurrence within a metacommunity, these distributions more realistically suggest species distributions and environmental drivers are independent of each other.

Where positive coherence is observed, species turnover is examined by the number of times each species replaces every other species between two sites, also tested using a z-test. Results from this stage (i.e. positive or negative turnover) are then tested for range boundary clumping (extent of clumping at the edges of species distributions) using Morista’s Index (MI) (Morista, 1971). Again, these values are then compared with the null expectation using a Chi² test.

Metacommunities with significantly positive turnover (greater species replacements) can be classified into Clementsian (clumped range boundaries), Gleasonian (random range boundaries) and evenly spaced gradients based on their boundary clumping. Significantly negative turnover (fewer species replacements), represents nested subsets. These can be sub-divided based on boundary clumping into random species loss, clumped species loss, and hyperdispersed species loss (Presley et al., 2010). Finally, the same patterns in boundary clumping can be detected for metacommunities with non-significant turnover (positive) or nestedness (negative), termed quasi-structures.

We ran these analyses on the full suite of organisms across the aquatic-terrestrial boundary (All), individual community groups (i.e. benthic invertebrates, beetles, spiders, riparian combined; Community), within benthic invertebrate groups (i.e. EPT vs. non-EPT, orders; Taxonomic), and within benthic invertebrate trait groups (e.g. short vs. long life cycles, and various other traits; Traits).

All statistical analyses were performed in R version 3.0.2 (R Core Team, 2013).

3. Results

Considerable variation in metacommunity structure was evident between groups, but Gleasonian distributions were the most common idealised structures identified on the primary axis (RA axis 1; Table 2; Figs. 2–3; Table S1). Axis 2 of the RA produced mostly random structures, thus we will focus our interpretation on axis 1 (Table S1). Overall, taking all groupings into account, random (32% of all matrices) and Gleasonian (31%) were the most commonly observed structures, followed by various quasi-structures (mostly quasi-Clementsian [17%] or quasi-Gleasonian [9%]) (Fig. 3).

Of the 52 possible first-order transitions between years (i.e. 26 groups, differences in structure between 2010–2011 and 2011–2012), 48% remained the same (i.e. stable structures). Of the 26 possible second-order transitions (i.e. 2010–2012), 35% remained the same between 2010 and 2012, and when considering all years together, 31% (8 of 26) of the structures remained stable across all three years. Of the 27 first-order transitions where a difference in structure was evident, there

Table 2

Results of elements of metacommunity structure analysis on aquatic and riparian organisms at 15 sites, sampled annually from 2010 to 2012 in the Kinzig River, central Germany. Presented are the best-fit idealised metacommunity structure for each group in each year. Only results from the primary axis of reciprocal averaging ordination are given here. Full results for both axes are given in Supplementary information Table S1 and coherence, turnover and boundary clumping results for axis 1 are given in Fig. 2.

Group	2010	2011	2012
all	Gleasonian	Gleasonian	Gleasonian
riparian	Gleasonian	Gleasonian	Gleasonian
inverts	Gleasonian	Gleasonian	Gleasonian
beetles	Clementsian	Gleasonian	Checkerboard
spiders	Gleasonian	Gleasonian	Gleasonian
ephemeroptera	Quasi-Gleasonian	Random	Random
trichoptera	Random	Random	Random
diptera	Quasi-Clementsian	Random	Random
ept	Random	Random	Random
non_ept	Gleasonian	Clementsian	Quasi-Clementsian
adult_naqua	Quasi-Clementsian	Quasi-Gleasonian	Gleasonian
adult_aqua	Gleasonian	Random	Random
ae_ac_disp	Random	Random	Random
aq_disp	Gleasonian	Clementsian	Quasi-Gleasonian
dc_high	Quasi-Clementsian	Random	Random
dc_low	Gleasonian	Clementsian	Quasi-Clementsian
mpe_s	Quasi-Gleasonian	Quasi-nested (random)	Quasi-nested (clumped)
mpe_l1	Gleasonian	Random	Random
lcd_g1	Quasi-Clementsian	Quasi-Clementsian	Quasi-nested (clumped)
univoltine	Quasi-Clementsian	Quasi-Clementsian	Random
multivoltine	Quasi-Clementsian	Quasi-Clementsian	Quasi-Gleasonian
shredder	Quasi-Clementsian	Gleasonian	Quasi-Gleasonian
scraper	Quasi-Clementsian	Quasi-Gleasonian	Random
filter_feeder	Gleasonian	Random	Random
predator	Random	Quasi-nested (clumped)	Random

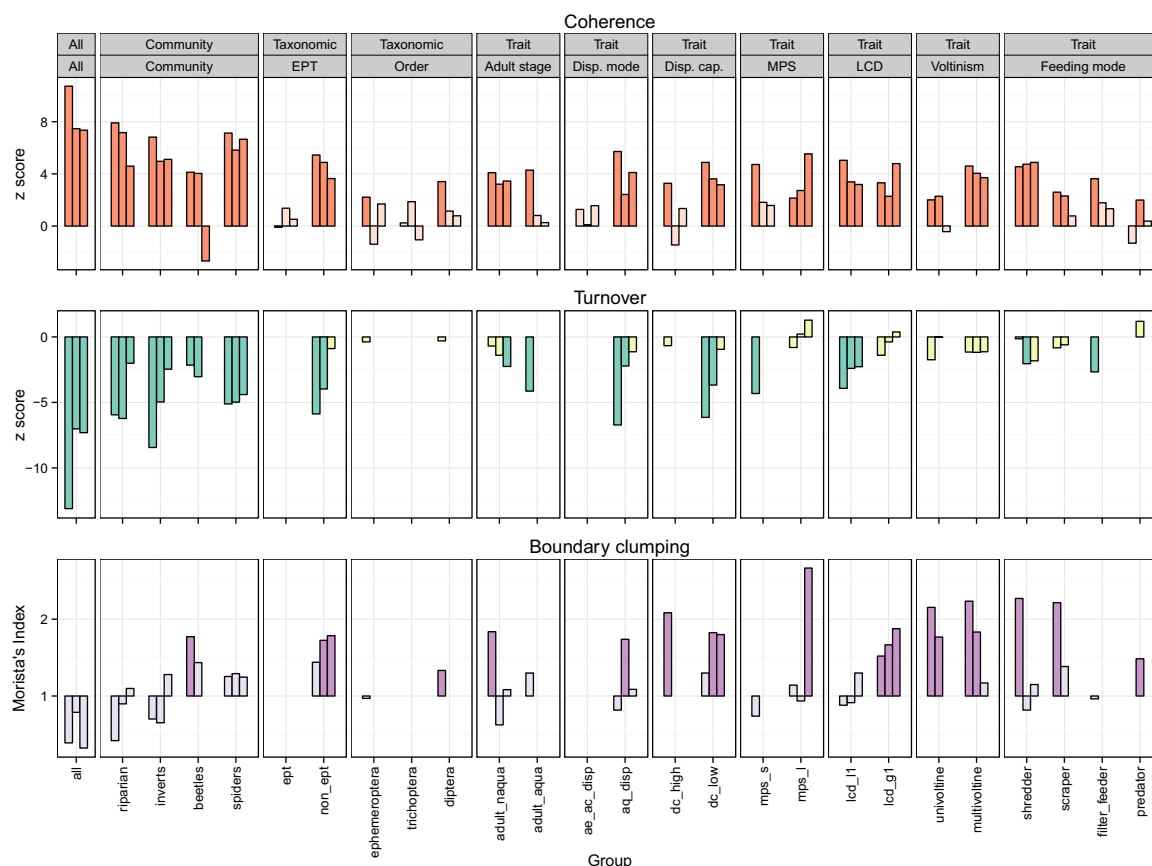


Fig. 2. Results of coherence, turnover and boundary clumping as part of analysis of elements of metacommunity structure on 15 sites, sampled annually from 2010 to 2012 in the Kinzig River, central Germany. Dark bars for each subplot represent the value for the given test is significant (i.e. coherence, turnover or boundary clumping are significantly different from the null expectation). Positive z scores for coherence represent fewer embedded absences than chance (coherence) and significantly negative are checkerboard. Negative z scores for turnover represent more species replacements than chance (turnover; opposite is nestedness). Morista's Index values significantly greater than one represent clumped boundaries, and significantly less than one represent hyperdispersed boundaries; non-significant are random. Results for turnover and clumping are only shown where coherence was significantly positive. Only on the primary axis of the reciprocal averaging ordination are given here. Full results for both axes are available in Supplementary information Table S1.

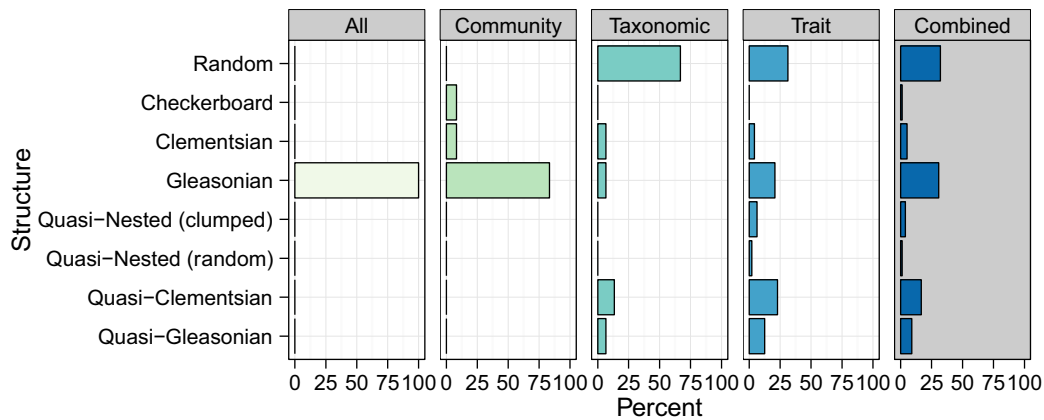


Fig. 3. Summary plot of the results of the primary axis of the elements of metacommunity structure analysis. The percentage a particular structure emerged for each classification group are given. The classification system is given in Table 1. The last panel (shaded) shows the overall results of all the groupings in the first four panels combined ($n = 78$). Each of the three years were treated as individual replicates. All: $n = 3$; community: $n = 12$; taxonomic: $n = 15$; trait: $n = 48$. Full results of idealised structures are given in Table 2 and complete results are in Table S1. Only idealised structures observed are listed in the table. Six remaining possible structures were not observed: nested (clumped), nested (random), nested (hyperdispersed), evenly spaced gradients, quasi-nested (hyperdispersed), and quasi-evenly spaced gradients.

were no dominant patterns, but the most common patterns were shifts between different quasi-structures or from quasi-structures to random patterns (Table 2).

3.1. Differences between taxonomic groups

For the full community matrices, with the exception of beetles (all combined, riparian combined, benthic invertebrates, riparian combined, and spiders), Gleasonian distributions were consistent (Table 2; Fig. 3; Table S1). Riparian beetles fluctuated from Clementsian to Gleasonian to checkerboard distributions (Table 2; Fig. 2; Table S1). Beetles were the only group to display checkerboard distributions on the primary axis of organisation, although checkerboarding was more common, but still rare, on the secondary axis (Table S1).

All order-based benthic invertebrate groups produced either random distributions or quasi-structures, likely resulting from their small dataset size (i.e. species richness; Table 2; Fig. 2; Table S1). Random distributions were largely found for the smaller datasets (Table 2; Fig. 2; Table S1). However, EPT combined were also consistently random, suggesting these patterns may not have been due to low sample number, as non-EPT taxa were either Clementsian, Gleasonian or quasi-Clementsian (Table 2; Fig. 2; Table S1). Groups mostly showed little variation from year to year, but some clear exceptions were evident (Table 2; Fig. 2).

3.2. Differences between trait groups

While the trait-derived groups commonly exhibited random distributions or quasi-structures, considerable variation was present. Poor dispersers (dc_{low}), for instance, were either Gleasonian, Clementsian or quasi-Clementsian, whereas good dispersers (dc_{high}) were either quasi-Clementsian or random (Table 2; Fig. 2; Table S1). Likewise, aerial active dispersers exhibited consistently random distributions, whereas aquatic dispersers were either Gleasonian, Clementsian or quasi-Clementsian (Table 2; Fig. 2; Table S1). Aquatic dispersers and poor dispersers (as well as non-EPT taxa) exhibited similar patterns in coherence, turnover and boundary clumping (Fig. 2).

Many of the traits showed clear differences between the different modalities (Fig. 2). Where these differences emerged was not consistent. For instance, dispersal groups differed clearly in terms of coherence, whereas different life cycle length groups exhibited similar coherence, but differed in terms of turnover and boundary clumping (Fig. 2).

One clear result to emerge was between short and long life cycled species (duration < 1 or > 1). These differences emerged mostly in the turnover metric. Short life cycle species had significant turnover and non-significant boundary clumping (i.e. Gleasonian distributions), whereas longer life cycles species exhibited non-significant turnover resulting in either quasi-Clementsian or quasi-nested distributions (Table 2; Fig. 1).

The only groups to indicate any form of nestedness were large species (mps_{l1}) and predators although these were quasi-structures (i.e. not significantly nested), with clumped range boundaries. Species with longer life cycle (lcd_{g1}) also had a quasi-nested structure in 2012 but with very little departure from null in terms of nestedness. The feeding mode groups mostly indicated non-coherent or quasi-structures, although shredders and filter feeders displayed Gleasonian gradients in 2011 and 2010, respectively (Table 2; Fig. 2; Table S1).

4. Discussion

4.1. What were the most common patterns?

We found considerable variation in the best-fit idealised metacommunity structure between several different group classifications, ranging from gradient structures, where turnover is strong, to checkerboards and various quasi-structures. Others have also found different metacommunity structure when examining different organismal groups in the same setting. For example, desert rodent parasites (Dallas and Presley, 2014) or small mammals in South American Atlantic Forest (de la Sancha et al., 2014). Structures can also differ between different environmental settings (Heino et al., 2015c) or gradients of environmental change, such as between different forest types, as found for terrestrial gastropods along elevational gradients (Willig et al., 2011). Heino et al. (2015d) recently found considerable variation in EMS patterns in a variety of freshwater systems and organisms. Interestingly, although there were clear differences within benthic invertebrate trait groups, there was little difference in the patterns across the aquatic-terrestrial ecotone.

Despite considerable variation in best-fit structures, only eight of the 14 possible structures were observed from 78 individual data matrices. For instance, we found very little evidence of checkerboarding in any of the groups. Checkerboarding, among others, can indicate strong interspecific competition (Diamond, 1975), hence our expectation of greater evidence of checkerboarding in trait groups through greater interspecific competition

between closely similar species, rather than those grouped taxonomically. This expectation of lower co-occurrence of species with similar functional traits should also depend on the trait being considered (e.g. dispersal mode, Heino, 2013a). Previous freshwater studies have found checkerboarding (e.g. Boschilia et al., 2008; Larsen and Ormerod, 2014), which can also reflect environmental heterogeneity (Heino, 2013a). Nonetheless, it is important to consider that EMS is a pattern-based approach, and to accurately get at competition one would need to focus at smaller scales, focus on abundances and take experimental approaches (e.g. Kohler, 1992).

In our study, the only group to display checkerboard distributions along the primary axis was the carabid beetles (for criticisms of checkerboard analysis see e.g., Gotelli and McCabe, 2002). However, this was not a consistent pattern, emerging only once in the three years, with Clementsian and Gleasonian in the other two years. Clementsian and Gleasonian distributions indicate species are responding to an environmental gradient, but either in compartments or individualistically, respectively. Moreover, there was no convincing evidence of nestedness in these communities, with only four quasi-nested structures emerging (with near-random turnover values). Of the eight observed patterns, four were quasi-structures; i.e. those with non-significant turnover or nestedness in distributions.

In addition to quasi-structures, random distributions were commonly found in our dataset. Importantly, Dallas and Drake (2014) argued against the assumption of non-significant coherence representing randomly-structured metacommunities. They reason that doing so is to mistakenly assert the null hypothesis and that an inability to distinguish between positive and negative coherence does not necessarily indicate random assembly. This is critical to the interpretation of our results. Random structures can emerge through species responding to alternative environmental gradients individually. However, some of these patterns in our results may reflect the low numbers of sites and species. After removal of singletons, many tests were run with low degrees of freedom, particularly for orders and feeding groups (Table S1). In fact, examining the full community matrices consistently returned significant structures. These issues are equally important for the interpretation of quasi-structures. Associated with small sample sizes may be short gradient lengths of environmental conditions, which could affect the observed patterns. For instance, large environmental gradients may facilitate various gradient structures (e.g. Clementsian, Gleasonian), and small environmental gradients nestedness (Heino, 2011). Nevertheless the majority of trait groups were significantly coherent (only 31% random structures), suggesting clear responses to latent environmental gradients. This contrasts the taxonomic groups, with two thirds having random structures.

4.2. Patterns for community-based groups

Gleasonian distributions emerged as the most common structure for the community-based groups or entire assemblage combined, indicating species responding to an environmental gradient and turning over between sites but responding individually to the main environmental gradient. The study river system flows through a mix of land use types, and Tonkin et al. (2015c) found a clear importance of surrounding land use on the linkages between these three organism groups. However, community compartments (i.e. Clementsian gradients; turnover of distinct groups of species) were rare in our study. While Gleasonian gradients are often found, Clementsian (or sometimes quasi-Clementsian) gradients are more commonly found in studies applying the EMS approach, such as alpine grassland plants (Meynard et al., 2013), bats (Presley and Willig, 2010), stream

fishes (Erős et al., 2013), woodlands (Keith et al., 2011), beetles at the regional scale in Scandinavia (Heino and Alahuhta, 2014), desert rodent parasites (Dallas and Presley, 2014), and regional-scale stream invertebrates in Germany (Tonkin et al., 2015d). The rarity of clumped distributions in our case likely reflects the small spatial scale compared to other studies that cross over different species pools (Heino and Alahuhta, 2014; Tonkin et al., 2015d), but clumped distributions may also emerge more clearly with more sites examined. In the present study, we were limited to the set of sampled sites based on the data being collected for LTER site monitoring. We are, nevertheless, confident in the sampling strategies employed being able to capture site-based variability in these summer metacommunities.

4.3. Patterns for deconstructed trait and taxonomic groups

Trait-based groups more regularly exhibited coherent structures than the taxonomic groups for benthic invertebrates. Heino (2013c) called for ecologists to compare patterns between different dispersal groups to enable a better understanding of factors structuring communities. We agree with this and went one step further to focus on a variety of different trait groups. The benefit of the trait-based approach was indicated in the study by Presley et al. (2009) who found Clementsian gradients structured a Paraguayan bat metacommunity, but different patterns when breaking into feeding groups (aerial insectivores: Gleasonian; frugivores and molossid insectivores: random distributions). While fluctuating between different structures (Gleasonian, Clementsian and quasi-Clementsian), we also found clear coherence in the combined taxonomic group of non-EPT rather than EPT species. This probably reflects the fact that many of the EPT are active fliers, hence their similarity in pattern with the aerial active and high dispersal capacity groups. Furthermore, EPT were relatively uncommon in this river and thus maybe exhibited somewhat weaker patterns than the non-EPT taxa as a result, despite being known to represent environmental conditions well (Tonkin, 2014).

Not unexpectedly, given the central role of dispersal in structuring metacommunities (Leibold et al., 2004; Holyoak et al., 2005), the clearest difference in metacommunity structure emerged between different dispersal groups compared to other trait groups. Linking dispersal directly with EMS is not straightforward though (Meynard et al., 2013), as the EMS approach organises communities, and thus focuses on patterns, along a latent environmental gradient. Aerial active dispersers were randomly distributed in contrast to the more strongly structured remainder of species, with either Gleasonian, Clementsian or Quasi-Gleasonian. Thompson and Townsend (2006) also found weak patterns for strong dispersers and suggest that this may be due to dispersal over scales greater than in their study. These patterns were similarly reflected in the dispersal capacity metric, with weak environmental structuring evident for strong dispersers. This differs from the conjecture of Heino (2013c) that strong dispersers would show the strongest environmental control and weak dispersers more spatial control. Of course, this depends on the scale of observation and connectivity between sites. The spectrum from dispersal limitation, to species sorting to mass effects (Heino et al., 2015b) should err on the side of dispersal limitation at large spatial scales and mass effects on fine spatial scales, with species sorting somewhat intermediate. Given the small spatial scale and high level of physical connectivity in our study, strong dispersers are likely to be structured more by mass effects, through overflowing into non-preferred habitats (Tonkin et al., 2015b). Findings such as these emphasise the benefit of using trait-based approaches to disentangle these relationships in metacommunity ecology.

Of the feeding groups, shredders exhibited the most coherent patterns. Thompson and Townsend (2006) found grazers (those that feed predominantly on periphyton) to be shaped by a combination of spatial and environmental control. Scrapers in our study displayed variable metacommunity structure, fluctuating between quasi-structures and random distributions. However, one clear pattern that emerged was the difference between short and long life cycle species, evident mostly in the turnover metric. Short life cycle species fit with the Gleasonian distribution best-fit model, whereas longer life cycle species did not show range turnover. This may be indicative of short-lived species tracking their currently available preferred conditions more efficiently (i.e. those present for the current population life cycle). Many aspects of the physical template of river systems are highly temporally variable, such as the hydrological regime (Resh et al., 1988) and associated substrate disturbance regimes (Tonkin and Death, 2012).

4.4. Temporal variability

Temporal variability was evident in the emergent metacommunity properties in our study across most groups, which is not an uncommon finding in stream systems (Göthe et al., 2013; Erős et al., 2013). Despite the Kinzig River being a relatively stable system, the high level of interannual variability in habitat conditions typical of river-floodplain systems can alter environmental gradients and thus may explain the high level of interannual variability observed in our data (somewhat answering Q3 despite the short timespan). While we can't specifically disentangle the relative importance of interannual variability compared to spatial variability, a previous study on this system found considerable variation in the microhabitat variables influencing communities, but suggested that overall land use was a more dominant structuring force than microhabitat conditions (Tonkin et al., 2015b). In fact, preceding flow conditions can determine the structure of stream metacommunities (Campbell et al., 2015). Thus short-lived species may reflect the conditions of the present year more accurately than species with longer life spans. Nevertheless, Lange et al. (2014) found a strong relationship between invertebrates with adult life durations of greater than a year and the percent of water abstraction. They argue this likely results from the ability of these long adult duration (mostly Coleoptera) species to withstand adverse instream conditions and recolonise new habitats.

5. Conclusions

Metacommunities remain difficult to predict, often with spatial and temporal variation in observed patterns, and processes acting differently on different subsets of organisms (Driscoll and Lindenmayer, 2009; Heino et al., 2012, 2015d; Tonkin et al., 2015a). Finding general patterns in stream metacommunities, in particular, has proven to be a major challenge for researchers (Heino et al., 2015a). We also found such context dependency in the present study with variation in emergent patterns between years and species groups at small spatial scales. Despite our expectation, we found little evidence of competition in trait groups (i.e. no checkerboarding), nor did we find nestedness, despite the non-pristine nature of the region. Instead, it appears abiotic conditions are structuring metacommunities but species are responding individually (i.e. Gleasonian or random distributions) to a variety of environmental filters in these river-floodplain metacommunities in an anthropogenically-dominated landscape. Moreover, the observed interannual variation in metacommunity structure points to temporal variability in environmental conditions driving assemblage distributions. Our approach unveiled a

variety of patterns in metacommunity structuring of these river-floodplain metacommunities, depending on the grouping level. The lack of differences between full communities across the aquatic-terrestrial ecotone but clear coherence and difference between trait groups for benthic invertebrates highlights the benefits of trait-based approaches for studying metacommunity patterns. Further studies should focus on disentangling context-dependent metacommunity patterns through the use of traits, highly replicated metacommunities at multiple spatial scales and multiple complementary methods (i.e. mechanistic and emergent matrix properties).

Conflict of interest statement

The authors declare that they have no conflict of interest.

Author contributions

JDT and SS conceived and designed the experiment; JDT analysed the data, wrote the manuscript and prepared the figures and tables; all authors contributed to drafts of the manuscript.

Acknowledgements

We thank three anonymous reviewers for constructive comments that helped improve this manuscript. SCJ acknowledges funding by the German Federal Ministry of Education and Research (BMBF) for "GLANCE" (Global change effects in river ecosystems; 01LN1320A).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecocom.2015.12.002>.

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