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Contrasting metacommunity structure and beta diversity in an aquatic-floodplain system

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Habitat connectivity and dispersal interact to structure metacommunities, but few studies have examined these patterns jointly for organisms across the aquatic–terrestrial ecotone. We assessed metacommunity structure and beta diversity patterns of instream benthic invertebrates, riparian carabid beetles (Order: Coleoptera; Family: Carabidae) and riparian spiders (Order: Araneae) at fifteen sites in a river-floodplain system. Sampling took place over a three-year period (2010–2012) in the Rhine-Main-Observatory LTER site on the Kinzig River, central Germany. This allowed disentangling the combined influence, and temporal variability, of habitat connectivity (i.e. between aquatic and terrestrial) and dispersal ability (i.e. between spiders and beetles, and aerial and aquatic dispersing invertebrates) on the dominant paradigms structuring these metacommunities. We found mostly consistent differences in the manner that metacommunities were structured between groups, with lower levels of variability explained for beetles compared to the other groups. Beetles were consistently structured more by turnover than nestedness components, with greater beta diversity than expected by chance and a minor spatial compared to environmental signal emerging with variance partitioning. Conversely, spiders and benthic invertebrates had lower beta diversity and greater nestedness than null expectation, and a clearer spatial signal controlling metacommunity structure. Our results suggest varying levels of mass effects and species sorting shape river-floodplain metacommunities, depending on habitat connectivity and dispersal ability. That is, greater connectivity and lower fragmentation along the river compared to the terrestrial zone promoted mass effects, and differences in overall dispersal ability and mode (i.e. active and passive) for instream and riparian communities shifted paradigms between mass effects and species sorting.

Metacommunity theory (Leibold et al. 2004, Holyoak et al. 2005) has facilitated a rapid expansion in empirical and theoretical research on the factors shaping communities connected through dispersal. Often the focus of metacommunity research is on differentiating patterns into one of the four original metacommunity paradigms (neutral, patch dynamics, species sorting (SS) and mass effects (ME); Cottenie 2005, Logue et al. 2011). The two most often examined and, in fact, invoked metacommunity paradigms, SS and ME (Cottenie 2005), primarily differ in the importance of dispersal in shaping metacommunity structure. In SS, species are expected to closely track preferred environmental conditions, which is dependent on organisms having an adequate dispersal ability. In the ME paradigm, dispersal processes are expected to potentially override habitat control through source–sink dynamics, leading to species also occupying unfavourable habitats (Leibold et al. 2004, Holyoak et al. 2005). Winegardner et al. (2012) recently argued that ME and patch dynamics are extensions of SS, reflecting differential control of dispersal (i.e. homogenisation versus limitation, respectively). Heino et al. (2015c) go on to suggest metacommunity research should focus on the relative roles of SS and dispersal, and hence a continuum from ME (small spatial scales and/or highly connected sites) to SS (intermediate) to dispersal limitation (DL; large spatial scales and/or disconnected).

Differences in the main paradigms shaping metacommunities are often a function of the connectivity of the environment and its association with dispersal (Heino et al. 2015c). At highly disconnected sites, it is likely that DL will shape communities (i.e. species do not fully track preferred conditions); at the other end of the spectrum, ME may occur with species flooding into non-preferred habitats (i.e. high dispersal rates) (Heino et al. 2015c). For instance, in river networks Brown and Swan (2010) suggested that isolated headwater stream communities are structured predominantly through SS, whereas mainstems are more influenced by ME through greater connectivity between local communities leading to a stronger spatial control. This may, in turn, lead to differential biodiversity in networks with a hierarchical structure such as rivers, where headwaters tend to support high beta diversity (Finn et al. 2011, Swan and Brown 2014), but more connected sites further down the network tend to support higher alpha diversity (Altermatt et al. 2013). Nevertheless,

where terrestrial areas may be subject to fragmented land use, rivers remain highly longitudinally connected along the river network (in the absence of man-made barriers), independent of the surrounding land use. Land use should therefore play a strong interactive role with dispersal mode in structuring stream and riparian metacommunities. Nonetheless, despite the key role land use plays in structuring stream community composition (Allan 2004), there are clear gaps in our understanding of how land use and dispersal interact in structuring stream metacommunities (Brown et al. 2011).

In a recent quantitative review, Soininen (2014) found SS to prevail at smaller spatial scales, where biogeographic processes are isolated. However, while environmental control has commonly been found to predominate over spatial control in stream systems (Siqueira et al. 2012, Göthe et al. 2013b, although there are exceptions to this), clear differences are often found between organisms with different dispersal modes and capabilities (Thompson and Townsend 2006, Grönroos et al. 2013, Canedo-Arguelles et al. 2015). This reflects the fact that benthic invertebrates comprise a wide range of dispersal abilities and modes, including flying and swimming/crawling. More capable dispersers, such as active aerial dispersers, may be able to reflect environmental conditions more clearly or, in highly connected habitats, actually override niche control through spreading into non-preferred habitats, leading to a stronger spatial signal. While benthic invertebrates harbor a range of dispersal modes, these differences in metacommunity dynamics may manifest more clearly when comparing aquatic and terrestrial species subject to clearly different dispersal strategies.

The riparian zone provides a unique ecosystem at the ecotone between terrestrial and aquatic ecosystems (Naiman and Henri 1997). Reciprocal flows of energy, nutrients and various materials strongly tie aquatic and terrestrial systems (Polis et al. 1997, Soininen et al. 2015), particularly for running waters and their adjacent riparian or floodplain zones (Baxter et al. 2005). Through their interaction with the aquatic environment, including flood and drought regimes, floodplains support highly heterogeneous habitat conditions, in turn supporting high levels of biodiversity (Tockner and Stanford 2002), including specialist ground-dwelling organisms such as carabid beetles and spiders (Bonn et al. 2002). These organisms are influenced by a similar set of environmental conditions in the floodplain area of river systems (Lambeets et al. 2008), such as the flood regime (Bonn et al. 2002) and microspatial heterogeneity (Antvogel and Bonn 2001). Nevertheless, clear differences exist in the long-distance dispersal strategies of these organisms, with spiders depending largely on semi-passive dispersal through 'ballooning' (Wise 1995); many are also susceptible to passive downstream drift dispersal through hunting on the water, but with little evidence of cross-river exchange (Lambeets et al. 2010). Conversely, carabid beetles are active dispersers, often with well developed flight ability (Bonn 2000). These differences likely translate into differences in the spatial and environmental control on these metacommunities. For instance, spiders should be more spatially structured (ME) through their enhanced passive, and thus non-selective, dispersal ability and the predominant along-river wind transport. This contrasts to carabid beetles, which, with their strong flying ability, are able to actively disperse and respond to flooding regimes (Bonn 2000), more effectively selecting preferred habitats in the riparian zone (reflecting SS, but not so strong as to lead to ME).

The relative importance of local- and regional-scale influences depends on several factors, particularly the scale of observation (Mykrä et al. 2007), and the relationship between environmental heterogeneity and beta diversity is highly scale dependent (Heino et al. 2015b). While small-scale environmental factors are merely a subset and finer resolution of factors at larger scales, the grain size of assessment may allow disentangling of multiple scales of influence. Previous research has found strong associations between local-scale variables and stream communities (Astorga et al. 2011, Tonkin 2014), but given the importance of the regional species pool on local communities (Poff 1997, Heino et al. 2003, Stoll et al. 2013, Tonkin et al. 2014b), it is clear that larger-scale factors are also fundamental. Thus, drivers of local stream communities manifest at a variety of spatial and temporal scales (Heino 2009).

Given the uncertainties regarding the importance of local habitat versus spatial control, differences in dispersal ability, and the connectivity of habitats on metacommunity dynamics, we examined metacommunity structure at fifteen sites in a river-floodplain system for both instream and terrestrial invertebrates over a three-year period. Specifically, we examined temporal variability in metacommunity structure of instream benthic invertebrates, riparian carabid beetles and riparian spiders in the Kinzig River (Rhine-Main-Observatory LTER site), central Germany between 2010 and 2012. Environmental control should be highest where dispersal rates are intermediate; this control may be weaker in highly connected sites (e.g. within a stream) where dispersal processes may override local environment (ME), or disconnected sites (e.g. across biogeographic regions) where DL inhibits species' ability to track their preferred conditions (Heino et al. 2015b, c). In this system, instream communities are highly connected through both active (swimming, crawling, flight) and passive dispersal (drift) and the longitudinal transport of water, compared to the more fragmented riparian and surrounding terrestrial zone (land use in this system is highly heterogeneous). We therefore expect differences in the physical connectivity (between aquatic and terrestrial) and dispersal ability (between spiders and beetles) would alter the dominant paradigms structuring these metacommunities. Nevertheless, we acknowledge that there are a range of dispersal modes and abilities of benthic invertebrates. We, therefore, also compared patterns between aerial active and aquatic dispersing benthic invertebrates.

Specifically, based on these points and our understanding of other factors shaping metacommunities, we formed and tested the following hypotheses. H_1: Spatial control would predominate on benthic invertebrates and spiders (ME), whereas SS would prevail in carabid beetles. Moreover, SS would be more important for structuring aquatic compared to aerial active (ME) dispersing benthic invertebrates. H_2: A greater ME control would lead to reduced beta diversity (homogenisation) for invertebrates and spiders compared to carabid beetles, which are structured more strongly by SS. H_3: H_1 and H_2 would lead to beta diversity more structured by nestedness for invertebrates and spiders, compared to spatial turnover shaping riparian carabid communities due to

land use fragmentation. H_4: More evidence would emerge for the surrounding broad-scale land use structuring riparian carabid beetle communities than benthic invertebrates or spiders. This would occur through a closer association with microhabitat conditions for beetles (SS) compared to ME control (spiders). As 1) few studies have examined temporal patterns in stream metacommunity structure (but see Erős et al. 2012, 2013), and 2) we were restricted to three years of data, we did not form a specific hypothesis regarding temporal variation in patterns.

Methods

Study site

The Rhine-Main-Observatory (RMO) is a long-term ecological research (LTER) site, situated on the Kinzig River, as part of the German LTER (LTER-D) network. The Kinzig River is situated in the central German state of Hesse, flowing through a variety of land uses, including forest, agricultural and urban. We sampled fifteen sites along a ~30-km stretch of the Kinzig River as part of the RMO, from one of three pre-defined land-use types (five sites in each): forest, open/pasture, and urban (Supplementary material Appendix 1 Fig. A1). Sites are arranged along the mainstem of the river, but with uneven spacing between, and thus differential spatial arrangement of sites along the network (Supplementary material Appendix 1 Fig. A1). Moreover, given the sinuosity of the river, aquatic and terrestrial dispersers are subject to different dispersal routes, depending on whether the river channel is used for dispersal or not. Land use along this segment is highly fragmented, creating a fragmented dispersal route for overland dispersers. We sampled each site once in late summer in each of three years consecutively from 2010 to 2012. Sites span a 100-m longitudinal reach of the river and spread laterally 30 m each side of the river from the centre point (ca 6000 m^2 area).

Sampling

Instream

We sampled benthic macroinvertebrates following the German EU Water Framework Directive (WFD) compliant multi-habitat sampling protocols (Haase et al. 2004). This involved taking 20 sub-samples from multiple instream habitats, representing the range of aquatic habitats available at the site (Table 1). That is, all available microhabitats in the 100-m long reach were first recorded in 5% coverage units, and each sampling unit (25 × 25 cm) sampled with a 0.5-mm mesh kick net. These samples were then pooled for later analysis (1.25 m^2 total sampling area). We stored samples in 70% ethanol for later identification in the laboratory, using the German WFD-compliant operational taxon list (Haase et al. 2006) as the level of taxonomy for identification. Using this method, most organisms are identified to either species or genus, with only few difficult taxa identified at higher levels. The microhabitat values were recorded (in percentage cover) for use in subsequent analyses (Table 1). Some of these microhabitat variables were grouped for analysis, resulting in five substrate size classes, artificial substrates, algae, macrophytes, terrestrial plants, deadwood, CPOM and FPOM (coarse and fine particulate organic matter, respectively), saprobic, and non-woody debris.

Table 1. List of terrestrial and aquatic microhabitat variables used in the analysis.

Terrestrial		Aquatic	
Variable	Abbreviation	Variable	Abbreviation
Annuals	ANN	Algae	ALG
Bare	BAR	Artificial	ART
Deadwood	DWD	CPOM	CPM
Forest ground cover	FGC	Deadwood	DWD
Garden	GAR	FPOM	FPM
Grass mown	GRM	Gravel	GRV
Grass not mown	GRN	Large substrate	LSU
Hard substrate	HSU	Macrophyte	MPY
Shrubs	SHR	Medium substrate	MSU
		Non-woody debris	NWD
		Sand	SAN
		Sapropel	SPR
		Silt	SIL
		Terrestrial plants	PLT

Riparian

We sampled riparian spiders (Order: Araneae) and carabid beetles (Order: Coleoptera; Family: Carabidae) using 5.5-cm diameter pitfall traps in the riparian zone. We used eight traps at each location, covering the range of terrestrial microhabitat conditions at each site (Table 1). We left traps in situ for two weeks in August each year, filled with Renner solution to kill and preserve organisms. We removed any juvenile spiders from the analyses. Each year, the traps were set up in the same locations.

Each year, the presence or absence of different microhabitat structures was assessed within a radius of three meters around each pitfall trap when setting the traps. Several microhabitat structures can be present in each zone. The following nine microhabitat structures were differentiated: bare soil, regularly mown grassland, not mown grassland, tall forb stands (annuals), shrubs, forests ground cover, dead wood (size larger than pencil), garden horticultural areas and artificial hard substrates. For the analyses, these variables were converted into a percentage of presence across all eight replicate trap locations (i.e. 3-m radius around the pitfall trap). That is, if a particular microhabitat structure was present in all eight locations, it had a value of 100%. The riparian zone varies substantially between sites, subject to, and somewhat reflecting, the surrounding land use (i.e. forest, pasture and urban).

Statistical analyses

Diversity patterns

We compared alpha diversity (taxonomic richness) and beta diversity between years for each organism group. To assess beta diversity, we used the betadisper function in 'vegan', based on the PERMDISP2 method (Anderson 2006). We used distance to group centroid as the method of assessing variability, based on Bray–Curtis distances on abundance data. We tested for differences in alpha diversity between

years for each group using one-way ANOVA and, where significant, tested for post hoc differences between individual years with Tukey's HSD test (*R* function Tukey-HSD). To examine difference between years in beta diversity (dispersion), we used a permutation test, with 999 permutations. As it is not relevant to compare raw diversity measures directly between the different groups, we did not test for differences statistically.

Null model analysis

To examine if beta diversity patterns of different organism groups were structured more through nestedness or turnover, we partitioned beta diversity into these two components (β_{SNE} and β_{SIM}, respectively), as well as overall Sorensen beta diversity (β_{SOR}), following the methods of Baselga (2010). We assessed whether these partitions were greater or less than expected by chance through comparison with null matrices, using 10 000 permutations. We constrained the null matrix using the R1 (fixed-incidence proportional) method, using the oecosimu function to run the simulations, and the nestedbetasor function to partition beta diversity in the 'vegan' package. These analyses were performed on species presence–absence data. This method uses the standardised z-score to examine if values in the observed data are greater than those expected by chance (null model) from the 10 000 permutations.

Additionally, as an indication of community turnover between years we compared temporal beta diversity using the beta.temp function on presence–absence data in the 'betapart' package (Baselga and Orme 2012). We used raw values of the turnover component of beta diversity (β_{SIM}), rather than comparing against a null model, and focused on year-to-year variability (2010–2011 and 2011–2012). For simplicity, we took the mean of all fifteen site turnover values to compare overall turnover between groups.

Spatial variables

We created a set of spatial vectors to represent the distribution of the fifteen sites in space along the river network using principal coordinates of neighbour matrices (PCNM) (Borcard and Legendre 2002) with the pcnm function in the 'vegan' package. This method transforms spatial distances based on a distance matrix into rectangular data for use in constrained ordination methods. To do this, we used geographic locations (i.e. latitude and longitude, rather than the along-river network distance) to create a Euclidean distance matrix. We restricted our distance measure to Euclidean (i.e. overland/direct) distance, as 1) we wanted to capture a distance relevant to both aquatic and terrestrial organisms, and 2) recent work has shown overland and watercourse distances correlate similarly with benthic invertebrate community dissimilarity (Kärnä et al. 2015). As we were interested in the main gradients of spatial structure, combined with the relatively linear arrangement of sites, we limited our focus to the first four PCNM vectors for our analyses (Supplementary material Appendix 1 Fig. A2). While sites were arranged along a single stem of the river, the arrangement is not strictly linear, with considerable sinuosity, and the spacing of sites is clumped (Supplementary material Appendix 1 Fig. A1). Therefore, the use of PCNMs is appropriate to generate spatial vectors in this dataset.

Variance partitioning

Prior to the following analyses, community data were Hellinger transformed as per Legendre and Gallagher (2001) using the decostand function in 'vegan' (Oksanen et al. 2013).

To examine the relative influence of spatial and local microhabitat variables on structuring community composition of the three groups, we employed a variance partitioning procedure (Borcard et al. 1992, Peres-Neto et al. 2006). This method uses partial redundancy analysis (pRDA) to partition the variation into the pure components of space, microhabitat and their shared contribution to the explanation of community structure. This was performed using the varpart function on Hellinger-transformed community (abundance) data in 'vegan'. We examined the amount of variation explained by each matrix (space or microhabitat) using the adjusted R^2. Before settling on a final pRDA model, to factor out highly multicollinear variables we ran RDA analyses on the full suite of microhabitat variables and excluded those with a variance inflation factor (VIF) greater than 10 sequentially, starting from the variable with the largest VIF.

To further examine the importance of dispersal mode on structuring benthic invertebrate metacommunities using variance partitioning, we also compared dispersal modes of benthic invertebrates by grouping into aerial active and aquatic dispersers. To do this, we used trait data compiled as part of the EU STAR project (Bis and Usseglio-Polatera 2004, Furse et al. 2006), where dispersal trait modalities are assigned scores on a scale of 0–3. Zero represents no affinity and three represents high affinity of a particular species for the dispersal trait modality. In this case, four dispersal modes are available: aerial active, aerial passive, aquatic active and aquatic passive. More than one trait modality can be assigned to a species for the same trait. For example, a species can have non-zero scores for both active aquatic and active aerial dispersal modalities. To form the two dispersal groups, any species with an aerial active affinity score of two or three was considered an aerial active disperser. In our data, if a species had a non-zero aerial passive score, it also had an affinity for either of the aquatic dispersal modes. Therefore, all remaining species were considered aquatic dispersers.

Ordinations

To examine the consistency of community patterns through years, as well as the importance of microhabitat variables and land use type on these patterns, we used ordinations on each community for each year. This allowed us to gain an understanding of the importance of overall land use structure compared to specific microhabitat variables. That is, if important microhabitat variables fluctuate year-to-year, it would imply communities are more structured by the larger-scale land use type.

Rather than focus on the constrained ordinations, we chose to examine the community patterns in unconstrained spacing using non-metric multidimensional scaling (nMDS) ordinations. We ran these using the metaMDS function in 'vegan', using Hellinger-transformed abundance data and Bray–Curtis distances. We examined the influence of coarse land use structure by fitting categories with ellipses (standard error, 99% confidence interval) and testing for significant

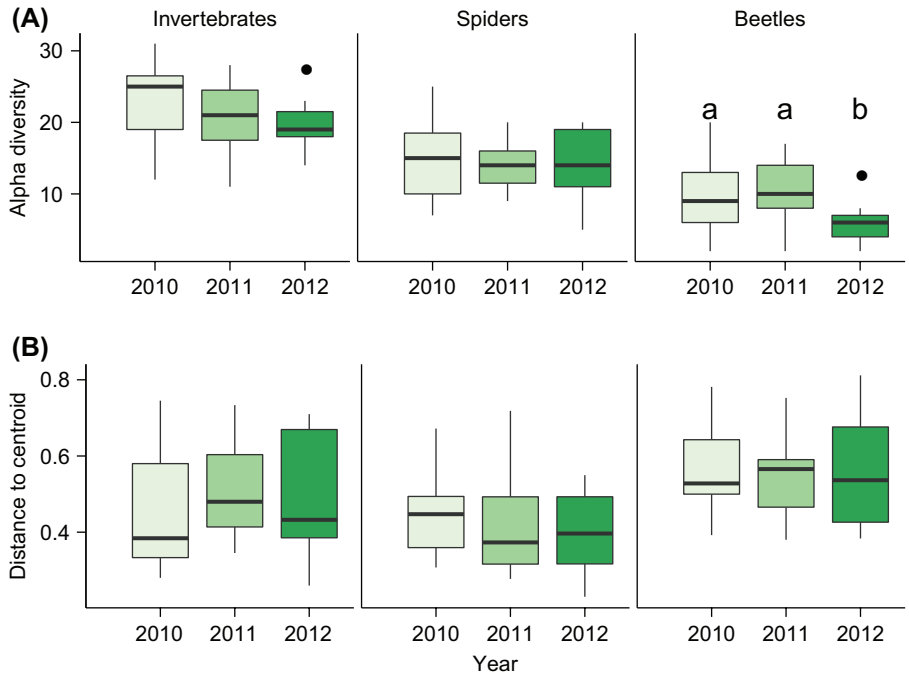

Figure 1. Alpha (A) and beta (B) diversity of instream macroinvertebrates, riparian carabid beetles and riparian spiders sampled from 15 sites annually between 2010 and 2012 in the Rhine-Main-Observatory, central Germany. Beta dispersion (based on Bray–Curtis distances on abundance data) was used to calculate beta diversity with the distance to group centroid as the method. A higher distance to centroid represents higher beta diversity. Only alpha diversity of beetles changed interannually ($p < 0.05$), with letters on the plot indicating the results of Tukey's HSD post hoc test.

differences with PERMANOVA using the adonis function in 'vegan'. We then fitted vectors of all microhabitat variables with $p < 0.05$, using the envfit function in 'vegan'.

All statistical analyses were performed in R ver. 3.0.2 (<www.r-project.org>).

Data deposition

Data available at <http://data.lter-europe.net/deims/site/LTER_EU_DE_018>

Results

Diversity patterns

Alpha and beta diversity were relatively stable interannually, with no differences for either benthic invertebrates (alpha: $F_{2,42} = 1.457$, $p = 0.244$; beta: $F_{2,42} = 0.503$, $p = 0.617$) or spiders (alpha: $F_{2,42} = 0.109$, $p = 0.897$; beta: $F_{2,42} = 0.480$, $p = 0.605$; Fig. 1). Nevertheless, beetle richness was lowest in 2012, but no change in beta diversity was evident (alpha: $F_{2,42} = 4.186$, $p = 0.022$; beta: $F_{2,42} = 0.174$, $p = 0.844$; Fig. 1). Benthic invertebrates exhibited contrasting patterns in alpha and beta diversity, with a lower beta diversity (measured as mean distance to group centroid) when alpha diversity was higher. Beetles had the highest beta diversity compared to the other groups, and spiders the lowest.

These lower values for beta diversity of benthic invertebrates and spiders, measured as distance to group centroid on abundance data, were reflected in the null model analysis of presence–absence data. That is, lower Sorensen diversity value than expected by chance, although these were not significant, based on the permutation tests (Fig. 2). Contrary to this, beetles had significantly higher Sorensen beta diversity than the null models in 2010 and 2012, but non-significantly higher in 2011. Beta diversity of invertebrates and spiders was structured by nestedness rather than turnover, although this was only significant for invertebrates across the three years. Beetle distributions, on the other hand, were driven by turnover between sites, although the strength of this differed year to year, with considerably higher turnover in 2012 (Fig. 2). Temporal turnover in community composition was greater for beetles (β_{SIM}: 2010–2011 = 0.44; 2011–2012 = 0.41), than for spiders (β_{SIM}: 2010–2011 = 0.36; 2011–2012 = 0.36) or benthic invertebrates (β_{SIM}: 2010–2011 = 0.38; 2011–2012 = 0.39).

Variance partitioning

In general, there was a stronger spatial or shared space and habitat control for benthic invertebrates and riparian spiders, compared to carabid beetles (Fig. 3). This was also reflected in a higher overall variance explained for these two groups. Spiders, in particular, were the best-explained group, reflecting a clear joint control of spatial processes and local microhabitat. Combined microhabitat and space were only able to explain 16–23% of the variation in beetle community structure compared to 55–60% for spiders and 37–62% for benthic invertebrates (Fig. 3). Breaking benthic invertebrates into dispersal groups indicated that aerial active dispersers were more clearly structured by spatial variables than aquatic

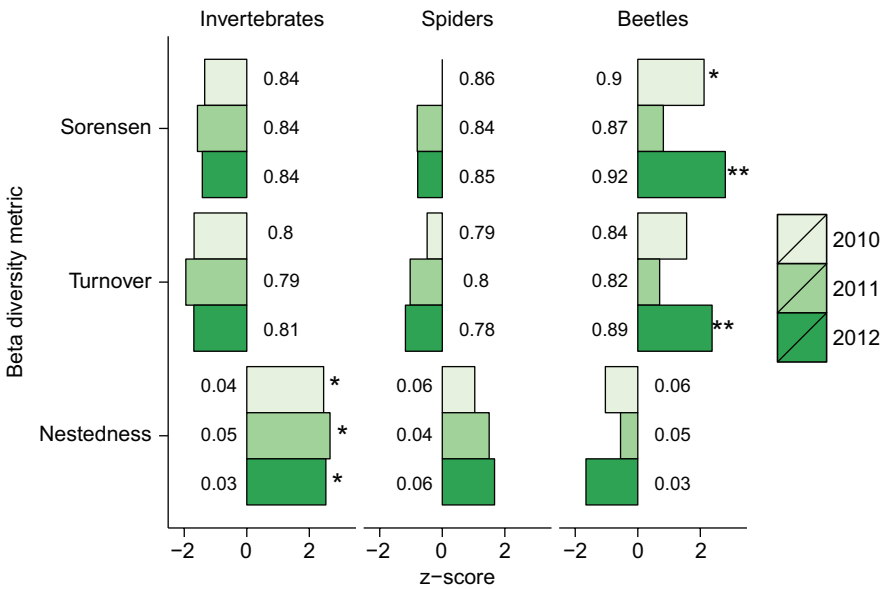

Figure 2. Results of partitioning beta diversity into overall (Sorensen), and turnover and nestedness components of beta diversity for instream macroinvertebrates, riparian carabid beetles and riparian spiders sampled from 15 sites annually between 2010 and 2012 in the Rhine-Main-Observatory, central Germany. Analyses are based on presence–absence data. Displayed with bars are z-scores resulting from comparison with 10 000 simulated communities, using the R1 method to constrain the null matrix. A higher z-score represents higher value for that facet of beta diversity than expected by chance and vice versa. Raw Sorensen, turnover and nestedness metrics are displayed as text corresponding with each bar. Significance of z-scores are indicated with asterisks. $^{**}p < 0.01$, $^{*}p < 0.05$.

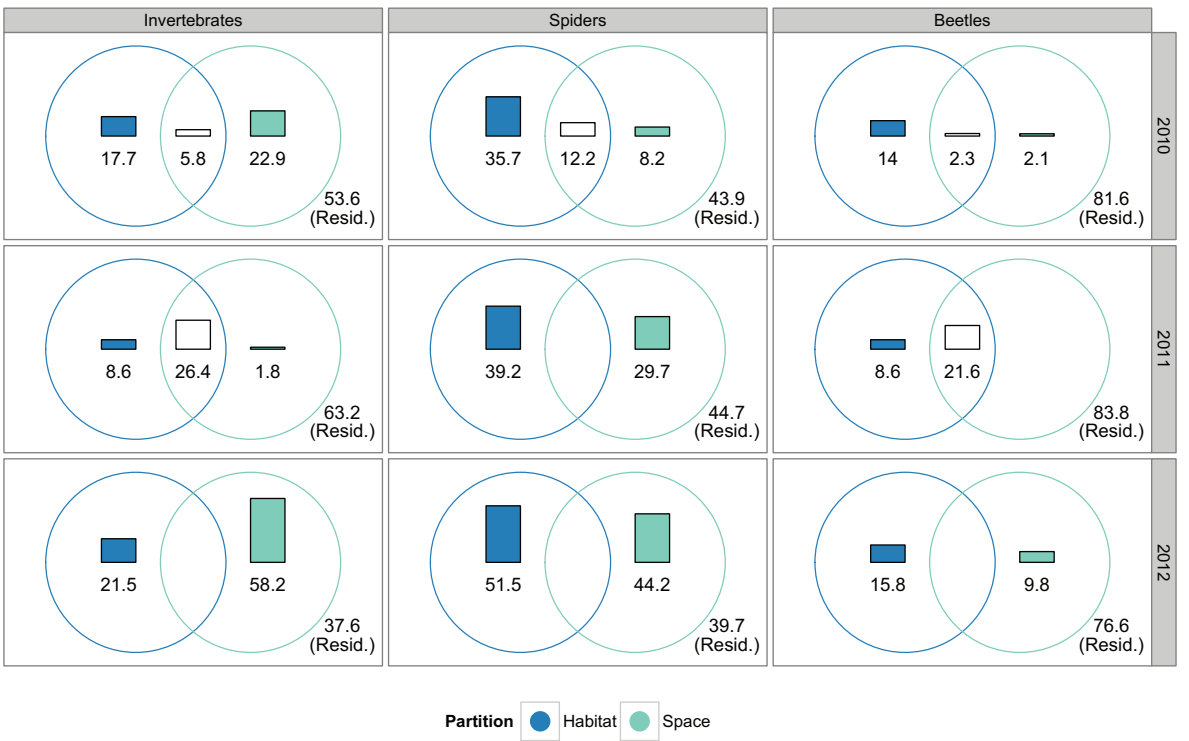

Figure 3. Results of variance partitioning analysis between environmental and spatial variables and community composition. Analyses are based on Hellinger-transformed abundance data for instream macroinvertebrates, riparian carabid beetles and riparian spiders sampled from 15 sites annually between 2010 and 2012 in the Rhine-Main-Observatory, central Germany. The plot indicates the amount of variation (%; Adj. R^2) in the community composition data explained by microhabitat variables, coarse level spatial influences (first four principal coordinate of neighbour matrices; PCNM), and the shared variance between habitat and space, as well as the remaining unexplained variance (Resid.). The full variance explained by the model is 100-residual variance. Negative values are not shown, thus some plots may sum to > 100.

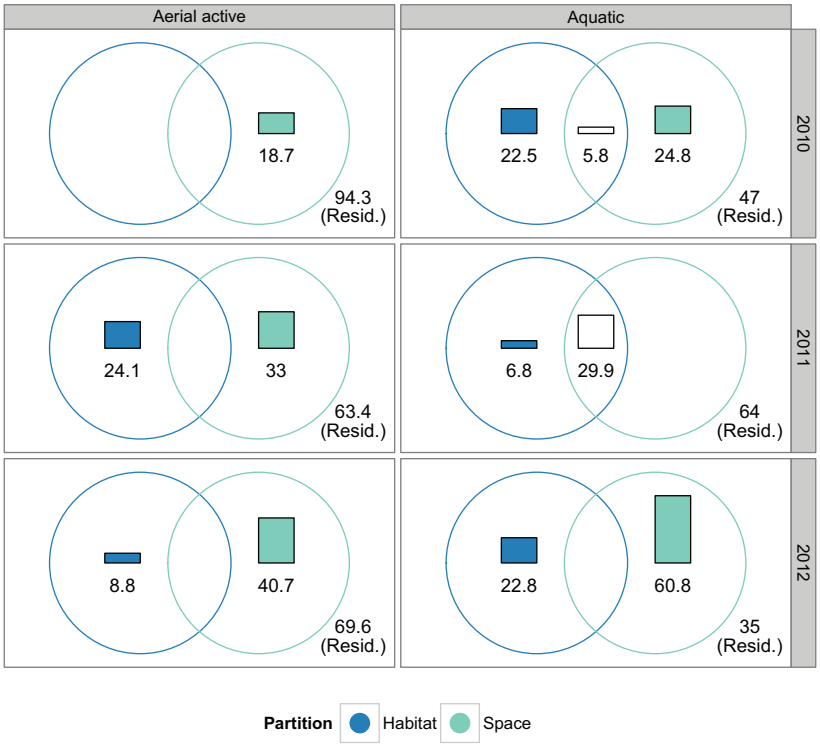

Figure 4. Results of variance partitioning analysis between environmental and spatial variables and community composition for instream macroinvertebrate dispersal groups. Analyses are based on Hellinger-transformed abundance data for aerial active and aquatic dispersers sampled from 15 sites annually between 2010 and 2012 in the Rhine-Main-Observatory, central Germany. The plot indicates the amount of variation (%; Adj. R^2) in the community composition data explained by microhabitat variables, coarse level spatial influences (first four principal coordinate of neighbour matrices; PCNM), and the shared variance between habitat and space, as well as the remaining unexplained variance (Resid.). The full variance explained by the model is 100-residual variance. Negative values are not shown, thus some plots may sum to > 100.

dispersers (Fig. 4). Moreover, habitat and spatial variables were able to explain much greater combined variation for aquatic (36–65%) compared to aerial active dispersers (6–37%; Fig. 4).

Ordinations

All nMDS ordinations fit the data well (2D stress < 0.13). Beetles and spiders were more clearly clustered into land-use sections along the river compared to the benthic invertebrates, although sites still tended to cluster into the three groups (Fig. 5). In particular, the most obvious differences for riparian communities were between forest and pasture sections, whereas for benthic invertebrates, forest and urban sites were more separated in ordination space. All groups across all years were significantly clustered into the surrounding land use groups except for benthic invertebrates in 2012 (PERMANOVA $p < 0.05$). Forest communities were most consistently tightly grouped, whereas urban communities were highly variables for both aquatic and terrestrial communities.

Important microhabitat variables tended to fluctuate from year to year, particularly for benthic invertebrates (Fig. 5). Grass predominated as an important microhabitat variable in the riparian communities, as did forest ground cover. These microhabitat variables aligned with the broader land use categories of pasture and forest.

Discussion

We examined biodiversity patterns as well as spatial and environmental (microhabitat) control on metacommunity structure in a river-floodplain system, with three organism groups comprising clearly different dispersal modes. We also examined differences in benthic invertebrates with different dispersal modes (i.e. aerial active and aquatic). Riverine landscapes are highly heterogeneous in space and time, which is reflected in their biodiversity patterns (Robinson et al. 2002, Ward et al. 2002). However, within the three year period examined, we found stability in metacommunity structuring, although the importance of habitat and spatial variables did fluctuate for benthic invertebrates. Of the three groups, it was in fact riparian beetles that exhibited the strongest temporal turnover in community composition. While stream metacommunity patterns have been found to be highly context dependent (Heino et al. 2012, 2015a, Tonkin et al. 2015a), few studies have examined temporal variability in stream metacommunity patterns. However, Erős et al. (2012) and Erős et al. (2013) examined temporal variability in freshwater fish metacommunity structure and found clear variation through time using various approaches.

Species sorting or mass effects?

Our results indicate a higher level of spatial control on benthic invertebrates and spiders than carabids and thus

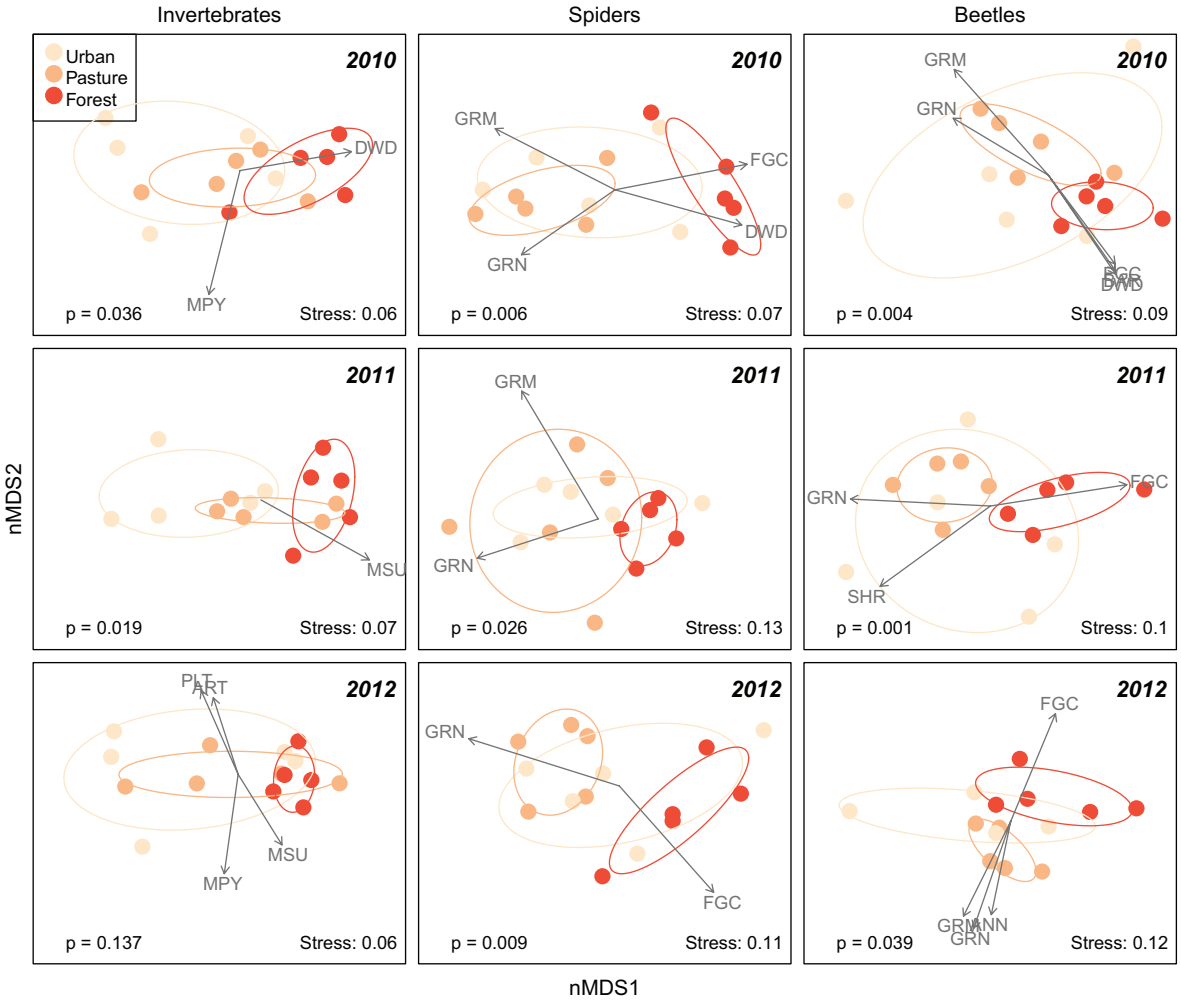

Figure 5. Non-metric multidimensional scaling (nMDS) ordinations (based on Hellinger-transformed abundance data and Bray–Curtis distances) for instream macroinvertebrates, riparian spiders and riparian carabid beetles sampled from 15 sites annually between 2010 and 2012 in the Rhine-Main-Observatory, central Germany. Sites are colour coded based on surrounding land use and land use groups are encircled in ellipses based on standard errors with 99% confidence limits. Vectors display significantly correlated microhabitat variables with community structure. Arrows indicate the direction of maximum change in a variable, with the length being proportional to its rate of change. p-values represent significance of PERMANOVA tests comparing group differences between the three land use types. 2D stress values are given in the bottom right of plots. Notes: Microhabitat variables are all based on percentage cover. See Table 1 for abbreviations of microhabitat variables.

provide some support for our primary hypothesis (H_1) that ME would predominate for these groups. While spatial signal can represent either ME or DL (Heino et al. 2015c), the small spatial scale examined here and the lack of dispersal barriers, points strongly to ME, which can have a strong homogenising effect, rather than DL. This was evidenced by greater beta diversity values using both abundance and presence–absence data (Fig. 2, 3). Stream organisms are typically more strongly structured by environmental than spatial variables (Landeiro et al. 2012, Siqueira et al. 2012, Göthe et al. 2013b), but this depends on the scale of observation, as well as being particularly dependent on dispersal traits (i.e. mode and capacity) (Thompson and Townsend 2006).

We found clearer evidence of ME for active aerial dispersers, with low overall variability explained, compared to aquatic dispersers, when considering dispersal modes of benthic invertebrates. These patterns, of course, depend on the spatial scale of observation, with our study being limited to a small spatial extent. Similarly, Thompson and Townsend (2006) found weak patterns for strong dispersers, but weak and moderate dispersers were predicted by a combination of environmental and geographical factors. Contrarily, Grönroos et al. (2013) found active aerial dispersers showed a stronger environmental control than either passive aquatic or aerial dispersers suggesting a better ability to track preferred conditions, but their metacommunities covered greater spatial extents than ours and also considered more complex river networks. Using distance decay relationships, Canedo-Arguelles et al. (2015) recently found strong dispersers did not exhibit a pattern in response to local and regional factors, whereas local and weak disersers reflected local-scale factors, and intermediate dispersers reflected landscape-scale factors.

The stronger spatial signal for instream and spider communities is likely a function of two factors directly related to the physical connectivity of sites: First, instream communities are strongly linked through both active (swimming,

crawling, flight) and passive dispersal (drift) and the longitudinal transport of water, compared to the more fragmented riparian zone in terms of major habitat conditions. Second, spiders harbour an enhanced passive and non-selective dispersal ability through ballooning (Wise 1995), and also through downstream drift for certain species that forage on the water surface, although little interbank exchange may occur (Lambeets et al. 2010). Spiders are thus well dispersed by wind (and have been known to travel significant distances in the air), which predominantly travels along river networks, facilitating a homogenisation of communities. On the other hand, carabid beetles have an enhanced flying ability, enabling them to effectively and actively disperse and respond to flooding regimes (Bonn 2000), thereby allowing selection of preferred habitats (SS). Moreover, it is important to consider here that differences in sampled environmental variables between the aquatic and terrestrial environments may have influenced differences in the relative importance of environmental variables in this study.

The greater spatial control was reflected in beta diversity patterns of spiders and benthic invertebrates, suggesting ME was more apparent in shaping these two groups compared to beetles. Beta diversity of these two groups was lower than beetles and much lower than expected through random assembly (i.e. null models), and this beta diversity indicated greater nestedness than chance expectation, particularly for benthic invertebrates (H_2 and H_3 partially supported). Nevertheless, it is important to bear in mind that the method we applied has been shown to detect the nestedness component in the absence of nestedness (Carvalho et al. 2013). Moreover, while we employed a null model approach, an important consideration is that nestedness is likely affected by the phylogenetic differences between the three groups. For instance, carabid beetles are limited to one Family, whereas benthic invertebrates consider multiple families, potentially altering the strength of patterns emerging. Nevertheless, it appears in this case that ME, an extension of SS indicating a homogenising effect of dispersal on local communities (Winegardner et al. 2012), exerted the strongest influence on benthic invertebrate communities, but spider communities were governed by factors more at the SS end of the spectrum. That is, connectivity and dispersal control did not override niche control on spider communities, but that dispersal was adequate for species to track their preferred conditions.

There was some evidence of SS structuring beetle communities, with a much greater environmental control compared to spatial influence, but the variability explained was low. Gerisch (2011) found little evidence of spatial control on riparian carabid communities, with little clustering in community composition, suggesting a strong environmental control or SS. The small spatial signal for these organisms, coupled with 1) the small spatial scale, and 2) the fact that spatial variables should be important if communities are indeed dispersal limited, suggests a lack of either ME or DL as a structuring paradigm. These riparian systems are highly stochastic, thus for organisms to track their preferred conditions, adequate dispersal is required to recolonise post-flooding. In fact, natural flow regimes enable the maintenance of patches within floodplain mosaics, which enables the maintenance of ground-dwelling arthropod biodiversity in these systems (Datry et al. 2014). However, riparian carabid communities can recover rapidly from flood disturbances, given their well developed flying ability (Bonn 2000, Bonn et al. 2002), and the higher temporal beta diversity we found for beetles may be somewhat reflecting this ability to actively respond to local condition changes. Thus, DL should not be occurring for these organisms.

Without some form of DL, the low overall variation explained is puzzling as it suggests organisms are indeed not tracking their preferred environmental conditions. However, our results suggest these communities were strongly structured by turnover between locations, so it may be that the abiotic microhabitat variables were not important in explaining their preferred niches, and the most important niche variables for carabids went unmeasured. Given the importance of the flood regime for these organisms (Bonn et al. 2002), one possible candidate variable would be the site-based susceptibility to inundation. The turnover component of beetles increased when local richness decreased in 2012, leading to strong spatial turnover in communities, but this did not clearly alter the variance partitioning patterns in 2012. Nevertheless, the consistently lower alpha diversity of beetles compared to the other groups likely contributed to their low overall explained variability. A recent quantitative review by Soininen (2014) highlighted that while SS may be prevalent in natural communities (Cottenie 2005), the overall influence may be relatively weak as an independent force. Biotic interactions are often a missing element in metacommunity studies of this nature (Göthe et al. 2013a, Soininen 2014), and we cannot rule this out as an important influence in our study. This is particularly the case for carabids and spiders, which directly compete for food. Future work on metacommunities should also incorporate biotic interactions (e.g. grazer abundance: Göthe et al. 2013a) as these may be important drivers of local community patterns. One final potential explanation would be historical land use (Harding et al. 1998), which may also represent some of the spatial structuring in these metacommuniies.

Microhabitat versus surrounding land use

Our results supported H_4 in that the surrounding land use had a clear structuring role on the communities, particularly in the riparian zone. According to the nMDS ordinations and associated tests, the surrounding land use was less important for structuring instream communities. Several factors are likely operating to produce this pattern: First, instream sites are less directly influenced by lateral than upstream processes. Second, microhabitat structure is a critical factor governing benthic invertebrate community assemblages, particularly regarding the structure or complexity of habitat-forming living material, such as macrophytes, bryophytes and periphyton (Costa and Melo 2007, Louhi et al. 2011, Tonkin et al. 2014a). Nevertheless, overall land use structure tended to consistently group out sites in ordination space, suggesting that while microhabitat influences were important, large-scale environmental control was most important in structuring these communities. Indeed, previous research on this system showed a clear influence of these broad land use categories, with alternative influences on the coupling between the three organism groups (Tonkin et al. 2015b). There is ongoing debate over the importance of local

and regional-scale variables on community structure, but of critical importance is the scale of observation (Mykrä et al. 2007, Astorga et al. 2011).

For the riparian communities, where the land use grouping was clearer, forest and pasture sites were more clearly separated, with urban sites often intermediate between the two. However, for instream communities, the clearest division was between urban and forest, with pasture sites being highly variable. While streams are typically highly heterogeneous within drainage basins (Heino et al. 2012), our sampling took place along a relatively homogeneous section of river, thus instream sites were likely more environmentally similar than the riparian sites. Beta diversity is dependent on environmental heterogeneity, as has been shown recently for stream invertebrates (Astorga et al. 2014). The lower beta diversity of instream organisms in the present study is thus likely reflecting this lack of habitat variability. This is to be expected as environmental gradients tend to increase with increasing stream order, hence the trend of decreasing beta diversity progressively downstream (Finn et al. 2011). This is particularly important as heterogeneous landscapes may allow for greater population persistence in climatically extreme conditions, providing a source pool of organisms for recovery from disturbance (Piha et al. 2007).

Microhabitat variables typically reflected surrounding land use in terrestrial ordinations, although there was some fluctuation in important variables between years. This is to be expected in a dynamic floodplain environment, and further supports the fact that large-scale environmental is control having a more consistent structuring influence than microhabitat. Beetles were more clearly grouped into land use sections of the river, reflecting a greater control of the surrounding environment, or a weaker ability to track preferred microhabitat conditions. Small-scale environmental conditions and microspatial heterogeneity may be particularly important for these organisms. Antvogel and Bonn (2001) found soil moisture, leaf litter cover and light intensity to be the main environmental drivers of alluvial carabid communities and emphasise the importance of microspatial heterogeneity for their distributions. Nevertheless, Bonn et al. (2002) found riparian spiders were structured more strongly by differences in habitat structure compared to carabid beetles, which were more strongly influenced by different flood regimes. They suggest that spiders tend to use the three-dimensional structure of their habitat more than ground beetles, but based on the variables we used, we found little difference in the important microhabitat variables shaping their presence. It remains clear that riparian ground beetle communities are maintained by a complex suite of environmental influences, particularly the flood regime, which interact with life history characteristics related to their ability to respond to disturbance regimes (Gerisch 2011).

Differentiating between DL, ME and SS is of fundamental importance, not only for enhancing our basic understanding, but for practical reasons, including biomonitoring and restoration (Heino et al. 2015c). Recent work clearly demonstrated that the response of stream communities to restoration was highly dependent on the availability of colonists in the surrounding regional pool, particularly the distance to the nearest colonist and species ubiquity (Stoll et al. 2014, Tonkin et al. 2014b). In their studies, these factors were the overriding drivers of restoration response. Thus, it is likely that DL was limiting the ability of certain species to colonise, but differentiating between SS and ME is difficult. To fully comprehend the utility of habitat restoration on local communities, we need to understand the mechanisms in which communities are assembling in space.

Conclusions

We tested the combined influence of habitat connectedness (aquatic versus terrestrial) and dispersal capacity (riparian beetles versus spiders, and aerial versus aquatic dispersing benthic invertebrates) on metacommunity structure in a low-mountain river-floodplain system. Using a set of locations sampled consistently over three years allowed the examination of interannual variability in patterns, and mostly consistent differences were found in the ways that metacommunities were structured between groups. Our results suggest some differentiation between ME and SS shaping river-floodplain metacommunities, depending on habitat connectivity and dispersal ability. First, greater connectivity and lower habitat fragmentation along the river compared to the surrounding terrestrial environment led to ME being the main structuring paradigm for benthic invertebrates. Second, the differences in control between riparian spiders and carabid beetles likely reflects their overall dispersal ability and mode (i.e. passive but strong and active, respectively), leading to communities shaped by a combination of ME and SS for spiders and by SS for beetles, but with low variability explained for beetles. Moreover, a clearer role of SS was apparent for aquatic dispersing benthic invertebrates compared to aerial active dispersers, which were poorly explained by environmental conditions. These patterns were, in turn, reflected in patterns of beta diversity between the groups. Our results demonstrate habitat connectivity, habitat type (i.e. river versus riparian), and dispersal ability and mode combine to shape metacommunities.

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Supplementray material (available online as Appendix oik-02717 at <www.oikosjournal.org/appendix/oik-02717>). Appendix 1.