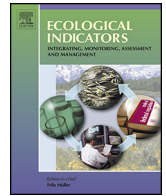




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Anthropogenic land-use stress alters community concordance at the river-riparian interface

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ABSTRACT

Organisms often respond in similar ways to environmental or spatial gradients, particularly at large spatial scales. Yet, while understanding these relationships is important for both basic and applied purposes, such as identifying surrogate taxa for conservation and monitoring purposes, patterns at finer scales and across ecotones are less certain. Our central aim was to explore patterns in community concordance at the river-riparian interface and examine whether concordance was decoupled by increasing anthropogenic stress (a gradient of local land-use intensity). We explored this at 15 sites over three years within the LTER site, Rhine-Main-Observatory, a low mountain river system in central Germany, assessing concordance between four organism groups: riparian spiders and carabid beetles, benthic macroinvertebrates, and combined aquatic macrophytes and riparian plants. This represented three different linkages: (1) predator-prey, (2) direct competition, and (3) habitat associations. While there were no correlations in richness patterns, multivariate community structure was highly concordant between all groups. Anthropogenic stress strongly reduced links between riparian spiders and carabid beetles, likely resulting from their shared resource requirements. However, increasing concordance generally occurred between plants and other groups, although inconsistently between the three groups. We posit that patterns may be resulting from two processes: (1) linkages between directly competing species decouple with increasing anthropogenic stress, and (2) stronger coupling may occur between habitat providers and dependent species when overall habitat complexity is reduced. Our results highlight the complex manner in which anthropogenic stress can influence ecosystem structure, particularly at small scales. Based on these complexities, we recommend considering the full suite of community data to adequately explore biodiversity patterns or when searching for surrogate taxa.

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1. Introduction

Biodiversity often responds to environmental or spatial gradients in a consistent manner over large spatial scales (Lamoreux et al., 2006; Qian and Ricklefs, 2008). The concordance in pattern between multiple taxon groups, also termed cross-taxon congruence, is important for both fundamental and applied reasons (Heino, 2010; Howard et al., 1998; Kati et al., 2004), such as understanding multi-organism responses to environmental gradients,

and surrogacy for conservation planning and biomonitoring purposes. The complexity of ecosystems can result in an inability to adequately describe biodiversity in many systems, through lack of financial resources or expertise, giving rise to the need for cost-effective solutions in biodiversity and conservation work (Gardner et al., 2008; Heino, 2010). Consequently, much of this research has focused on the development of surrogate or indicator taxa for applied purposes. However, while concordance has been found in a variety of systems and between a wide range of organisms (Bilton et al., 2006; Heino, 2002; Lund and Rahbek, 2002; Su et al., 2004), linkages may be weaker at smaller spatial scales (Kati et al., 2004; Paavola et al., 2006).

Communities showing concordance at large spatial scales may be reflecting similar responses of organisms to environmental factors and comparable latitudinal gradients of community structure (Paavola et al., 2006). Concordance in patterns between organism

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groups at finer spatial scales should theoretically depend on the levels of ecological and physical connectivity between these groups. Spatial subsidies between habitats, for instance, can significantly influence many ecosystem properties and the dynamics of receiving food-webs (Anderson and Polis, 1999; Polis et al., 1997), and dissimilar habitat types have as much potential for cross-boundary transfer of material as do similar habitats (Talley et al., 2006). Freshwater and terrestrial ecosystems are a prime example of such an inter-habitat connection, being strongly linked through the riparian ecotone (Gregory et al., 1991; Talley et al., 2006). Riparian zones represent a unique ecotone with strong interactions and dynamic communities, as well as often harbouring high levels of biodiversity (Naiman and Henri, 1997). Running water ecosystems, in particular, are highly connected to adjacent riparian zones through flows of nutrients (Gende et al., 2002), detritus (Wallace et al., 1997), and organisms (Nakano et al., 1999), but these processes are vulnerable to anthropogenic stressors (Baxter et al., 2005).

Strong biotic interactions can occur between different organism groups across the river-riparian interface, such as between emerging aquatic insects and riparian arthropod predators (i.e. predation) (Hering and Plachter, 1997; Sanzone et al., 2003). These linkages, whether biological or physical, should theoretically influence the level of concordance between different groups and differ depending on the type of associations being considered. For instance, competitive interactions, which play an important role in shaping local communities (Kohler, 1992; McAuliffe, 1984), are likely to be stronger between groups inhabiting the same zone, such as riparian arthropods, rather than spanning across the ecotone. Another important association to consider is the role of habitat provision by plants, with highly concordant relationships previously found between aquatic macro-flora and invertebrates, possibly reflecting a microhabitat provision role of plants (Ormerod et al., 1987).

While ecosystems spanning the globe are currently subjected to a suite of global change related stressors (Tylianakis et al., 2008), rivers in particular are under significant threat (Dudgeon et al., 2006; Vörösmarty et al., 2010). Land-use change related stressors form a major component of the threats to freshwater biodiversity (Dudgeon et al., 2006; Vörösmarty et al., 2010). Land use plays a key role in shaping river ecosystems (Allan, 2004), with urbanisation typically having a greater stress on natural communities than agricultural land use (e.g. Lenat and Crawford, 1994). Urbanisation, can bring with it major changes in pollutant runoff, hydrological regimes, temperature regimes and channel morphology (Allan, 2004). Stressors on these systems can operate in a variety of manners. For instance, recent work has highlighted that human-derived stressors alter the co-occurrence patterns of stream invertebrates through changes in community assembly patterns (Larsen and Ormerod, 2014). As it is well understood that natural external factors can alter stream food webs and processes, it is likely that other processes and community linkages decouple with external anthropogenically-driven influences, such as land-use stress, at the river-riparian interface. For instance, sustained stream pollution can impact riparian spider populations through alteration of cross-system subsidies (Paetzold et al., 2011).

As a transitional area from aquatic to terrestrial, river-riparian interfaces provide an ideal focal area to test concordance between taxon groups across coupled habitats subject to the reciprocal exchange of resource subsidies (metaecosystem flows *sensu* Loreau et al., 2003). Therefore, combined with the importance of understanding linkages between multiple organism groups at fine spatial scales and across ecotones, our central aim was to explore patterns in community concordance at the river-riparian interface and examine whether concordance was decoupled by increasing anthropogenic stress (a gradient of local land-use intensity). We assessed cross-taxon congruence/community concordance of riparian spiders and carabid beetles, benthic invertebrates, and

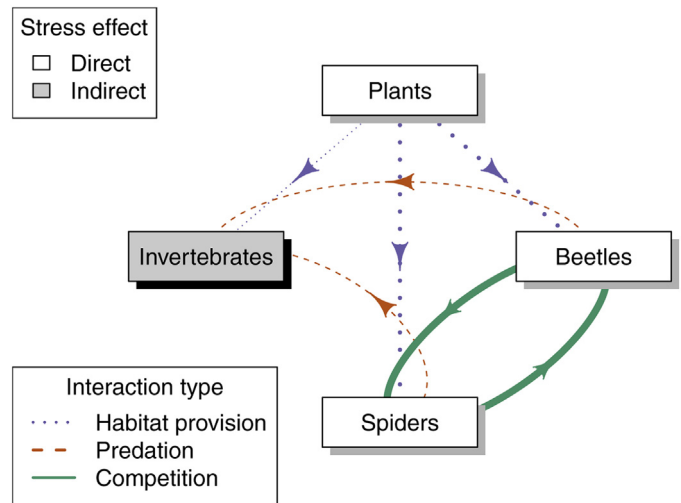


Fig. 1. Hypothesised linkages between the four different organism groups. Different interaction types are indicated by different line types. Hypothesised concordance strengths are indicated by line weights (heavier lines represent stronger concordance in patterns). Whether or not stress is hypothesised to be direct vs. indirect is also displayed. We expect stress will be less direct on the instream communities.

riparian and instream plants in the Rhine-Main-Observatory, a low-mountain river system in central Germany, over three consecutive years. This provides us with three different putative linkages to compare between in the form of: (1) predator-prey (riparian predators-benthic invertebrates), (2) direct competition (spiders-beetles), and (3) habitat associations (i.e. flora-fauna associations such as beetles using plants as habitat; Fig. 1).

Specifically, we assessed whether the degree of concordance of richness and community structure at 15 sites, each sampled consecutively over 3 years, differed between three levels of anthropogenic stress (a local land use gradient). We developed the following set of hypotheses as indicated in Fig. 1: (1) due to the small spatial scale compared to that which concordance is often examined, concordance between richness and community patterns of different organism groups would be weak in general; (2) highest concordance would be between beetles and spiders, given their shared habitat/resources, and previously reported similarity in important environmental conditions (Lambeets et al., 2008); (3) concordance would decrease between different communities with increasing anthropogenic stress, resulting from more impaired communities and lower functional connectivity (although the opposite might also be true, assuming no asymmetry in the stressor; Ormerod et al., 1987); (4) due to the buffering capacity of rivers (i.e. more indirect effects of terrestrial stressors), and the distance across the aquatic-terrestrial interface, the weakest concordance would occur between benthic invertebrates and the remaining groups.

2. Materials and methods

2.1. Study site

Fifteen sites were sampled along the Kinzig River as part of the Rhine-Main-Observatory (RMO), a long-term ecological research (LTER) site (Fig. A.1). The Kinzig River is a low-mountain river catchment situated in central Germany and flows through a mosaic of different land uses, including forested (mostly low intensity managed forest), agriculture (a mosaic of pastoral and cropping uses) and urban areas (a variety of different settlement sizes). The mean water temperature of the full study reach over the three years was 11.42 ± 1.81 °C (1 SD). Dissolved oxygen averaged 9.78 ± 0.71 mg L⁻¹, pH had a mean of 7.74 ± 0.14 , and conductivity

$447.71 \pm 75.06 \mu\text{S cm}^{-1}$. More details of the RMO LTER can be found in Kuemmerlen et al. (in this issue). The sampling design was set up to maximise the coverage of sites across a land use intensity gradient. Sampling sites were situated in one of three land use types, which represented a clear gradient in anthropogenic stress (five replicates of each category), ranging from low to high stress. The negative influences of urbanisation on stream ecosystems emerge at smaller percentages of cover in the catchment than for agriculture (Allan, 2004). Thus it is well known that streams in urban zones are typically more degraded than those in agriculture, which are in turn more degraded than those in forest (e.g. Lenat and Crawford, 1994). Therefore, forest represented the low stress sites, open agricultural land was medium and urban zones represented high stress sites. Sampling was performed annually in summer 2010–2012 at each of the 15 sites. Each site covers a 100-m river reach and spans 30 m laterally from the centre of the river (area = 6000 m²).

2.2. Vegetation mapping

Riparian vegetation and large emergent instream macrophytes were mapped at each of the sites in a two-step approach. First, areal coverage of vegetation types according to Oberdorfer (1992) was mapped in a field survey supported by aerial photographs using GIS. Second, for each vegetation type determined at each of the sites, three replicate assessments of individual species abundances (relevés) were performed using the Braun-Blanquet scale (Braun-Blanquet, 1964). For vegetation types comprising predominantly herbaceous species, each assessment covered an area of 10 m²; for vegetation types including woody plants larger areas of 100 m² each were assessed. Sampling took part in summer, when the vegetation was fully developed. Only forested sites were visited twice, in spring and summer, to also cover the geophytes that are only visible in spring. For this approach, terrestrial and aquatic (macrophytes) plants were considered together. Due to the sampling strategy (vegetation mapping approach), we cannot treat these groups separately. However, in general, macrophytes are uncommon along this stretch of river, consisting of few species. Where present, they are clearly visible during summer (the sampling period).

2.3. Riparian spiders and carabid beetles

Riparian spiders (Order: Araneae) and carabid beetles (Order: Coleoptera; Family: Carabidae) were sampled using 5.5-cm diameter pitfall traps in the riparian zone. Eight pitfall traps were used at each site, covering the range of microhabitat conditions available (i.e. bare, mown grass, unmown grass, annuals, shrubs, low forest ground cover, high forest ground cover, garden, hard substrate, deadwood). Each year, traps were left in situ for a period of two weeks in August, and were filled with Renner solution to kill and preserve the specimens. Due to their ballooning dispersal mode, juvenile spiders can disperse widely through the landscape in a non-selective manner, hence overriding niche control. Therefore, to reduce variability and minimise random spatial compared to niche structure, we excluded juvenile spiders from the analysis.

2.4. Benthic macroinvertebrates

Benthic macroinvertebrates were sampled following the official EU Water Framework Directive (WFD) multi-habitat sampling protocols (Haase et al., 2004a). This process involves 20 sub-samples being taken from multiple locations covering the range of microhabitats present at a site (i.e. seven substrate size classes, two artificial substrate classes, algae, submerged macrophytes, emergent macrophytes, terrestrial plants, deadwood, CPOM, FPOM, saprobic, non-woody debris), to accurately represent the sample reach. Samples were then stored in 70% ethanol and later identified

in the laboratory to the level of the EU WFD-compliant operational taxon list (Haase et al., 2004a,b).

2.5. Statistical analysis

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

To assess differences in taxonomic richness between the three stress levels and years, we used two-way analysis of variance (ANOVA) using the 'aov' function the package 'stats'. To assess whether species richness patterns were congruent between the four organism groups across all sites and years we performed Pearson's correlations between all groups using the 'rcorr' function in the Hmisc package (Harrell, 2014). We also correlated richness associations for each local land use separately to assess if richness congruence was stronger for certain stress levels.

For multivariate community analyses, we used presence-absence data to best enable standardised between-group comparisons. Presence-absence data also represents the next step in complexity of information from the taxonomic richness data for comparison, compared to the greater jump in information with full abundance data. To visualise differences in community structure between the three stress categories and years, we used non-metric multidimensional scaling (nMDS) ordination, with the function 'metaMDS' in Vegan (Oksanen et al., 2013). Given presence-absence is the most extreme form of data standardisation, we also compared ordination stress scores with those from ordinations on log-transformed data. These scores, and the general arrangement of sites in ordination space, remained similar to presence-absence data (stress for log-transformed data increased for beetles, decreased for invertebrates, and remained the same for spiders and plants). We used Bray-Curtis as the distance measure and fit vectors to compare year-to-year changes in community structure between the groups and stress levels. To statistically assess differences in community structure between the three stress levels and years, we used two-way PERMANOVA, using the 'adonis' function in Vegan. Again we used Bray-Curtis distances and performed 9999 permutations.

To assess pairwise community concordance between the four groups we compared the two-dimensional nMDS ordination structures using a Procrustes superimposition approach (Gower, 1971). This process attempts to minimise the sum-of-squared residuals of points (sites) on two ordination structures by scaling and rotating ordination structures. Essentially, one ordination structure is superimposed onto a second ordination, while maximising the association between corresponding points on the two ordinations. The fit is based on minimising the sum-of-squared residuals ($M12^2$), which is lower when the concordance is higher. This is essentially similar to the Mantel test but dealing only with the two-dimensional ordination structure rather than the entire distance matrix. Thus, it has the advantage over Mantel tests of reducing dimensionality of the original data and allowing a visual inspection of the compared structures (Peres-Neto and Jackson, 2001).

We then tested for significant associations between these structures on a pairwise basis using a PROTEST permutation procedure (Jackson, 1995) implemented with the 'protest' function in Vegan using 9999 permutations. This approach uses randomisation to test the significance of the Procrustean fit (Jackson, 1995; Peres-Neto and Jackson, 2001). More specifically, the test randomly permutes observations from one dataset among all possible other observations in that dataset. $M12^2$ is calculated for each permutation and thus the significance of the observed fit can be calculated based on these random permutations.

To test our hypothesis that anthropogenic stress influences community concordance, we assessed pairwise differences in ordination structures between the four groups. To do this, we extracted

residual differences between individual ordination points resulting from the Procrustean rotations. A longer residual for a single point (i.e. site) between two ordinations suggests a strong deviation between communities (e.g. spiders vs. beetles) at that particular site. A smaller residual indicates similar communities, and thus strong concordance. We grouped residuals for each land-use stress category and tested for differences in residuals between the three stress categories using one-way ANOVA. Where significant differences were evident, we assessed individual differences between stress levels using Tukey's HSD post hoc test with the 'TukeyHSD' function.

Finally, we were interested in whether differences in concordance may have been influenced by different levels of spatial structuring or spatial autocorrelation between different groups. To do this, we performed mantel tests for each group, and for each year separately, between distance matrices of presence-absence data and geographic coordinates of sites using the 'mantel' function and 1000 permutations with the ecodist R package (Goslee and Urban, 2007).

3. Results

3.1. Richness patterns

Richness of plants and benthic invertebrates did not differ either between the three stress levels or between years (Fig. 2). Riparian beetle richness was higher at the medium compared to high stress sites (Tukey's HSD: $P < 0.01$), but there were no other pairwise differences between stress categories (Tukey's HSD: $P > 0.05$; Fig. 2). Further, beetle richness was significantly lower in 2012 than both 2010 and 2011 (Tukey's HSD: $P < 0.05$; Fig. 2). Spider richness

Table 1

Results of two-way PERMANOVA tests comparing community structure of four different organism groups collected from the Kinzig River, Hesse, Germany from 2010 to 2012 between three land-use stress levels and years. Degrees of freedom for all factors are 2,40.

Factor	Sums sq.	Mean sq.	F Model	R ²	P
<i>Plants</i>					
Stress	2.923	1.462	13.57	0.387	<0.0001
Year	0.314	0.157	1.46	0.042	0.131
<i>Beetles</i>					
Stress	2.527	1.263	4.77	0.183	<0.0001
Year	0.686	0.343	1.30	0.050	0.142
<i>Spiders</i>					
Stress	2.331	1.166	7.97	0.267	<0.0001
Year	0.574	0.287	1.96	0.066	0.032
<i>Invertebrates</i>					
Stress	1.009	0.504	3.45	0.137	<0.0001
Year	0.495	0.248	1.69	0.067	0.035

was significantly higher at medium compared to both low and high stress sites (Tukey's HSD: $P < 0.0001$), with no difference between low and high stress sites (Tukey's HSD: $P > 0.05$; Fig. 2).

There was no correlation between taxonomic richness of any of the organism groups within each anthropogenic stress level or for all stress categories combined (Fig. 3).

3.2. Multivariate structure

Multivariate structure of all organism groups differed strongly between stress levels, but only spiders and invertebrates differed between years (Fig. 4; Table 1). Plants had the lowest variation from year to year (Fig. 4; Table 1)

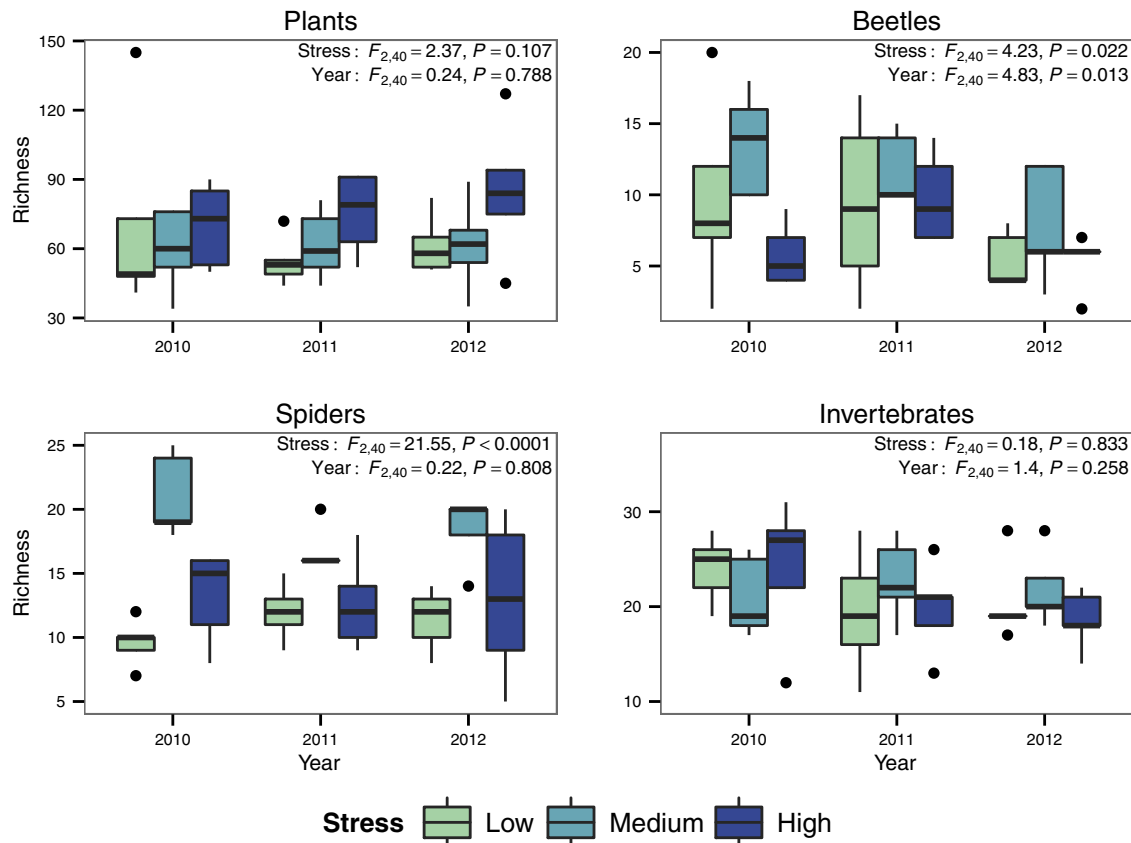


Fig. 2. Taxonomic richness for each organism group for three stress levels collected from 15 sites annually between 2010 and 2012 on the Kinzig River, Hesse, Germany.

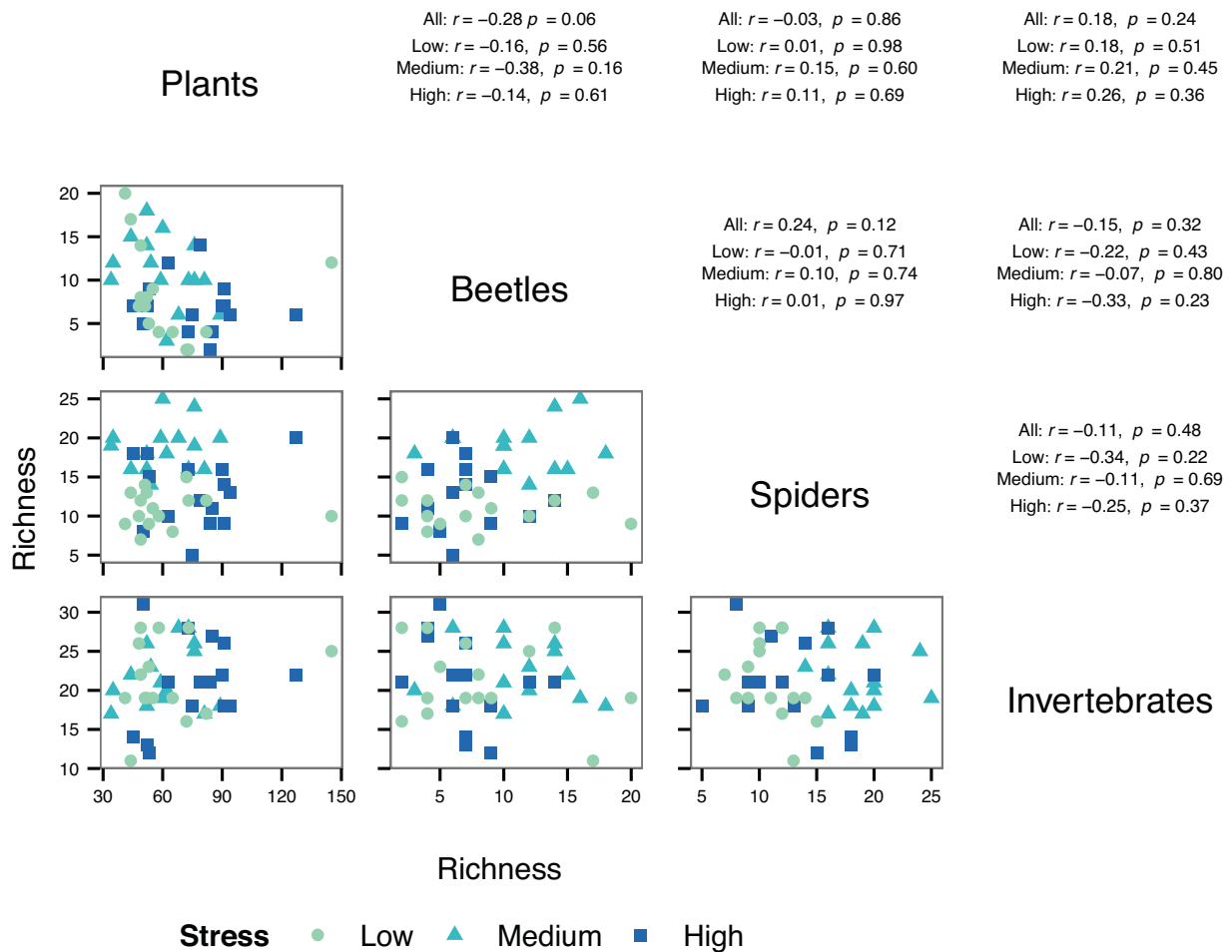


Fig. 3. Pairwise comparisons of species richness between each organism group for three land-use stress levels and all land uses combined for data collected between 2010 and 2012 on the Kinzig River, Hesse, Germany. Results on right are Pearson's correlations. Note *P* values have not been corrected for multiple comparisons, but there were no significant values.

All pairwise ordination similarities were highly significantly related, with correlations ranging between 0.431 and 0.711 (Fig. 5). Plant and spider ordinations were the most similar, whereas the least similar structures were those between invertebrates and both beetles and spiders (Fig. 5). Benthic invertebrates had the lowest concordance with other groups (Fig. 5).

Anthropogenic stress had variable influences shaping concordance between organism groups (Fig. 5). Extracted pairwise ordination residuals between the four organism groups exhibited significant differences between stress types for plants–spiders, plants–invertebrates, beetles–invertebrates and beetles–spiders comparisons. Residuals between plant and spider assemblage ordinations were greater (implying lower concordance) at low than medium, but not high stress sites (Fig. 5), and the same trend was apparent for the beetles–invertebrates comparison. Concordance between plant and benthic invertebrate assemblages increased with increasing stress (i.e. residuals reduced), with intermediate concordance at medium stress sites (Fig. 5). Concordance decreased between riparian beetles and spiders with increasing stress, with significantly higher residuals at high compared to low and medium stress sites (Fig. 5).

Invertebrates exhibited significant and consistent, albeit minor, spatial structuring, with a clear distance decay pattern each year (Table A.1). With the exception of beetles in 2010, there was no evidence of spatial structuring in the other three groups (Table A.1).

4. Discussion

Cross-taxon congruence is of fundamental importance for the selection of indicator (or surrogate) taxa, often with the focus on whether or not surrogate taxa are able to predict spatial patterns in other taxa. This topic has received significant attention in conservation biology and applied ecology (Fattorini et al., 2012; Heino, 2010; Kati et al., 2004), stemming from the lack of resources to effectively monitor every component of highly complex ecosystems. We examined the congruence in species richness and community structure between four organism groups in a river–floodplain system, and whether or not these linkages were influenced by anthropogenic land-use stress. While there was no evidence of concordance in taxonomic richness between organisms at the river–riparian interface in this study, community structure was strongly linked between all groups. We hypothesised concordance would decrease between different organisms with increasing anthropogenic stress, resulting from more impaired communities and lower functional connectivity. However, the influence of stress shaping concordance of community structure varied between pairwise comparisons. We posit that two processes are operating to reveal these relationships: (1) increasing anthropogenic stress leads to decoupling of directly competing species (e.g. riparian beetles and spiders), whereas (2) stronger coupling occurs between habitat providers (i.e. plants) and other species when overall habitat complexity is reduced.

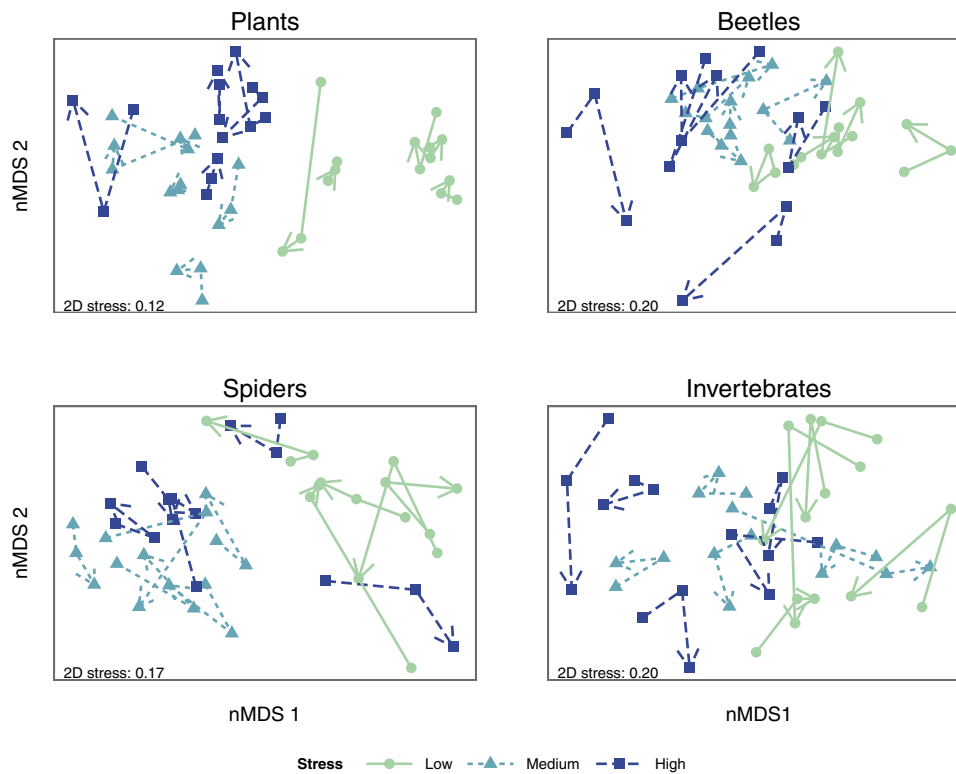


Fig. 4. nMDS ordinations on presence-absence community data of four organism groups collected between 2010 and 2012 on the Kinzig River, Hesse, Germany. The arrow represents community shifts from 2010 to 2012. Two-dimensional stress values are given on the plots. Differences between land-use stress levels and years can be found in Table 1.

Due to both groups being active ground hunters and competing for the same resources, we hypothesised riparian beetles and spiders would exhibit the most concordant patterns at the community level. However, Tonkin et al. (2015c) found little evidence of competition within these assemblages and highly variable metacommunity structure across the aquatic–terrestrial ecotone. A previous study examining lowland river bank spider and carabid beetle assemblages found similarities in the predominant environmental variables influencing their structure (Lambeets et al., 2008). While the strongest link for multivariate structure was between spiders and plants, riparian beetles and spiders exhibited strongly concordant patterns at the community level. The association between these two groups was most clearly affected by anthropogenic stress, with a strong decoupling with increasing stress, which we hypothesise is a function of their shared resource requirements. In low-stress environments, species interactions shape community structure, resulting in a strong coupling between different taxonomic groups, particularly those with shared resource requirements such as riparian spiders and carabid beetles. With increasing stress, this species network that is structured by competitive interactions and limiting similarities is broken up and communities are increasingly shaped by abiotic controls. A recent meta analysis showed that increasing stress may facilitate positive species interactions, but this paper focused solely on plant communities (He et al., 2013). Nonetheless, there is evidence that increasing stress can strengthen antagonistic interactions (Thomson et al., 2002; Tylisanakis et al., 2007). Furthermore, it is important to emphasise here that we focused on occupancy data only and were thus not focusing on changes in abundances of organisms along this stress gradient, despite more subtle differences potentially occurring. Previous work in Finland found that, while abundances of carabids and ground spiders did not differ

along a rural-urban forest gradient, more subtle effects were found when considering species traits (Alaruiikka et al., 2002)

In line with our hypothesis, whilst being significantly linked, benthic invertebrates had consistently the lowest concordance with the remaining groups. This is likely a result of two key factors: first, contrary to riparian communities, instream communities are buffered from the influence of the immediately surrounding terrestrial zone and are shaped by the entire upstream catchment processes (Allan, 2004). Of course, major point source discharges could also decouple instream communities from those in the riparian zone, although we are unaware of any such major discharges along the study reach. Second, benthic invertebrates were the only taxonomic group to be limited to the aquatic zone (at least for part of their life cycle) in our analyses and consequently were the most disconnected of the groups across the aquatic–terrestrial boundary. Finally, a third explanation for the weaker link between invertebrates and the other groups was a greater influence of spatial structuring (i.e. mass effects) in the instream environment. Indeed, invertebrates were the only group to exhibit consistent significant, but minor, distance decay of similarity, indicating a greater level of connectivity between the aquatic sites compared to terrestrial. Nevertheless, patterns remained strongly concordant with other groups, reflecting the importance of reciprocal aquatic–terrestrial connectivity in stream ecosystems (Baxter et al., 2005), which can occur in many forms, including energy, materials, and organisms (Talley et al., 2006).

As plants in the present study were combined riparian vegetation and instream macrophytes and thus spanned the river-riparian boundary, it is not surprising they were the most strongly linked of the three remaining groups with benthic invertebrates. A previous study in Welsh streams found strong concordance between aquatic macro-flora and many invertebrate groups in relation to acidity

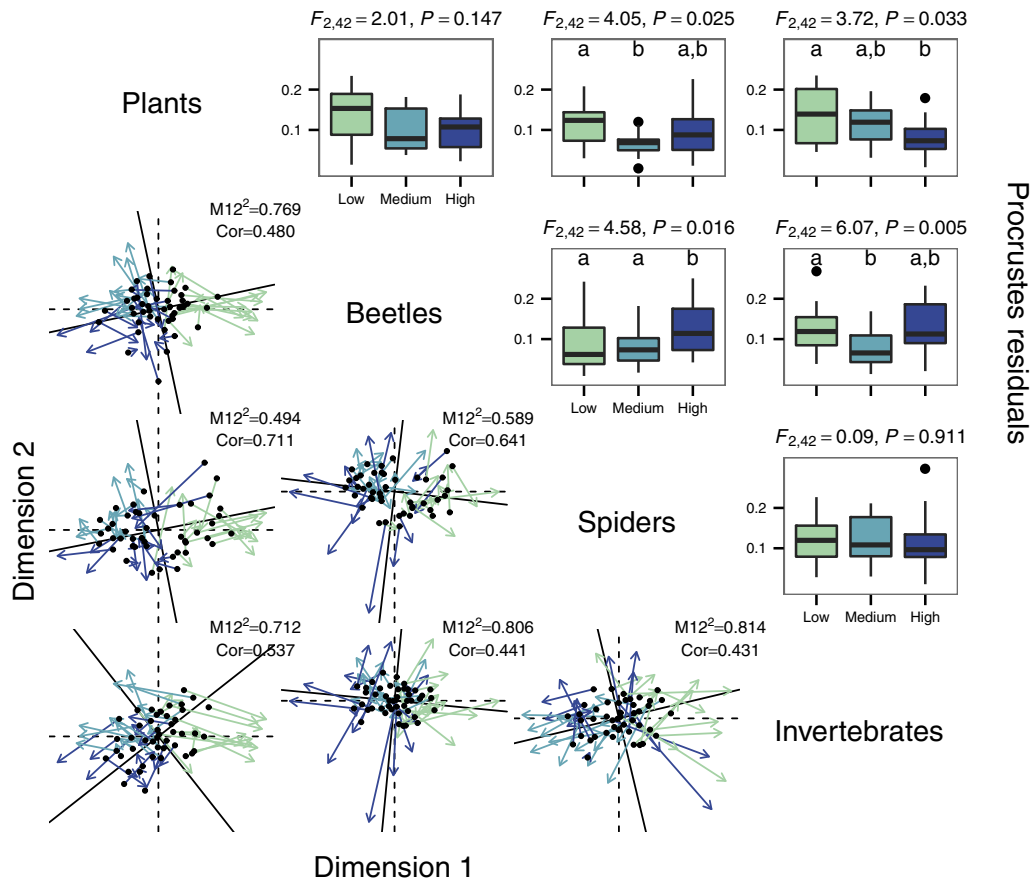


Fig. 5. Results of Procrustes rotations and PROTEST permutation tests on nMDS ordination plots from Fig. 4 on presence–absence community data of four organism groups collected between 2010 and 2012 on the Kinzig River, Hesse, Germany. Bottom left plots show Procrustes superimposition plots indicating the level of rotation required to align pairwise ordinations between different organism groups and lines indicate shifts in individual site points between the two ordinations, colour coded for each stress level. $M12^2$ is the sum of squares of the symmetric Procrustes analysis and Cor represents the correlation between the two ordinations. All Procrustes tests were significant at $P < 0.0001$. The top right box plots represent residual differences between points on pairwise Procrustes rotations for each land-use stress level. One-way ANOVA results for residual differences are displayed above the plots and where significant differences were evident, Tukey's HSD results, where $P < 0.05$, are displayed on the graphs.

(Ormerod et al., 1987). They hypothesise three different causes for this concordance: (1) food provision by plants; (2) microhabitat provision by plants; and (3) independent (but similar) responses to environmental factors. This final hypothesis of course may promote non-concordant responses to environmental gradients, particularly if certain groups are more buffered from the gradient of interest. For instance, in our case, instream organisms are less directly influenced by activities in the immediate riparian zone than riparian organisms.

While invertebrates were less strongly linked with riparian predators, studies have found strong associations between benthic invertebrates and riparian communities (Burdon and Harding, 2008; Sabo and Power, 2002; Sanzone et al., 2003). For instance, stream insect biomass was found to be strongly associated with riparian spider biomass and web densities in New Zealand streams (Burdon and Harding, 2008), and this association weakened with distance from the stream for spider webs. Riparian web-building spiders derive a significant proportion of their carbon from aquatic sources (Collier et al., 2002; Sanzone et al., 2003), and riparian carabid beetles also largely feed on aquatic insects, particular those that emerge through crawling (Hering and Plachter, 1997). However, the use of aquatic subsidies by riparian ground beetles and spiders can be separated seasonally, indicating clear plasticity in their diets (O'Callaghan et al., 2013), likely as a result of their life-history characteristics (Paetzold et al., 2006), and our study was based on one-off sampling in late summer/autumn. Finally, as we included both mero- and hololimnic benthic invertebrate species (i.e. those

with and without an adult flight stage) in our analyses, and the fact that riparian predators feed predominantly on emerging insects, it may be assumed that the link between riparian predators and benthic invertebrates would be stronger with merolimnic species alone.

Contrary to expectation, concordance between plants and other groups increased with increasing stress. This trend likely reflects the habitat provision role that plants have for associated groups, rather than direct competition as per beetles and spiders. For beetles and spiders, concordance increased mostly from low to both medium and high stress sites. This pattern is challenging given the contrasting richness trends between medium and high stress sites for these communities. That is, richness of both beetles and spiders was highest in the medium stress sites and lower in high stress sites. Despite these variable richness patterns, it appears there is an increased dependence on plant structure with increasing local habitat stress. Greater concordance at high stress sites, in particular, likely results from reduced richness leading to a strengthening of the link of remaining species on plant habitat. Habitat loss is one of the principal causes of biodiversity decline worldwide (Brookes et al., 2002), and riverine habitats are particularly vulnerable to land-use change (Allan, 2004; Vörösmarty et al., 2010). Remaining species under these stressed conditions are likely those able to cope under conditions of reduced habitat complexity. Modifying habitats can influence food-web structure without altering conventional community metrics (Tylianakis et al., 2007). Vegetation is one important aspect of habitat, and habitat complexity can mediate

species interactions such as predation and competition (Beukers and Jones, 1997; Grabowski, 2004).

The increased coupling of remaining benthic invertebrates and beetles to plants with increasing environmental stress, is likely a result of the overall reduction of site-wide habitat complexity leading to an increased dependence on remaining vegetation habitat; a trend that may also be operating for the riparian communities. Furthermore, while invertebrate richness did not change with stress level, community structure fluctuated the least year-to-year in the high-stress sites. This trend, coupled with the high plant temporal stability, helps to further explain this strengthened invertebrate–plant association. While spiders were more spatiotemporally variable, they followed the same general pattern as the other two animal groups.

Our finding of weak congruence between richness of all groups, but strong concordance of community structure has important management implications, particularly for identifying surrogates or indicator taxa. A variety of previous studies spanning a range of organism sizes, habitat types and trophic levels have reported similar patterns (Bilton et al., 2006; Su et al., 2004). For instance, Su et al. (2004) found highly varied associations between richness of birds, butterflies and vascular plants, but consistent and strong when assessing community similarity. Moreover, Bilton et al. (2006) found weak richness associations but strong similarity in community patterns for pond inhabiting macroinvertebrates. These examples and our results exemplify the importance of not overlooking more complex responses to environmental variables and relying on richness as a measure of congruence, particularly at small spatial scales. Global change not only operates on communities by directly influencing richness, but by altering species interactions (Tyllianakis et al., 2008).

The lack of association of richness between groups likely reflects the small spatial scale of observation in this study. While biodiversity often corresponds with environmental or spatial variation similarly over large spatial scales (Qian and Ricklefs, 2008; but see Tonkin et al., 2015b), the link is less clear at smaller spatial scales (e.g. Kati et al., 2004; Paavola et al., 2006). The spatial scale of observation is critical with regard to many relationships in nature, such as the response of biodiversity to productivity (Chase and Leibold, 2002; Tonkin and Death, 2013). For instance, in boreal streams, Paavola et al. (2006) found weaker concordance patterns within individual stream drainages compared to between drainages and ecoregions. In general, cross-taxon congruence has been too weak to find reliable predictors of biodiversity in freshwater ecosystems (Heino, 2010), possibly reflecting the prevalence of context dependency in these systems (Heino et al., 2012; Tonkin et al., 2015a). Our results suggest that these relationships are highly dependent on anthropogenic stress and underlying processes. First, increasing anthropogenic stress decouples the link between directly competing organisms, and second, when overall habitat complexity is reduced, the link between habitat providers (i.e. plants) and other species will strengthen. Nevertheless, we did not specifically quantify these putative linkages and therefore recommend this as an important avenue of future research to disentangle the mechanisms driving these patterns. Moreover, future work seeking to find appropriate surrogate or indicator taxa for conservation or biomonitoring purposes would benefit from focusing on multiple spatial scales and the community rather than individual species level, particularly at finer spatial scales.

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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.ecolind.2015.08.037>.

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