Context dependency in biodiversity patterns of central German stream metacommunities

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SUMMARY

1. Context dependency is an emerging topic that is challenging our understanding of the factors shaping biodiversity in metacommunities. River networks and other dendritic systems provide unique systems for examining variation in the processes shaping biodiversity between different metacommunities.

2. We examined biodiversity patterns in five benthic invertebrate data sets, from two catchments in central Germany, with the aim of exploring context dependency in these systems. We used variance partitioning to disentangle the variation explained in three biodiversity metrics: taxonomic richness, Simpson's diversity and local contribution to beta diversity (LCBD; a measure of the uniqueness of a site). As explanatory variables, we used proxies of network position (i.e. catchment size and altitude) and habitat conditions.

3. Contrary to our expectation, we found no evidence of a decline in LCBD downstream in our study. Local habitat conditions and catchment land use played a much stronger role than catchment size and altitude in explaining variation in the three biodiversity metrics. Observed patterns were highly variable between different data sets in our study. These findings suggest that factors shaping biodiversity patterns in these systems are highly context dependent and less related to their position along the river network than local habitat conditions.

4. Given the clear context dependency between data sets, we urge researchers to focus on disentangling the factors driving the high levels of variability between individual systems through the study of a number of replicate, rather than single, metacommunities.

Keywords: benthic invertebrates, beta diversity, local contribution to beta diversity, river network, variance partitioning

Introduction

While clearly linked, the alpha, beta and gamma components of biodiversity (Whittaker, 1960) can be shaped by a different suite of processes operating at different scales (Angeler & Drakare, 2013). The metacommunity concept (Leibold *et al.*, 2004; Holyoak, Leibold & Holt, 2005), by emphasising the importance of processes operating beyond the local scale, led to a rapid advancement in both our understanding of and the analytical tools used to examine spatial patterns in biodiversity. Disentangling metacommunity patterns and underlying processes requires an understanding of not only local environmental influences (i.e. species sorting), but also spatial processes such as dispersal (Holyoak *et al.*, 2005). Given the strong ties between the theoretical foundations of meta-

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community ecology and the drivers of beta diversity, understanding beta diversity patterns also necessitates hypotheses developed in the context of metacommunity theory (Heino, Melo & Bini, 2015a).

Metacommunity organisation remains difficult to predict, with various processes operating fleetingly and acting differently on different subsets of organisms (Driscoll & Lindenmayer, 2009). Community ecology in general is riddled with contingency so complex that general repeatable patterns are rare (Lawton, 1999). Contingency is the most problematic in this middle ground between low levels of ecological organisation (e.g. populations), and higher levels at greater spatial and temporal scales (e.g. macroecology) where generalisations are more readily available (Lawton, 1999). Beyond communities, factors governing metacommunities can, therefore, be highly context dependent between regions (Driscoll & Lindenmayer, 2009; Heino et al., 2012). As with community ecology in general (Lawton, 1999), context dependency in metacommunity structuring may emerge through differences in the characteristics of different organisms. For instance, there are often differences between different trait modalities, such as dispersal modes (Thompson & Townsend, 2006; Canedo-Arguelles et al., 2015; Tonkin et al., 2015b), or in the characteristics of the environmental setting (Heino et al., 2015d). Such context dependency can lead to differences in the importance of environmental or spatial factors on metacommunities within different regions (Heino et al., 2012). Among others, such as floodplain lake fish communities (Fernandes et al., 2013), one particular system shown to exhibit strongly context-dependent patterns is the running water system, where different patterns typically emerge between different catchments, studies, locations and years (Erős et al., 2013; Heino et al., 2015b Heino et al., 2015e).

Metacommunity studies have been biased towards systems with discrete habitat boundaries (Logue et al., 2011). However, streams and rivers are ideal systems for testing metacommunity concepts and beta diversity patterns, due to their isolated position embedded within the terrestrial landscape and owing to their hierarchical dendritic organisation (Campbell Grant, Lowe & Fagan, 2007; Altermatt, 2013), variety of habitat types and disproportionately high biodiversity (Vinson & Hawkins, 1998; Vörösmarty et al., 2010). This organisation and unidirectional flow can have strong implications on the way in which organisms disperse, dictating metacommunity dynamics and subsequently the organisation of biodiversity (Campbell Grant et al., 2007; Brown & Swan, 2010; Altermatt, 2013; Swan & Brown, 2014). Contrary to previous views, such as the River Continuum Concept (Vannote et al., 1980), headwaters are now understood to harbour much of the catchment-wide biodiversity in river systems (Finn et al., 2011; Besemer et al., 2013), although alpha diversity should be promoted in sites more central within catchments (Altermatt, Seymour & Martinez, 2013). Higher beta diversity in headwaters may result from their spatial isolation and thus limited dispersal rates (Brown & Swan, 2010; Finn et al., 2011), considerable environmental heterogeneity between streams (Clarke et al., 2008), a potentially higher level of specialisation compared to downstream sections (Hughes, Schmidt & Finn, 2009) and their numerical dominance over downstream sections due to the dendritic organisation (Benda et al., 2004). Accordingly, a reasonable expectation is to observe an increase in alpha diversity and decline in beta diversity moving downstream in moderately sized-river systems (Finn et al., 2011).

Greater beta diversity in headwaters suggests that each stream contributes a larger proportion to both overall beta diversity and gamma diversity compared to other sections. In fact, the local environmental (e.g. niche-related processes) versus regional (e.g. dispersal-related processes) control is likely to differ between different locations in the river network (Brown & Swan, 2010). Therefore, in this study, we applied techniques to disentangle the local contribution to beta diversity (LCBD), a measure of the uniqueness of individual sites within a metacommunity (Legendre & De Cáceres, 2013), in relation to their position within the river network. Given the indication of strong context dependency in metacommunity patterns, it is important to explore these issues across multiple environmental settings (see Heino et al., 2015b). Thus, we focused on five separate benthic invertebrate data sets spread between 3 years and two separate catchments with similar spatial extents. Benthic invertebrates contribute significantly to the biodiversity of streams (Strayer, 2006) and have a central position in the functioning of these ecosystems (Allan & Castillo, 2007), making them ideal focal organisms to test metacommunity concepts and biodiversity patterns.

We tested the following hypotheses: H1. Alpha diversity increases downstream with increasing catchment size and with decreasing altitude, but LCBD decreases simultaneously. This is based on the notion that headwater sites are more isolated and more physically variable than downstream sites, leading to more unique assemblages within the catchment (higher LCBD), but also have lower local richness (Finn et al., 2011). H2. Due to the largely non-pristine nature of our central German study region and impaired regional species

pools (Tonkin *et al.*, 2014), environmental variables (a combination of habitat and catchment land use) are more important in explaining biodiversity than the physical position within the network. More specifically, we expect H1 to hold, but network position to exert a weaker influence than environmental variables. We also examined whether biodiversity patterns and environmental predictors were consistent or variable between the different data sets, owing to context dependency, as has been observed regularly in examinations of stream metacommunities (Heino *et al.*, 2012, 2015b,e). Consistent patterns between the five data sets would indicate similarity in processes shaping these stream metacommunities, whereas different patterns would indicate a certain level of context dependency between data sets (i.e. different factors may drive biodiversity patterns in different environmental settings). To test these hypotheses, we partitioned the variation in our response variables between catchment size (as a direct proxy for position along the river network; larger streams are further downstream), altitude (indirectly related to network position) and selected environmental variables for predicting stream macroinvertebrate biodiversity patterns.

Methods

Study sites

We collated benthic invertebrate community data from 124 low mountain streams and rivers in the central German state of Hesse. These streams belong to the Central Highlands ecoregion [stream types 5–9, and 19 (small streams in riverine floodplains, independent of ecoregion)] (Pottgiesser & Sommerhäuser, 2004, http://wiki.reformrivers.eu/index.php/River_typology_in_Germany). Sites were sampled between 2005 and 2007 and each site was sampled once during this period. Precipitation fluctuated over this period, but there were no major differences between the 3 years (source: NOAA – National Oceanic and Atmospheric Administration; http://www.ncdc.noaa.gov/; Station: GHCND: GMW00035032 – RHEIN MAIN, GM).

For this study, we delineated two catchments, a northern and southern: the Weser River to the North and the Main River to the South. To adequately examine metacommunity dynamics, it is important to limit metacommunities to those that can interact through dispersal and thus to consider individual years separately (Heino *et al.*, 2015b). Therefore, we divided these two catchments into different years as individual metacommunities. To ensure adequate replication, we employed a criterion of a mini-

mum of 15 sites per catchment per year to be included in the analysis. The statistical models we employed can better be trusted if they are based on a moderate number of sites. This resulted in five replicate data sets, two from the northern catchment (2005, 2007) and three from the southern (2005–2007), with a final number of 124 sites (North: data set a – 18, b – 27; South: c – 28, d – 28, e – 23; Fig. 1). We hereafter refer to these as data sets, rather than catchments as, while each site was only considered once, only two broad catchments are included, with temporal replicates. Nevertheless, these datasets represent five different replicate metacommunities, given that no individual sites were replicated over the 3 years (i.e. each site was only sampled once over the 3-year period).

We removed all sites with catchment sizes greater than 300 km^2 as these few sites can bias the patterns observed. Thus, catchment sizes ranged between 7 and 280 km^2, with a mean of 64 km^2 (see Table S1 in Supporting Information). Mean site altitude was 167 m a.s.l., ranging between 84 and 379 m a.s.l. Both catchment size (one-way ANOVA: $F_{4,119} = 7.09$, $P < 0.0001$) and altitude ($F_{4,119} = 22.58$, $P < 0.0001$) differed significantly between the five data sets. Sites in the two northern data sets (the same general region but sampled in different years and different individual sites) were at higher altitude than those in the southern data sets (Tukey's HSD $P < 0.05$ between all data sets of northern and all southern basins, but not within the basins). Catchment size differences were less clear, however, with data sets D and E having greater catchment sizes than data set C, and data set E greater than A (Tukey's HSD $P < 0.05$).

Sampling

Benthic invertebrates were sampled by German governmental environmental agencies following the official EU Water Framework Directive (WFD) compliant sampling protocols for German streams (Haase *et al.*, 2004). This sampling method uses a multi-habitat approach by taking 20 sample units from each site, based on the proportion of microhabitats present at a site. More specifically, all microhabitats in a 100-m long reach were first recorded in 5% coverage units based on visual assessments, and each sampling unit (25 × 25 cm) sampled with a 0.5-mm mesh kick net. Twenty sample units were taken from each site and then pooled for later analysis (1.25 m^2 total sampling area). These microhabitat values were recorded for use in subsequent analyses and can be found in Table S2. They consisted of substratum composition of various sizes, algal cover, coarse particulate organic matter, macrophytes (submerged and emergent),
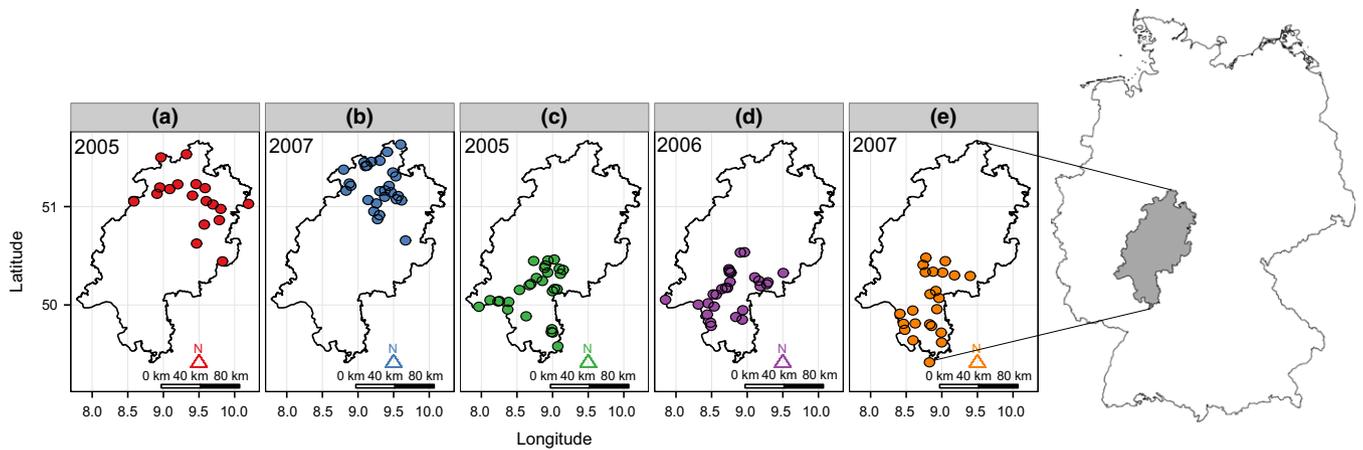
Fig. 1 Map of the five data sets sampled between 2005 and 2007 in the central German state of Hesse. The five data sets comprise one northern and one southern catchment (Weser and Main Rivers, respectively, sampled each year). Insufficient sites were sampled in 2006 in the northern basin to be included.

woody and non-woody debris, terrestrial plants and decaying material (Table S2). Collected samples were stored in 70% ethanol and identified in the laboratory to consistent levels between sites, as proposed by Haase, Sundermann & Schindehütte (2006) (i.e. EU-WFD-compliant operational taxon list for German running waters). To partially control for major anthropogenic stressors, we removed heavily polluted sites using the German saprobity index (Rolauffs *et al.*, 2004). We thus removed all sites with worse than 'medium' saprobity scores.

Environmental variables

In addition to the microhabitat variables (see Table S2), catchment land use was calculated for the entire upstream catchment area of each site using data from the CORINE Land Cover database (Bossard, Feranec & Otahel, 2000). We grouped CORINE classes into seven coarser classes (artificial, agriculture, forest, shrub, natural bare, wetlands, water), but due to low percent coverage of some classes, only artificial, agriculture, forest and shrub were kept for our analyses. These were used as explanatory variables in the analyses.

Data analysis

Differences in environmental conditions. To test the null hypothesis that there was no difference in the degree of environmental heterogeneity between the five data sets, we tested for homogeneity of group dispersions (PERM-DISP2) (Anderson, 2006) using the 'betadisper' function in the *R* package vegan (Oksanen *et al.*, 2013). This method uses the ANOVA *F*-statistic to compare the within-group distances to each group centroid, and tests

for significance between groups using permutation. We tested for differences using normalised environmental variables and Euclidean distances. Where significant, we compared between individual data sets using pairwise Tukey's HSD tests. We ran these tests, both inclusive and exclusive of catchment size and altitude, in order to observe their influence.

As beta diversity should increase with increasing spatial extent (Bini *et al.*, 2014; Heino *et al.*, 2015a), we also assessed whether there were any differences in the spatial extent of each data set using the same approach on geographical coordinates and found no differences ($F_{4,119} = 1.09$, $P = 0.364$).

Differences in biodiversity. Multiple approaches to measure beta diversity are often required, depending on the question of interest, as different measures describe distinct aspects of beta diversity (Anderson *et al.*, 2011). Accordingly, there is a plethora of methods now available for its calculation, which can be largely broken down into two broad categories: one measuring turnover and another measuring overall variation (Anderson *et al.*, 2011). Turnover refers to the directional change in composition from one location to another in relation to some form of gradient (e.g. environmental, spatial or temporal). Variation in community composition, on the other hand, does not consider a gradient of change, but simply the overall variation in community composition between a set of sites. Legendre & De Cáceres (2013) recently proposed a highly adaptable method to quantify beta diversity as the total variation in a species-by-site community matrix, based on a variety of transformations and distance measures. One benefit of this method is its ability to also identify the local site-based contributions (LCBD) to over-

all beta diversity in a data set. LCBD allows, for instance, identification of individual sites or areas that contribute more or less than average to overall beta diversity. This, in turn, enables the disentanglement of factors underlying metacommunity (or regional) biodiversity patterns, but also the ability to identify sites with high conservation value (or restoration potential in the case of species poor communities), those with invasive species or those with unique environmental conditions (Legendre & De Cáceres, 2013).

To calculate catchment-specific beta diversity measures, we followed the methods developed by Legendre & De Cáceres (2013). We examined overall (i.e. data set) beta diversity (BD_Total) using the beta.div function, based on the R code provided by Legendre & De Cáceres (2013). To examine the uniqueness of individual assemblages for testing our two hypotheses (H1 and H2), we calculated local (i.e. individual site-based) contribution to beta diversity (LCBD) using the same method. We based our approach on Hellinger-transformed data (i.e. raw abundance data, using the 'hellinger' method in 'beta.div'), a suitable method for handling heteroscedastic community data for statistical methods with assumptions of linearity (Legendre & Gallagher, 2001). Significance of individual LCBD values was tested for using the permutation procedure of Legendre & De Cáceres (2013).

To summarise differences between the biodiversity of the five data sets, we compared local taxonomic richness, Simpson's diversity index, data set gamma diversity and data set beta diversity (BD_Total). We calculated Simpson's diversity index ($1 - D$) using the 'diversity' function in the R package vegan (Oksanen *et al.*, 2013). We compared mean taxonomic richness and Simpson's diversity index using one-way ANOVAs, followed by pairwise Tukey's HSD tests, when significant differences were observed. Gamma diversity and BD_Total could not be compared statistically as they only had one value per data set.

To test our first hypothesis (H1), linking catchment size (as a proxy for network position) and altitude, and taxonomic richness, Simpson's diversity and LCBD, we ran simple linear regressions, using log-transformed catchment size and altitude.

To examine the extent of context dependency between data sets and the importance of environmental variables (H2), we partitioned the variation in our response variables between combined local habitat and catchment land use (environmental), altitude and catchment size separately for each data set. This allowed us to examine whether the relative positioning of a community within a river catchment (representative of regional processes) or whether local environmental conditions (local pro-

cesses) were more important for structuring biodiversity. As we were specifically interested in both catchment size and altitude, we always forced them in the variance partitioning approach. For the environmental variables, we used forward selection of normalised variables to select significant variables using the 'ordistep' procedure in linear regression (i.e. with a single response variable) in the vegan package (Oksanen *et al.*, 2013). We set models to include variables with a $P < 0.05$ and subsequently remove them with a $P > 0.1$, and we set the number of permutations to the number required for each case with respect to our defined P value.

We ran variance partitioning (Borcard, Legendre & Drapeau, 1992; Anderson & Gribble, 1998; Peres-Neto *et al.*, 2006) for each of the single response variables in each data set, using the 'varpart' function in vegan. Given we modelled single response variables, the partitioning was based on partial linear regression (Oksanen *et al.*, 2013). This method partitions the variation between the pure effects of each variable (i.e. catchment area or altitude), or group of variables (i.e. local environmental variables) and the shared variance explained. In this case, we had three independent variable groups. This resulted in seven individual components of variation and unexplained variation.

All statistical analyses were carried out in R 3.1.1 (R Core Team 2013).

Results

Congruence between data sets

Environmental heterogeneity differed between the five data sets (between data set A and C specifically; Tukey's HSD $P < 0.05$), both with ($F_{4,119} = 3.84$, $P = 0.006$) and without ($F_{4,119} = 4.53$, $P = 0.001$) catchment size and altitude included (see Figure S1 in Supporting Information).

A total of 325 taxa was found across the five data sets. Trichoptera was the most diverse order with 78 taxa, followed by Diptera (52), Coleoptera (45), Ephemeroptera (43), Plecoptera (18) and Gastropoda (17). Taxonomic richness averaged 28 taxa per site and was lower in data set C than A, but no pairwise differences were evident between any other data sets ($F_{4,119} = 3.94$, $P = 0.005$; see Figure S2 in Supporting Information). Simpson's diversity index averaged 0.81 at each site, but did not differ between the five data sets ($F_{4,119} = 2.19$, $P = 0.074$; see Figure S2). Catchment-level gamma diversity ranged between 148 taxa in data set B to 184 in data set D, and BD_Total between 0.51 in data set B to 0.67 in data sets C and E (see Figure S2). Mean alpha diversity was lowest (and gamma diversity second lowest behind data set

B) and beta diversity highest in data set C, corresponding with the highest environmental heterogeneity in this data set (see Figure S1). LCBD averaged 0.04 ± 0.001 (± 1 SE) and was highest in data set A compared to the other four data sets ($F_{4,119} = 14.11$, $P < 0.0001$; Tukey's HSD $P < 0.05$). Few LCBD points per catchment were significant (Fig. 2).

Linkages between catchment size or altitude and the three response variables were highly variable between the five data sets (Fig. 2; Table 1). Likewise, forward-selected environmental variables differed considerably between the data sets and three biodiversity metrics, although some of this variability resulted from inversely correlated variables being selected, such as the different land-use variables (Table 2). In fact, there were very few selected variables shared between different data sets or metrics. Finally, variance partitioning showed a high level of variability between the different data sets and biodiversity metrics (Fig. 3).

Effects of network position

Catchment size was rarely important for predicting biodiversity, with only one identified relationship with rich-

ness or LCBD and none for Simpson's index (Fig. 2; Table 1). The significant relationships exhibited increases with increasing catchment size (Fig. 2; Table 1). Altitude was more often linked with the indices. Richness increased with altitude in three of the five data sets, Simpson's index in two and LCBD index in one.

Combined relative effects of network position and environmental variables

Of the forward-selected environmental variables, land-use variables were often selected, but these differed between data sets and included agriculture, forest, shrub and artificial landforms. In the variance partitioning framework, environmental variables regularly explained a much higher proportion of the variability than catchment size or altitude for all biodiversity metrics. The pure effect of the environment ranged from 2 to 68% for richness, 23 to 43% for Simpson's index and 13 to 55% for LCBD. Richness tended to have the highest variance explained (Adj. R^2: mean = 0.65, min = 0.39, max = 0.84), followed by Simpson's index (Adj. R^2: mean = 0.40, min = 0.21, max = 0.64) and LCBD index (Adj. R^2: mean = 0.36, min = 0.23, max = 0.54). How-
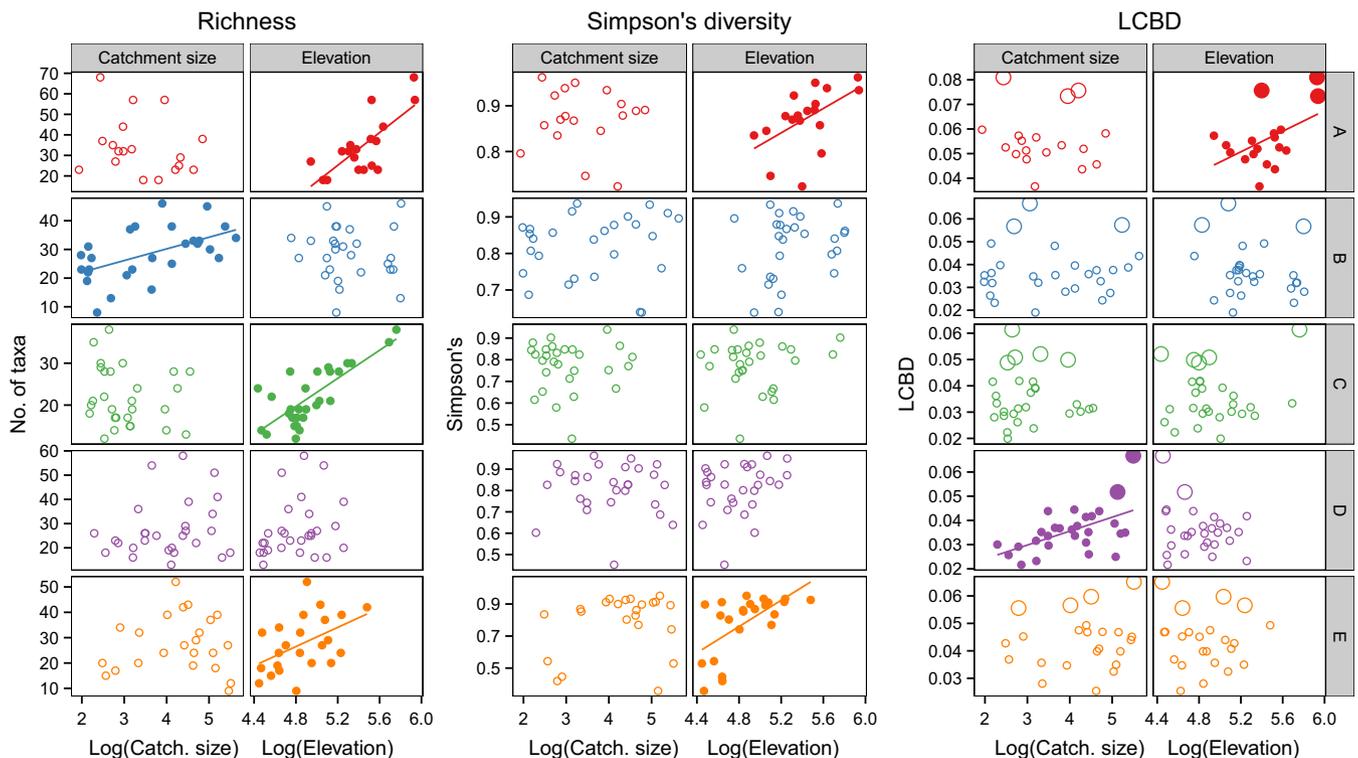

Fig. 2 Taxonomic richness, Simpson's diversity and local contribution to beta diversity (LCBD) as a function of log-transformed catchment size and altitude, across five data sets from two catchments in central Germany, sampled between 2005 and 2007. Significant relationships are shown with filled circles and plotted linear regression lines. In the LCBD sub-plot significant LCBD values at $P = 0.05$ are larger. Full regression results can be found in Table 1.

Table 1 Results from regressions between log-transformed catchment size and altitude and the three macroinvertebrate community metrics: taxonomic richness, Simpson's diversity index (1 − D) and local contribution to beta diversity (LCBD). Significant *P* values are marked in bold. d.f., degrees of freedom.

Independent	Metric	Catchment	d.f.	Intercept	Slope	F	R^2	P
Catchment size	Richness	A	16	47.64	−3.90	0.90	0.053	0.3558
Catchment size	Simpson's	A	16	0.88	0.00	0.02	0.002	0.877
Catchment size	LCBD	A	16	0.06	0.00	0.11	0.007	0.744
Catchment size	Richness	B	25	13.92	4.06	10.22	0.290	**0.0037**
Catchment size	Simpson's	B	25	0.79	0.01	0.24	0.010	0.6257
Catchment size	LCBD	B	25	0.04	0.00	0.09	0.004	0.7629
Catchment size	Richness	C	26	26.66	−1.54	0.67	0.025	0.4193
Catchment size	Simpson's	C	26	0.76	0.00	0.01	0.000	0.9352
Catchment size	LCBD	C	26	0.04	0.00	0.00	0.000	0.9448
Catchment size	Richness	D	26	15.75	2.94	1.34	0.049	0.2572
Catchment size	Simpson's	D	26	0.83	0.00	0.02	0.001	0.8759
Catchment size	LCBD	D	26	0.01	0.01	10.91	0.296	**0.0028**
Catchment size	Richness	E	21	25.55	0.48	0.04	0.002	0.8497
Catchment size	Simpson's	E	21	0.57	0.05	1.43	0.064	0.2459
Catchment size	LCBD	E	21	0.04	0.00	0.30	0.014	0.5888
Altitude	Richness	A	16	−181.98	39.84	19.66	0.551	**0.0004**
Altitude	Simpson's	A	16	0.15	0.13	6.42	0.286	**0.0221**
Altitude	LCBD	A	16	−0.06	0.02	4.95	0.236	**0.0408**
Altitude	Richness	B	25	40.63	−2.29	0.14	0.006	0.7104
Altitude	Simpson's	B	25	0.45	0.07	1.52	0.057	0.2297
Altitude	LCBD	B	25	0.08	−0.01	1.05	0.040	0.3153
Altitude	Richness	C	26	−60.69	16.75	38.97	0.600	**<0.0001**
Altitude	Simpson's	C	26	0.49	0.06	0.72	0.027	0.4026
Altitude	LCBD	C	26	0.02	0.00	0.31	0.012	0.5849
Altitude	Richness	D	26	−35.24	13.06	2.09	0.074	0.1606
Altitude	Simpson's	D	26	0.24	0.12	1.73	0.062	0.2002
Altitude	LCBD	D	26	0.08	−0.01	1.33	0.049	0.2594
Altitude	Richness	E	21	−64.29	18.91	6.32	0.231	**0.0201**
Altitude	Simpson's	E	21	−1.21	0.41	12.97	0.382	**0.0017**
Altitude	LCBD	E	21	0.05	0.00	0.03	0.001	0.8738

ever, there was considerable variability in the adjusted R^2 between data sets for each metric (Fig. 3).

This variability was reflected in the individual variation partitions. For instance, the pure effect of catchment size was unimportant in most data sets (mostly 0% explained). However, pure catchment size explained 25% for richness in data set B and combined with the shared influence of environmental variables, this was increased to 34%. The pure effect of altitude more regularly explained a substantial proportion of variation in all metrics, but was also highly variable (0–35% for richness, 0–17% for Simpson's index and 0–7% for LCBD).

Discussion

Congruence between data sets

We examined patterns of biodiversity in stream macroinvertebrate communities in relation to key environmental gradients in central Germany. Our five data sets (two

catchments and 3 years with non-overlapping study sites) showed considerable variability in the amount of variance explained, the importance of catchment size or altitude for local taxonomic richness, diversity and LCBD, and the effects of environmental variables selected for variance partitioning. These differences did not reflect differences in environmental heterogeneity between the data sets, although mean alpha and overall beta were somewhat aligned with environmental heterogeneity. Moreover, there were no clear differences in precipitation between the years, which might have influenced the results.

The mechanisms with which metacommunities are governed can be highly variable and may operate intermittently (Driscoll & Lindenmayer, 2009; Eros *et al.*, 2012; Fernandes *et al.*, 2013). Therefore, we hypothesised that there would be strong context dependency in the observed patterns, not least because the structuring of stream metacommunities in particular can be highly context dependent between different catchments (Heino *et al.*, 2012). Not only are there differences between

Table 2 Results of forward selection of environmental variables on the three macroinvertebrate community metrics. The variables column lists the variables selected for use in the variance partitioning due to being significantly linked with the macroinvertebrate metric. Catch, catchment/data set; d.f., degrees of freedom.

Metric	Catch	d.f.	F	P	Variables
Richness	A	1,16	9.40	0.006	Agriculture
Richness	B	1,25	5.41	0.031	Sub_meso
Richness	C	1,26	10.99	0.002	Artificial
Richness	D	6,21	16.89	0.001	Sub_meso, Shrub, CPOM, Terrestrial_plants, Woody_debris, Sub_mega
Richness	E	6,16	21.67	0.001	Sub_macro, Sub_gravel, Forest, Sub_meso, CPOM, Artificial
Simpsons	A	3,14	10.98	0.002	Agriculture, CPOM, Algae_cover
Simpsons	B	1,25	11.89	0.004	Artificial
Simpsons	C	1,26	9.43	0.026	Decaying_matter
Simpsons	D	1,26	10.31	0.005	Artificial
Simpsons	E	3,19	7.83	0.004	Sub_sand, Shading_stream, Sub_macro
LCBD	A	1,16	6.12	0.020	Sub_meso
LCBD	B	2,24	5.98	0.012	Algae_cover, Emergent_macrophytes
LCBD	C	2,25	7.27	0.002	Sub_micro, Forest
LCBD	D	3,24	12.01	0.002	Decaying_matter, Terrestrial_plants, Non_woody_debris
LCBD	E	2,20	9.46	0.004	Shading_stream, Forest

catchments, but also between different locations, seasons and years (Erős *et al.*, 2013; Fernandes *et al.*, 2013; Göthe, Angeler & Sandin, 2013; Heino *et al.*, 2015b,e; Tonkin *et al.*, 2016), and depending on preceding flow conditions (Campbell *et al.*, 2015). Indeed, we found clearly context-dependent patterns in the factors regulating biodiversity in these five data sets. Streams are highly stochastic systems, with strong fluctuations in environmental conditions, particularly the flow regime (Resh *et al.*, 1988) with its associated substratum disturbance (Tonkin & Death, 2012). This represents a key issue with one-off sampling, as species that are present one year due to favourable preceding conditions can be missing the following year (Erős *et al.*, 2013; Andersson *et al.*, 2014). Thus, incorporating a temporal aspect in metacommunity research has the potential to increase predictive power in our statistical models (Hill & Hawkins, 2014).

Effects of network position

Because the balance between local and regional processes may differ between different locations in the river net-

work (Brown & Swan, 2010), we incorporated altitude and catchment size as proxies for network position to represent regional controls of metacommunity structuring. However, our results contrast with the suggestion of Finn *et al.* (2011) that the positioning within a river network (i.e. headwaters versus downstream) may override other factors (including stressors) shaping stream biodiversity (particularly beta diversity), such as climate, flow and biogeography. The importance of neutral processes relating to river network structure has been clearly demonstrated both empirically (Muneepeerakul *et al.*, 2008) and experimentally (Carrara *et al.*, 2012). Yet, local variables can potentially override regional processes on stream metacommunities if there is substantial heterogeneity in conditions across space and time (Canedo-Arguelles *et al.*, 2015), and if dispersal processes do not interfere with species sorting (Heino *et al.*, 2015a).

Regional environmental heterogeneity did, in fact, promote data set beta diversity, but had no effect on gamma diversity (see Figures S1 and S2). This reflects a greater availability of niches and is consistent with some previous findings (see Heino *et al.*, 2015a). In addition to habitat heterogeneity (e.g. Astorga *et al.*, 2014), beta diversity can be promoted through a suite of different processes, including dispersal limitation (Shurin, Cottenie & Hillebrand, 2009), productivity (Bini *et al.*, 2014), and spatial extent (Heino *et al.*, 2015c). Although streams are highly heterogeneous systems with strong differences even between different riffles, this heterogeneity in both habitat and biota is likely to decrease downstream (Heino, Louhi & Muotka, 2004; Finn *et al.*, 2011). Moreover, as physical isolation is a key factor governing metacommunity dynamics (Driscoll & Lindenmayer, 2009), we hypothesised (H1) that LCBD would decline downstream (i.e. with increasing catchment size), and alpha diversity would increase simultaneously. Substantial evidence exists that although headwaters may have lower alpha diversity (but see Besemer *et al.*, 2013), they contribute substantially to overall gamma diversity through high site-to-site variation (i.e. beta diversity) between streams (Finn *et al.*, 2011). Recent work has shown this high beta diversity in low-order streams to be independent of altitude in the Rocky Mountains (Harrington, Poff & Kondratieff, 2016). Yet, we found no evidence to support this reasoning, with the only trend for LCBD being an increase downstream (i.e. with increasing catchment size) in one data set.

Catchment size was a poor predictor of biodiversity in our study in general, but more regular and clearer links were found with altitude. Where a link between the two network location variables (catchment size and altitude)
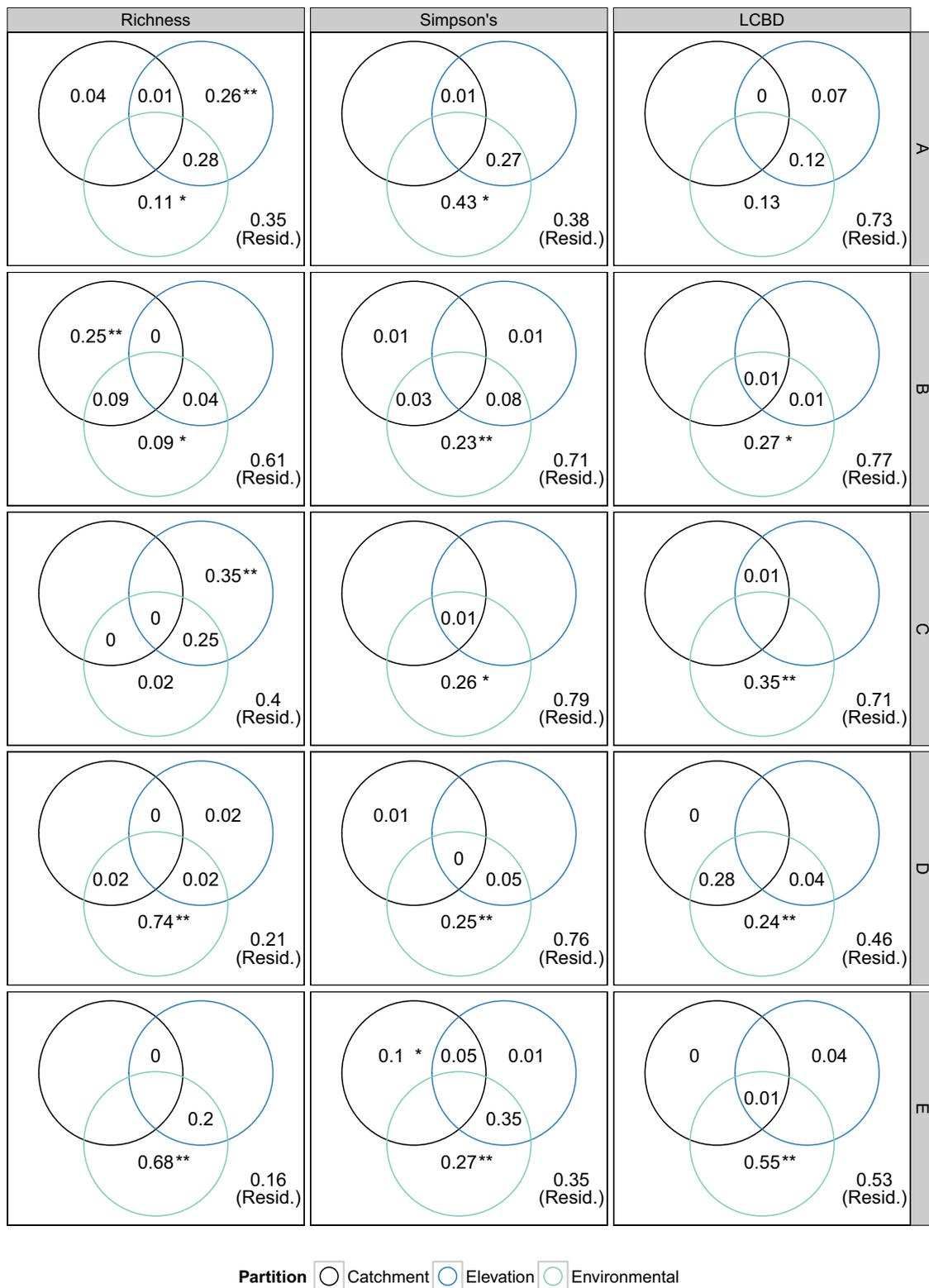
Fig. 3 Results of variance partitioning in each of the five data sets (A–E) on three macroinvertebrate community metrics: taxonomic richness, Simpson's diversity (1 − D) and local contribution to beta diversity (LCBD). Catchment size, altitude and forward-selected environmental variables were examined in separate partitions. Values displayed are the adjusted R^2 and negative values are not shown. The unexplained portion is shown in the bottom right of panels (Resid. = Residual). Forward-selected environmental variables can be found in Table 2. The full regression results can be found in Table 1. Significance of the pure effects of catchment size, altitude and local environment are show as asterisks. *$P < 0.05$, **$P < 0.01$.

and biodiversity was present, biodiversity always increased. One possible reason for such weak linkages is an uneven representation of sites along the full environmental gradient in our data sets (i.e. small headwater streams were underrepresented). However, while we had few first order streams, 41 sites in total had catchment sizes of less than 20 km^2 (all data sets had at least four sites smaller than this threshold). Thus, we believe an adequate gradient was covered to observe patterns along the river size gradient (catchment size ranged from 7 to 280 km^2). At the heart of the river continuum concept is the idea that environmental conditions change predictably downstream and lead to biodiversity peaking in mid-order streams through greater environmental heterogeneity, with headwaters being relatively depauperate (Vannote *et al.*, 1980). Our results cannot refute this suggestion, but it may be that external stressors are influencing the context-dependent patterns in our system. The strong increase in biodiversity variables with altitude in many cases suggests more suitable environmental conditions are available for the biota at higher altitudes and that increasing stressor effects emerge in downstream sites. Nevertheless, given the well documented increase in beta diversity in isolated positions within dendritic networks (Finn *et al.*, 2011; Carrara *et al.*, 2012), we would expect to see greater contributions to beta diversity at smaller catchment sizes and with increasing altitude.

Effects of environmental variables

As hypothesised (H2), the selected environmental variables, representing local drivers, captured a substantial proportion of the variability in biodiversity in our study, more than either catchment size or altitude. Local habitat conditions have been clearly demonstrated as a key factor determining stream invertebrate communities in pristine streams (Heino *et al.*, 2012; Tonkin, 2014), and the importance of land use in shaping stream communities is well understood (Harding *et al.*, 1998; Allan, 2004). Moreover, the 'local' component regulating stream community composition may also incorporate associations between taxa (i.e. biotic interactions) (Johnson & Hering, 2010). Given that LCBD essentially represents the uniqueness of a community in relation to other communities within a metacommunity (Legendre & De Cáceres, 2013), it appears that niche-related processes are operating to govern biodiversity in our study regions.

The weaker link between the environment and LCBD compared to that between the environment and rich-

ness may have emerged from impacted species pools in this region, through a long history of anthropogenic modification. Göthe *et al.* (2015) also recently found no evidence of higher beta diversity in headwater streams in a degraded landscape. Recent work has highlighted the importance of intact species pools for restoration to succeed (Sundermann, Stoll & Haase, 2011; Tonkin *et al.*, 2014), but also that anthropogenic degradation can alter associations between different species in streams (Larsen & Ormerod, 2014; Tonkin *et al.*, 2015a). In degraded environments, some of the key factors promoting beta diversity in headwaters, such as their ability to harbour more habitat specialists (Meyer *et al.*, 2007), may not be operating. While environmental control may typically be greater in headwaters (Brown & Swan, 2010; Göthe *et al.*, 2013), their communities, as in other environments, are governed by an interplay between local and regional species pool-related factors (Heino, Muotka & Paavola, 2003; Grönroos & Heino, 2012). These local-regional interactions will, in turn, be controlled by the characteristics of regional species pools. Furthermore, a potentially greater amount of variation might have been captured if we had incorporated chemical stressors in our analysis (e.g. Leps *et al.*, 2015), but consistent data for these sites was unfortunately unavailable. We omitted highly polluted sites to reduce the influence of pollution on our results, but despite the lack of such variables, we were able to explain a sizable portion of variation in our response variables using the measured environmental variables.

The poorer prediction of LCBD compared to the other metrics may also simply reflect the fact that it is a difficult metric to predict, and the evidence is currently scarce as this metric is relatively new (but see Lopes *et al.*, 2014; Silva & Hernández, 2014). However, it is noteworthy that a substantial proportion of LCBD could be predicted by local environment alone, particularly for the degraded nature of this region. Thus, regions with greater chemical and physical heterogeneity might be expected to produce even clearer results. While other factors, such as the preceding flow regime, water quality and the effects of fish predation may have also contributed to the explanation of biodiversity, we believe we incorporated the most important structuring environmental variables. Land use, for instance, is closely tied with many water quality variables (Varanka & Luoto, 2012). Moreover, it remains that stream metacommunities can be notoriously difficult to predict. This has been demonstrated in a recent global study that showed weak and variable patterns in the factors

shaping beta diversity and assemblage structure (Heino *et al.*, 2015b).

One of the key findings to emerge through considering river systems from a network perspective is the knowledge that headwaters are critical biodiversity reservoirs (Meyer *et al.*, 2007; Finn *et al.*, 2011). However, we found no evidence to support this in our study, with no decline in LCBD downstream. We instead found a much stronger role of local habitat and catchment land-use variables than catchment size and altitude (proxies of network position). In these anthropogenically altered catchments, local habitat was a reasonable descriptor of biodiversity compared to other factors governing metacommunity structure, such as the role of dispersal and positioning within the stream network. This is an interesting finding, particularly from an applied standpoint, indicating that unique assemblages emerged out of environmental control rather than physical isolation (cf. dispersal limitation).

We found highly context-dependent patterns between different data sets in our study. Context dependency is a clear challenge for the study of metacommunities, making extrapolation of findings beyond individual studies difficult and thus posing a key obstacle to overcome for the development of general ecological theories. This is not a new phenomenon, as Lawton (1999, p. 178) stated that: '...community ecology is a mess, with so much contingency that useful generalisations are hard to find'. This level of contingency is even more challenging at the even more complex level of metacommunities. Therefore, we urge researchers to continue disentangling the primary drivers of this variability between metacommunities through studies on replicate, rather than single, metacommunities.

Acknowledgments

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Supporting Information

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

Figure S1. Results of tests of homogeneity of dispersions (PERMDISP/betadisper) on environmental variables between the five data sets.

Figure S2. Summary of drainage basin biodiversity values, for five data sets in central Germany, sampled between 2005 and 2007.

Table S1. Summary of elevation and catchment size between the five data sets, sampled between 2005 and 2007 in the central German state of Hesse.

Table S2. Environmental variables and units used in this study. Variables beginning with 'Sub_' represent stony substrates.