Local contribution to beta diversity is negatively linked with community-wide dispersal capacity in stream invertebrate communities

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ABSTRACT

It is increasingly well understood that stream communities are regulated by both local niche and regional dispersal processes, but comprehensive tests of these factors with datasets that cover extensive spatial and temporal scales are rare. Based on 1180 benthic invertebrate community samples from 2005 to 2012 in central low mountain streams of Germany, we tested the hypotheses that: 1) local contribution to beta diversity (LCBD: a measure of the uniqueness of communities) would decline with increasing average community dispersal capacity; and 2) owing to the relatively large spatial extent of the study region, regional dispersal processes would override local niche controls in structuring community composition. We found considerable temporal variation in LCBD and a negative correlation between LCBD and community dispersal capacity. However, no statistically significant correlation between species contribution to beta diversity (SCBD) and species dispersal capacity was observed. The large-scale spatial structure among locations (representative of dispersal limitation) was important in structuring benthic communities. Although much of the variation was explained by the shared effects of local processes and large-scale spatial variables, environmental controls were stronger than regional processes in few cases in the variance partitioning analysis, with the annual mean temperature and mean diurnal range of temperature being the important drivers. Given the highly varied correlates of beta diversity over time, we urge researchers to focus on not only spatial variation in diversity, but also the context of temporal variation.

1. Introduction

Research in recent decades has increasingly shifted from considering local or regional species richness (i.e., alpha and gamma diversity) as independent entities to considering the variation in species composition among sets of connected local communities (i.e., beta diversity) (Anderson et al., 2011; Heino and Gronroos, 2017). A key focus in the study of beta diversity is how communities are structured over space and time. The mechanisms promoting beta diversity can be disentangled through a combined consideration of local (e.g., environmental filtering and biotic interactions) and regional processes (e.g., dispersal related processes) (Brown et al., 2018; Heino et al., 2015b; Leibold et al., 2004). While local processes are important drivers of species distributions (Al-Shami et al., 2013; Anderson et al., 2006; Schmera et al., 2013), regional processes such as dispersal from the regional species pool can be equally important (Altermatt et al., 2013;

Brown et al., 2018; Heino et al., 2015a; Heino et al., 2015b; Tonkin et al., 2018a). The relative roles of these processes can depend on the spatial scale being considered and can be heavily dependent on the environmental context (Brown et al., 2018; Heino et al., 2015b; Leibold et al., 2004; Li et al., 2018; Schmera et al., 2018).

Running waters provide an ideal model system to distinguish the roles of local niche and regional dispersal processes in structuring communities (Brown and Swan, 2010; Heino et al., 2015c). Stream ecosystems are structured in dendritic networks with high geomorphological heterogeneity (Altermatt et al., 2013; Cañedo-Argüelles et al., 2015; Fagan, 2002; Tonkin et al., 2018b). Owing to this structure, combined with clear boundaries and isolation within the terrestrial matrix, streams harbor exceptional levels of biodiversity relative to their small spatial occupation of the Earth's surface (Strayer and Dudgeon, 2010), particularly in headwaters, which are relatively more isolated than downstream sections (Finn et al., 2011). Dispersal rates

can strongly affect species richness and community composition in river ecosystems by regulating the relative role of species sorting at different locations in the network (Altermatt and Fronhofer, 2018; Li et al., 2018). Species sorting can be decoupled through two process related to the rates of dispersal: first, weak dispersal capacity of species can restrict species from tracking their preferred environmental conditions; second, strong dispersal capacity can override the effect of species sorting through mass effects and these factors can differ depending on the position of a site in the river network (Brown et al., 2018; Schmera et al., 2018; Tonkin et al., 2018a). By influencing the relative functional isolation of a location within the river network, dispersal can affect the outcome of restoration efforts or regulate the relative conservation value of a location. Therefore, it is important to integrate both niche-based and dispersal processes in order to develop effective biomonitoring and biodiversity conservation practices in river networks (Heino, 2013).

In addition to a more integrative river management focus, an understanding of what promotes the uniqueness of a local site across a broad geographic extent can generate important insights into the management of biodiversity in rivers. Through the approach of Legendre and de Cáceres (2013), one can evaluate the contribution of localities (i.e., local contribution to beta diversity: LCBD) and species (i.e., species contribution to beta diversity: SCBD) to overall beta diversity along an ecological gradient, which can help to identify unique sites in a biodiversity conservation context (Landeiro et al., 2018; Vilmi et al., 2017). We examined LCBD and its environmental drivers across a broad spatio-temporal scale in Germany, disentangled the role of local niche and regional dispersal mechanisms structuring metacommunities, and evaluated the temporal patterns of LCBD and the driving mechanisms for community structure. We tested the following two hypotheses in our study: 1) communities comprising weak dispersers should be more unique in the landscape as a result of lower recruitment rates and thus harbour higher LCBD values; and 2) given the relatively large spatial scale of our study, dispersal limitation should be the predominant structuring force, thus regional dispersal processes should override local niche controls in structuring community composition.

2. Materials and methods

2.1. Biotic data collection

We compiled 1180 benthic invertebrate samples from low mountain streams in Germany comprising 527 taxa, and covering an elevational gradient from 65 to 1114 m above sea level and catchment areas between 0.2 and 99.8 km^2 (Fig. 1). 1053 of the 1180 samples were obtained in March, April, and May, thereby minimizing seasonal effects and allowing examination of annual variation in benthic invertebrate communities in spring. These multihabitat samples were collected using a kick net (20 replicates of 25 cm × 25 cm sampling area and 500 μm mesh size) between 2005 and 2012 (Haase et al., 2004). The following criteria were applied to filter the data down to 1,180 samples: 1) Only sites with an "Ecological Quality Class" (European Commission, 2000) better than "poor" were included; 2) sites were restricted to small low mountain streams (types of 5, 5.1, 6, and 7); 3) only one random sample was used if temporally replicated samples (i.e., multiple years) were recorded at the same sampling site; 4) a minimum number of 75 samples was required per year; and 4) all the involved taxa were then filtered by the "Operational Taxalist" to ensure comparable taxonomic resolution (Haase et al., 2006).

2.2. Abiotic data collection

For each sampling site, 21 key abiotic variables out of four categories known to have strong effects on biota were selected as candidate variables for the following analysis: spatial, geohydrological, land use, and bioclimatic. Spatial data comprised the coordinates of each site,

which were recorded *in situ* using a GPS device. Geohydrological data included elevation, slope, aspect, accumulated flow, and catchment area, which were calculated based on digital elevation maps (resolution: 25 m; Federal Agency for Cartography and Geodesy of Germany; http://www.geodatenzentrum.de) using ArcGIS (version 10.1; Environmental Systems Research Institute, Inc.; http://www.esri.com). Land use data included the proportion of forest, agriculture, urban, grass/shrub, and wetland cover (resolution: 100 m; Corine land cover 2006, version 12/2009; http://www.eea.europa.eu). The proportion of each land use type at a given sampling site was calculated using the surrounding 1 km buffer zone. Bioclimatic data included nine bioclimatic variables (i.e., Bio1 = annual mean temperature, Bio2 = mean diurnal range of temperature, Bio3 = isothermality of temperature, Bio4 = temperature seasonality, Bio5 = maximum temperature of warmest month, Bio6 = minimum temperature of coldest month, Bio7 = temperature annual range, Bio10 = mean temperature of warmest quarter, and Bio11 = mean temperature of coldest quarter) and was sourced from the BIOCLIM database at the sampling point (resolution: 250 m; http://gis.cri.fmach.it/eurolst-bioclim). Prior to further calculations, we excluded highly correlated variables ($|r| > 0.75$ in the Pearson correlation analysis) to reduce the redundancy of environmental variables. We retained all variables under the category of spatial, geohydrological and land use, as well as four bioclimatic variables (Bio1-4) as the final abiotic variables for the following analyses (Appendix 1).

2.3. Dispersal capacity

To address our first question regarding the dispersal capacity of benthic invertebrates, we calculated the overall community dispersal capacity metric (DCMc) for each community. To do so, the species dispersal capacity metric (DCMs) for 459 out of 527 taxa was obtained according to Li et al. (2016). In the study of Li et al. (2016), an integral DCMs based on four dispersal modes (aquatic active, aquatic passive, aerial active, and aerial passive) was developed, which ranged between 0 and 1. As aerial dispersal can enable greater potential dispersal distance than aquatic dispersal, Li et al. (2016) assigned more weight to the aerial dispersal mode to increase the accuracy of the DCMs. The final equation of the DCMs was defined in Li et al. (2016) as follows (Eq. (1)):

$$DCMs = \frac{(aqa_i + aqp_i + 2 \times aea_i + 2 \times aep_i) - min_c}{max_c - min_c} \quad (1)$$

where *DCMs* refers to species dispersal capacity metric, aqa_i refers to the aquatic active dispersal mode of species *i*, aqp_i refers to the aquatic passive dispersal mode, aea_i refers to the aerial active dispersal mode, and aep_i refers to the aerial passive dispersal mode, min_c and max_c refers to the species with the lowest and the highest sum of dispersal capacity values within the whole community *c* (n = 459), respectively.

The DCMc of a given sample was calculated as the average DCMs weighted by species abundance. DCMc was defined in Li et al. (2016) as follows (Eq. (2)):

$$DCMc_j = \frac{\sum_{i=1}^{n} DCMs_i \times AP_{ij}}{\sum_{i=1}^{n} AP_{ij}} \quad (2)$$

where $DCMc_j$ refers to community dispersal capacity metric at site *j*, $DCMs_i$ refers to dispersal capacity metric of species *i*, $Abund_{ij}$ refers to the abundance of species *i* at site *j*.

Four dispersal groups representing from weak to strong dispersers were firstly categorized by splitting the data into four quartiles ranked by dispersal capacity. Taxa in the 1st quartile with lower DCMs were categorized as weak dispersers. Taxa in the 2nd and 3rd quartiles were defined as weak-medium and strong-medium dispersers. The remaining taxa in the 4th quartile with higher DCMs were categorized as strong dispersers.
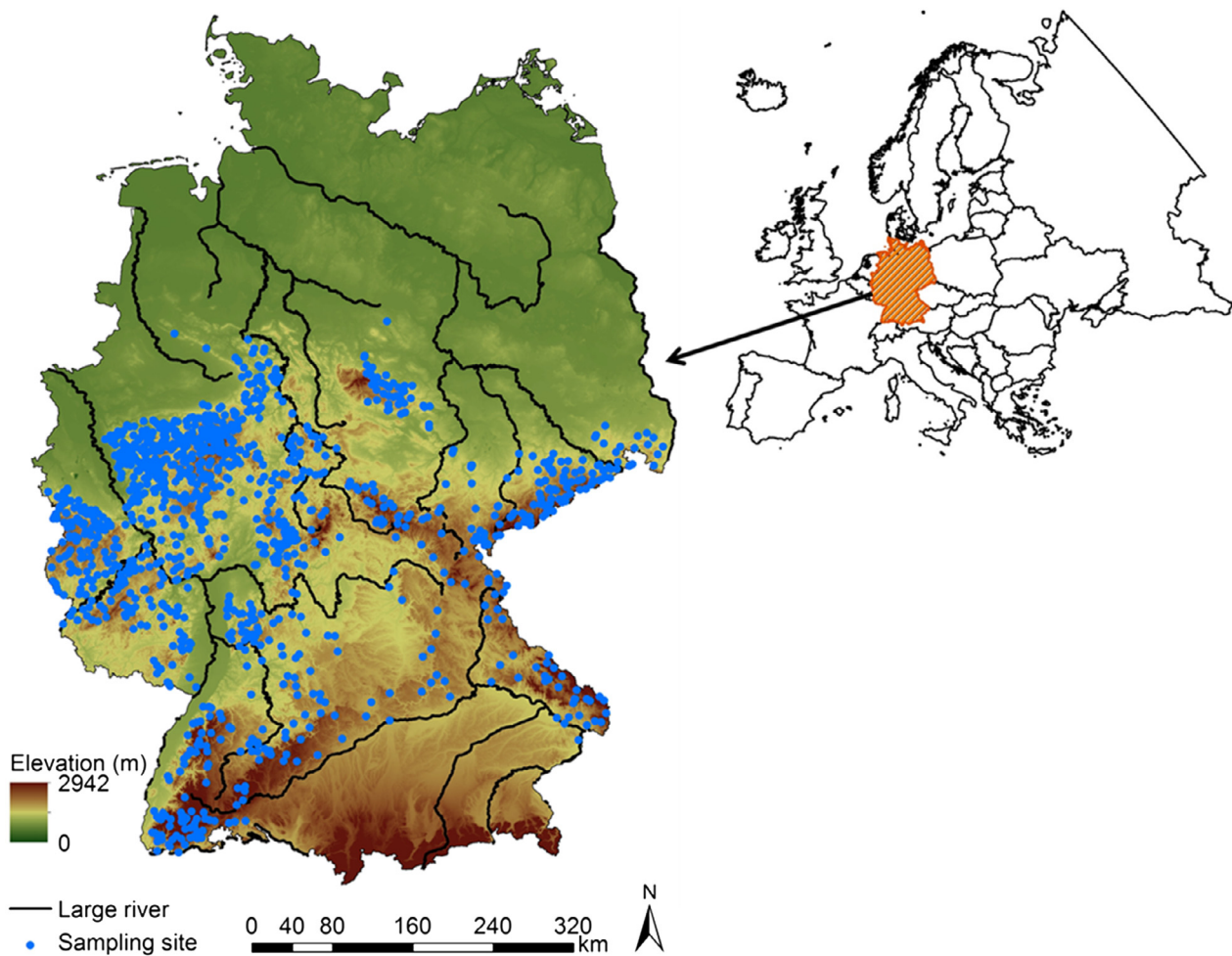
Fig. 1. Distribution of sampling sites in Germany.

2.4. Statistical analyses

To calculate beta diversity, we followed the approach proposed by Legendre and de Cáceres (2013). We examined the total beta diversity (BDtotal, a measure of the total variation of the community matrix), the local contribution to beta diversity (LCBD, a measure of ecological uniqueness of each sampling site), and the species contribution to beta diversity (SCBD, a measure of relative contribution of individual species to beta diversity) in our study. To evaluate the temporal variation in beta diversity of benthic invertebrates, we calculated BDtotal, LCBD, and SCBD for each year's dataset ('annual'), as well as for the combined years ('combined'). Simple linear relationships between BDtotal and year, between DCMc and LCBD, and between DCMs and SCBD were then examined using the *lm* function in R 3.0.2 (R Core Team, 2018). The linear relationship between the environmental variables and LCBD were examined using the *corrplot* package (Wei et al., 2017) in R 3.0.2 (R Core Team, 2018). Using the code provided by Legendre and de Cáceres (2013), the value of LCBD for each sampling site was calculated with 999 permutation on Hellinger-transformed species abundance data, in combination with the *vegan* package (Oksanen et al., 2018) in R 3.0.2 (R Core Team, 2018). To indicate the spatial and temporal variation in LCBD, the significance of LCBD in a given sampling site was calculated using the above approach.

To evaluate the pure and shared fractions of community structure explained by different variables, we modeled the multivariate response of entire community as well as weak and strong dispersers to a matrix of local environmental, large- and small-scale spatial variables using variation partitioning (our second hypothesis). Both annual and combined data were used for the entire community, but only the combined data were specifically used for weak and strong dispersers. Fourteen environmental variables (i.e., five geohydrological, five land use, and four bioclimatic variables) were used as the first explanatory set, and two spatial matrices were created using principal coordinates of neighbor matrices (PCNM) based on geographical coordinates of each sampling location. PCNM transforms pairwise spatial distances based on a distance matrix of geographic coordinates of sites into rectangular data for use in constrained ordination methods. The output vectors of PCNM were split into two sections. The first half of the eigenvalues represented large-scale spatial variation (including large and intermediate spatial variations) and the second half small-scale spatial variation (including small and intermediate spatial variations). Because the gradient length of the first detrended correspondence analysis (DCA) axis was smaller than 3 (Table 1), partial redundancy analysis (pRDA) was employed to carry out the variation partitioning analysis for species abundance (Hellinger-transformed). After first checking for significance of overall RDA models, forward selection was used to choose the most significant and important variables for each of three explanatory sets (Dray et al., 2006). A double stopping criterion was performed in the forward selection to avoid type I error and overestimating the amount of explained variance in species communities (Borcard et al., 2018). Selection of variables stopped if the significance level alpha ($P > 0.05$) was reached or if the adjusted R^2 (Adj. R^2) of the model exceeded the Adj. R^2 of the predefined global model (Blanchet et al., 2008). The above analyses were carried out using the *PCNM* (Dray et al., 2006), *packfor* (Legendre et al., 2005), and *vegan* packages (Oksanen et al., 2018) in R 3.0.2 (R Core Team, 2018).

Table 1

Summary of the number of samples per year, the total beta diversity (BDtotal), the length of detrended correspondence analysis (DCA) axis 1, and the number of variables involved in each explanatory set for variation partitioning analysis. *Df* refers to degree of freedom. Local = local environmental control, L-Spa = large-scale spatial variable, S-Spa = small-scale spatial variable. The statistical tests of the selected variables are available in Appendix 2.

Data source	Nr. sample	BDtotal	DCA	*df* of community		
				Local	L-Spa	S-Spa
2005	109	0.62	0.15	6	7	6
2006	111	0.63	0.14	7	4	4
2007	378	0.63	0.25	11	13	12
2008	144	0.65	0.18	6	6	5
2009	75	0.68	0.21	5	4	3
2010	145	0.62	0.20	7	3	2
2011	75	0.63	0.18	2	3	3
2012	143	0.62	0.15	7	6	6
Combined	1180	0.65	0.27	9	48	47

3. Results

3.1. Dispersal capacity and its correlation with LCBD and SCBD

The DCMs varied greatly among taxonomic groups. All taxa of Oligochaeta, Crustacea, Hirudinea, Turbellaria, Planipennia, Gastropoda, Porifera, and Megaloptera were weak dispersers, whereas most of the Ephemeroptera, Diptera, and Trichoptera were strong dispersers (Fig. 2).

BDtotal ranged between 0.62 and 0.68 (Table 1), indicating no overall temporal trend (simple linear regression: $F_{1, 6} = 0.01$, Adj. $R^2 = 0.00$, $P = 0.91$). Overall, the unique sites differed throughout the years (Fig. 3). For annual data, LCBD ranged between 1.50 and 28.02×10^{-3}, and on average 13.6% of sites (range of annual replicates 9.5–21.1%) were significant (Fig. 3). LCBD declined with increasing community dispersal capacity (simple linear regression: $F_{1, 1178} = 12.05$, $R^2 = 0.010$, $P = 0.0005$; Table 2). For combined data, LCBD ranged between 0.46 and 1.67×10^{-3}, and on average 12.12%

Fig. 2. The proportion of the taxonomic richness among the four dispersal groups for each taxonomic group.

of sites were statistically significant (Fig. 3). Combined-year LCBD was also negatively linked with the DCMc (simple linear regression: $F_{1, 1178} = 10.02$, $R^2 = 0.008$, $P = 0.0016$; Table 2). SCBD ranged between 0.001 and 20.28×10^{-3}, and no statistically significant relationships between SCBD and DCMs were observed (simple linear regression for the combined data: $F_{1, 457} = 1.94$, $R^2 = 0.004$, $P = 0.1649$; Table 2).

3.2. Regional and local controls

Variation partitioning showed some fluctuation in the amount of variation explained by the pure explanatory sets of variables with community data (Fig. 4). On average, the full amount of variation explained in benthic invertebrate communities was 17.6% and 20.0% with annual and combined data, respectively. Overall, large-scale spatial variables explained a higher amount of variation than small-scale spatial variables or environmental variables (ca. 5.5% and 10.7% with annual and combined data, respectively). For annual data, a higher amount of variation was explained by local environmental controls (5.1%) than by small-scale spatial variables (2.1%), whereas an opposite pattern was detected for combined data (local environmental controls vs. small-scale spatial variables = 2.2% vs. 2.6%). Most models had a certain amount of shared effects between two explanatory sets, with particularly high values observed between local environmental controls and large-scale spatial variables (4.7% and 5.0% with annual and combined data, respectively; Fig. 4).

All three explanatory datasets explained less variation in strong dispersers (residual = 84.5%) than in the entire community (residual = 80.0%) data and weak dispersers (residual = 80.3%; Fig. 4 & Appendix 3). Similar to the entire community data, the large scale spatial variables explained a much greater amount of variation than other two explanatory datasets with both weak (large scale:small scale:local = 7.3%:3.2%:2.6%) and strong dispersers (large scale:small scale:local = 7.6%:3.6%:1.4%; Appendix 3). Overall, there was very little difference between weak and strong dispersers.

Temporal variation was evident in the environmental drivers determining community structure (Table 3). Overall, climatic variables including Bio1 (annual mean temperature) and Bio2 (mean diurnal range of temperature) were important environmental drivers, followed by slope, elevation, and land use variables (Table 3). The environmental drivers were further used to correlate with LCBD. In general, latitude and longitude positively correlated with LCBD, most geohydrological and land use variables showed weak correlations with LCBD (Fig. 5). LCBD declined with increasing annual mean temperature (Fig. 5). In contrast, LCBD positively correlated with mean diurnal range of temperature and temperature seasonality (Fig. 5).

4. Discussion

Our analyses revealed that the uniqueness of benthic invertebrate communities (LCBD) varied over time in rivers across Germany, and this uniqueness was negatively related to community-wide dispersal capacity. While accounting for both local and regional processes in structuring communities, we found that most variation was explained by large-scale spatial variables, as well as their shared effects with local niche controls. However, niche controls were stronger than regional processes in few cases in the variance partitioning, with the annual mean temperature and mean diurnal range of temperature being the important drivers.

4.1. Dispersal capacity and its correlation with LCBD

As hypothesized, we found a negative relationship between LCBD and community-wide dispersal capacity. Knowing the factors that drive site uniqueness can allow for better prioritization of biomonitoring, conservation and other general management initiatives for the maintenance of riverine biodiversity (Heino, 2013). Sites with high LCBD
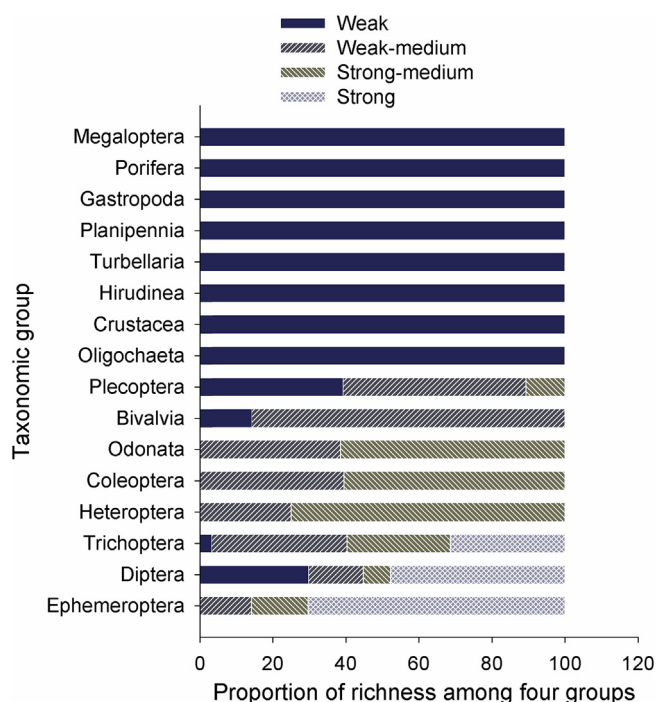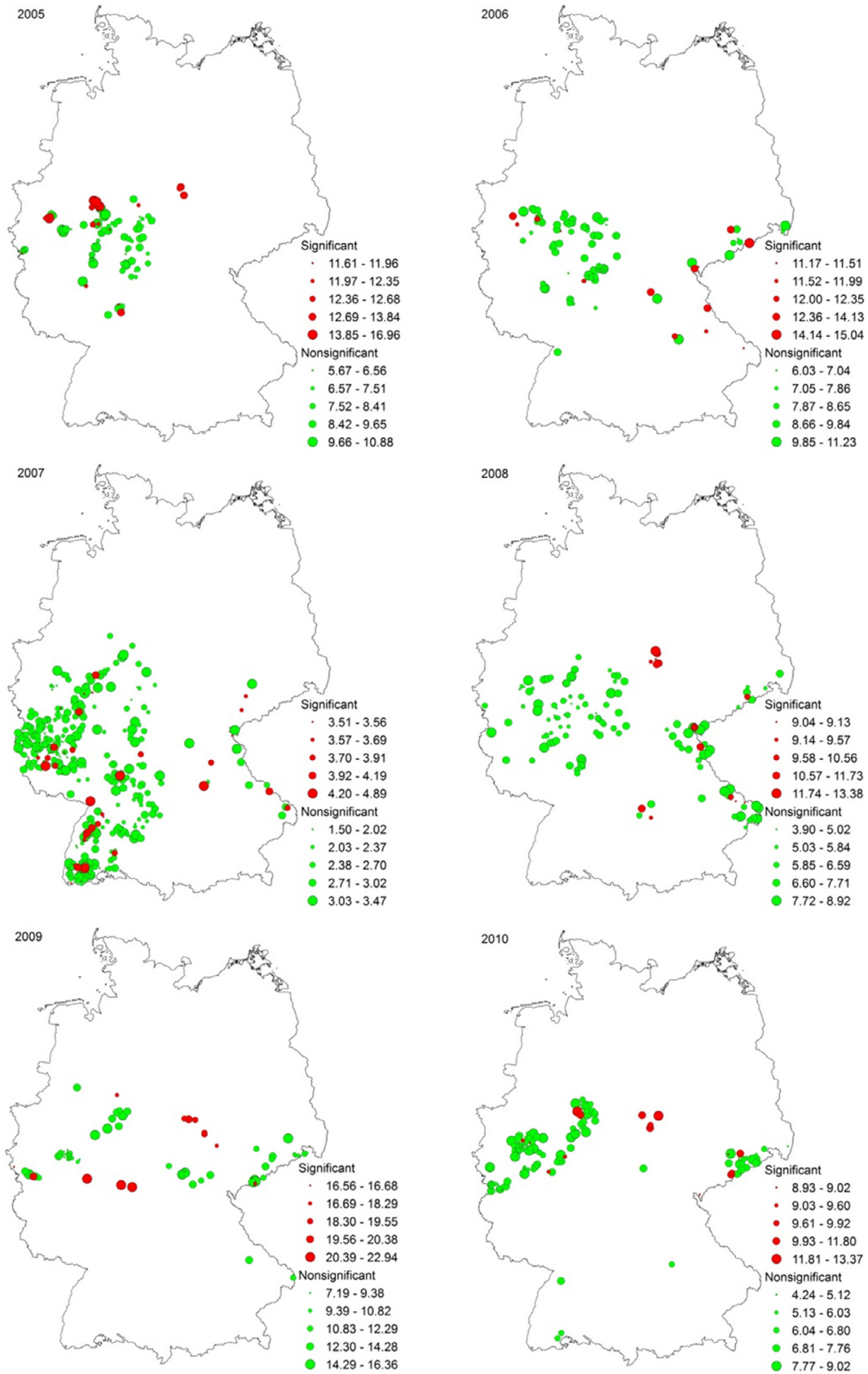
Fig. 3. Maps of significant (red point; *P* < 0.05) and nonsignificant values (green point) of local contribution to beta diversity (LCBD × 10^{-3}) with annual and combined data, respectively.
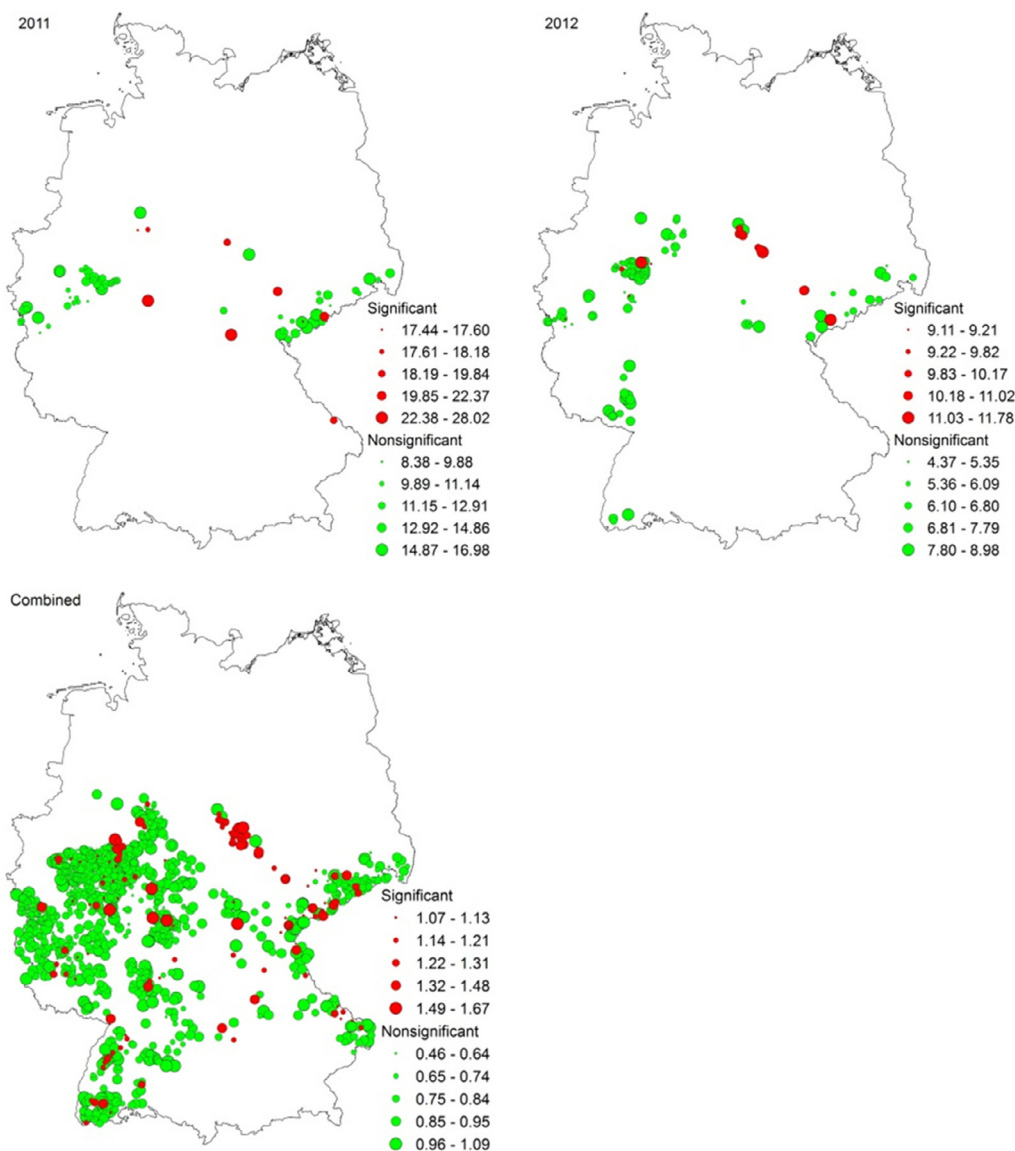
Fig. 3. (*continued*)

Table 2

Linear relationships between community dispersal capacity metric and local contribution to beta diversity (LCBD) and between species dispersal capacity metric and species contribution to beta diversity (SCBD). *Df* refers to degree of freedom.

Category	Variable	Coefficient	Intercept	*df*	*F*	R^2	*P*
LCBD	Annual	−0.0035	0.0090	1,1178	12.05	0.0101	0.0005
	Combined	−0.0002	0.0009	1,1178	10.02	0.0084	0.0016
SCBD	2005	0.0015	0.0011	1,457	1.94	0.0042	0.1649
	2006	0.0015	0.0011	1,457	2.06	0.0045	0.1523
	2007	0.0019	0.0009	1,457	3.57	0.0077	0.0595
	2008	0.0020	0.0008	1,457	2.49	0.0054	0.1155
	2009	0.0015	0.0011	1,457	1.81	0.0039	0.1790
	2010	0.0004	0.0017	1,457	0.16	0.0004	0.6890
	2011	0.0011	0.0013	1,457	0.99	0.0022	0.3211
	2012	0.0018	0.0008	1,457	3.19	0.0069	0.0748
	2013	0.0010	0.0014	1,457	0.61	0.0013	0.4347
	Combined	0.0015	0.0011	1,457	1.94	0.0042	0.1649

values are associated with a unique species composition, potentially representing locations of particular conservation or management concern (Legendre and de Cáceres, 2013; Legendre and Gauthier, 2014).

Our results indicate that dispersal is a key factor determining site uniqueness, highlighting the importance of incorporating metacommunity ecology into applied management contexts.

A community composed of species with strong dispersal capability is likely to have a lower contribution to beta diversity or LCBD than a community comprising weak dispersers (Heino, 2013), as we have demonstrated here. This discrepancy results from communities with weak dispersers being more heterogeneous than those with strong dispersers (in line with our first hypothesis) as a result of dispersal limitation. Given the strong role of spatial structuring and the negative link between DCMc and LCBD, limited dispersal appears to be the main factor promoting the uniqueness of assemblages in these German streams. Indeed, strong dispersal capacity can increase the community similarity among sites to the point of homogenizing communities at extreme rates of dispersal (Gronroos et al., 2013; Vonesh et al., 2009). For example, previous studies in river networks showed that increased connectivity in mainstem river sections compared to headwaters can lead to more similar communities among mainstem locations (through mass effects) than those in headwaters (with species sorting operating) (Brown and Swan, 2010). Some have even suggested that the physical position of sites within the dendritic network may override niche mechanisms in structuring communities (Finn et al., 2011). Yet, Tonkin et al. (2016a)
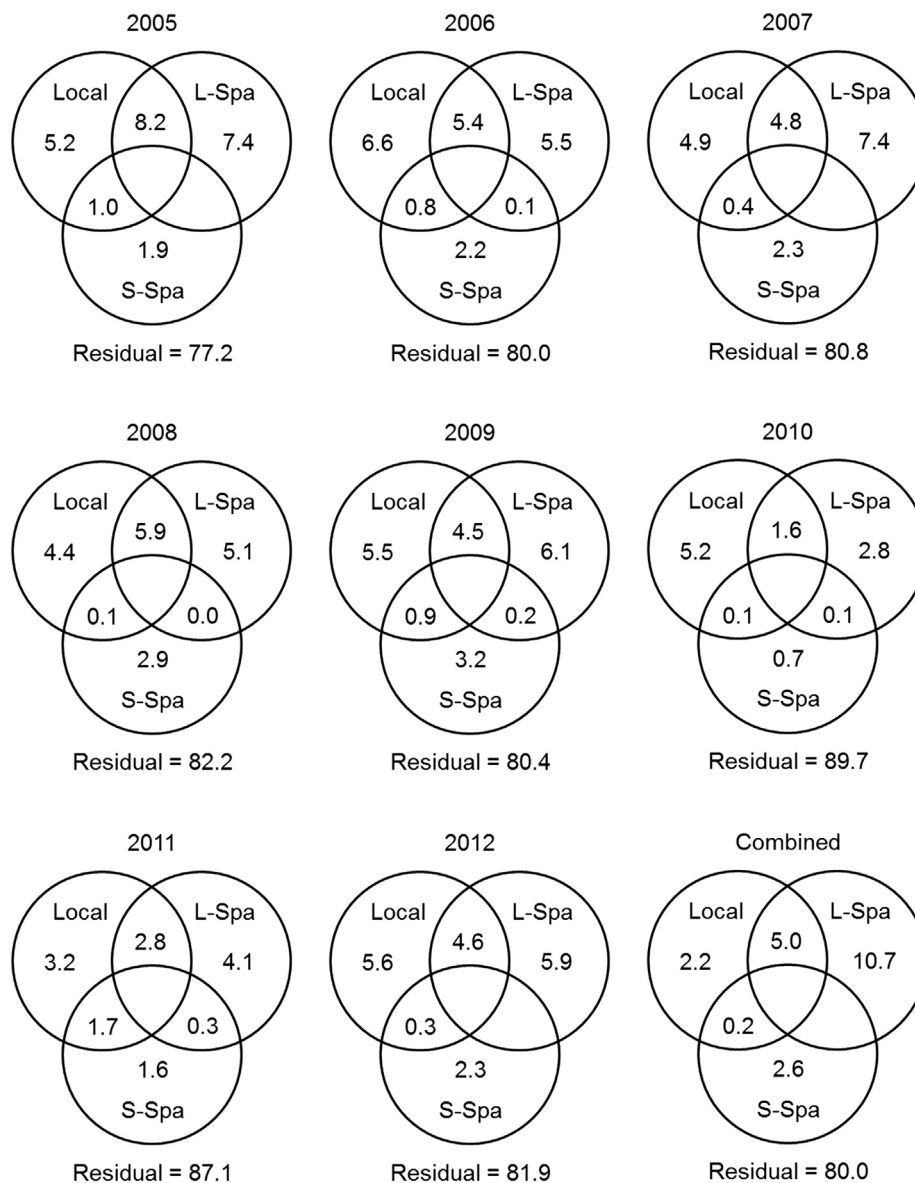
Fig. 4. Fractions of variance explained by local environmental (Local), large-scale spatial (L-Spa), small-scale spatial variables (S-Spa), and their shared effects using the variation partitioning analysis with community data. Values shown in the diagrams are the proportions of variation in each analysis, and negative values are not displayed.

found no evidence of a decline in LCBD downstream in German river networks.

In our study, there were some cases where local niche controls (e.g., annual mean temperature and mean diurnal range of temperature) emerged as more important drivers of community structure and LCBD. The negative correlation between annual mean temperature and LCBD is in line with the correlation between DCMc and LCBD, as most headwaters, which typically have lower temperature, harbor communities with lower dispersal capacity (Li et al., 2018). The positive link between mean diurnal range of temperature and LCBD might be the consequence of niche control, where only a few species, which can result in high LCBD, can adapt to habitats with large temperature fluctuations.

4.2. Comparison between regional and local controls

Although both local and regional processes drive the patterns of biodiversity, the relative importance of each process may vary. We found a higher amount of variation in benthic invertebrate communities explained by large-scale spatial variables both alone and combined with local environmental variables. This indicates the importance of spatial processes (e.g., isolated sites can harbour more unique species) in structuring community composition, and also reflects potential dispersal limitation and/or local niche controls being spatially structured. From a conservation perspective, strong dispersal capacity is important to maintain species abundance and distribution range, with dispersal limitation being associated with reduced dispersal capacity (Heino, 2013). As the interaction between local and regional processes is scale dependent (Heino et al., 2015b), local niche conditions tend to be the best predictors of stream communities at intermediate spatial extents (reflecting species sorting) (Landeiro et al., 2018). Two temperature variables were determined as the most important environmental variables explaining community structure. This is not surprising given the large temperature gradient within the study area, and supported by the importance of the large-scale spatial variables, which reflects increasing dispersal limitation at large spatial scales (Heino, 2013; Shurin et al., 2009) (supporting H2). Historical processes can also be reflected in the large-scale spatial variables; e.g., isolation by

Table 3
The forward selected environmental variables in variation partitioning analysis predicting community structure. All the selected variables are statistically significant as $P < 0.05$. The given number refers to the importance of the abiotic variable. A value of 1 indicates the most important variable and the importance reduces with the increasing of the value. Bio1 = annual mean temperature, Bio2 = mean diurnal range of temperature, Bio3 = isothermality of temperature, Bio4 = temperature seasonality, flow = accumulated flow, and area = catchment area. The results of statistical tests are shown in Appendix 2.

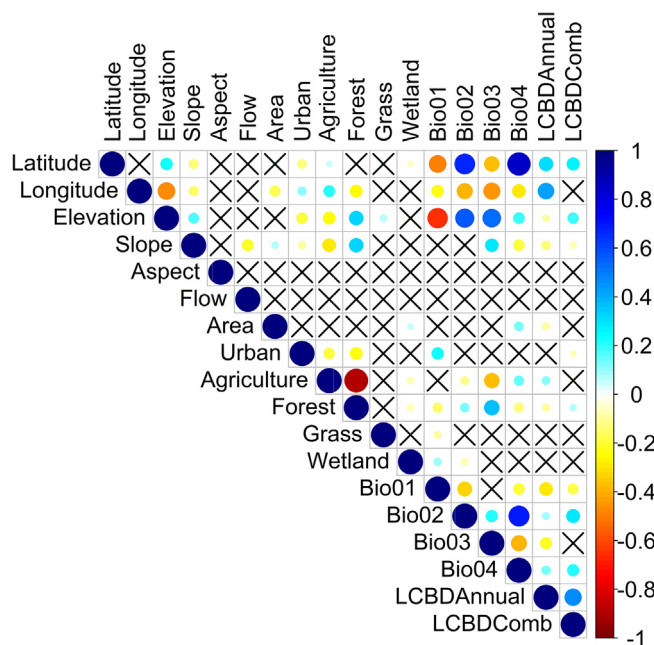| Variable	2005	2006	2007	2008	2009	2010	2011	2012	Combined
Elevation		4	5	4		2	1	3	5
Slope			9		7				9
Flow			8						
Area	6	3	3	2		5		4	3
Urban			10						8
Agriculture		7		6	4	4		2	4
Forest	4		7					5	
Grass									
Wetland			11						
Bio1	1	1	2	1	1	1		1	1
Bio2	3	5	6	3	5	3		6	2
Bio3	5	6	1		3				7
Bio4	2	2	4	5	2	6	2	7	6

Fig. 5. Linear relationships between environmental variables and local contribution to beta diversity (LCBD). Size of symbol is proportional to the maximum absolute value of the correlation coefficient (i.e., 1). The cross symbol means that the given correlation is not statistically significant at $\alpha = 0.05$.

geographical barriers (Thomas, 2011). Such a finding suggests that bioassessment may be more effective across larger spatial extents for strong dispersers than that for weak dispersers (Heino, 2013). It is also apparent that improved knowledge of how dispersal and local niche control interact is not only useful for the development of metacommunity theory, but also important for conservation practice (Heino, 2013; Li et al., 2016; Tonkin et al., 2014; Tonkin et al., 2017).

We found considerable temporal variation in the drivers and structuring of these communities, which may reflect changing metacommunity dynamics. This temporal dynamic deserves considerable attention for examination of beta diversity given the highly dynamic nature of lotic systems. Equally feasible in this case given the nature of the data is the fact that different sites were incorporated each year. Thus the different observed patterns, and the different combination of

samples each year may have either partially or fully covered the overall biological and environmental information of the study area. One may get inconsistent results from such data (Langenheder et al., 2012), as species that occur in one or several continuous years may not be present in following years due to the lack of preferred habitats being sampled. Associated with these different configurations of sampling localities, there was likely variation in the spatial arrangement, extent and therefore level of connectivity among sites in the different years. As the ecologically unique sites were different throughout the years, we assume that the fractions explained by spatial variables somehow also indirectly illustrate temporal variation.

While the explanatory power of our variation partitioning models were low (residuals: 77.2–89.7), these values are in line with many previous studies (Göthe et al., 2013; Gronroos et al., 2013; Heino, 2011; O'Hare et al., 2012; Tonkin et al., 2016b). There are several possible reasons for this; two obvious reasons are: First, the involved environmental variables may not adequately account for the variation in benthic invertebrate communities. Beside the selected environmental variables, there are a wealth of potentially important variables shaping benthic invertebrate communities including physiochemistry, hydromorphology, primary production, fish predation force, species pool, landscape characteristics, disturbance regimes, and the history of glacial retraction (Vinson and Hawkins, 1998). However, we believe we incorporated a realistic set of predictor variables for our broad-scale data, given the availability of data at this scale. Second, stochastic factors, such as rare events of colonization, extinction, and disturbance may lead to a low explanatory power (Pimm et al., 2014; Stoll et al., 2014).

5. Conclusions

In this study, we found a negative correlation between LCBD and community dispersal capacity. This suggests that dispersal rates may be controlling the presence of unique stream communities; unique sites are those comprising weaker dispersers. We found regional dispersal processes were important in structuring benthic communities in our study, likely reflecting the large spatial extent of the study. Given the highly variable drivers of communities observed in our study over time, we suggest that examining the drivers of temporal variation in the factors structuring biodiversity in streams is as important as spatial variation. However, this ideally requires a long-term, harmonized and standardized measurement programs (Haase et al., 2018). The spatio-temporal complexity of our results and the importance of dispersal capacity in driving community uniqueness highlight the importance of considering metacommunity dynamics in river management and conservation practice.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.105715.

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