

Dispersal capacity and broad-scale landscape structure shape benthic invertebrate communities along stream networks



Fengqing Li^{a,*}, Jonathan D. Tonkin^{a,b}, Peter Haase^{a,c}

^a Senckenberg Research Institute and Natural History Museum Frankfurt, Department of River Ecology and Conservation, Gelnhausen, Germany

^b Oregon State University, Department of Integrative Biology, Corvallis 97331, OR, USA

^c Faculty of Biology, University of Duisburg-Essen, Essen, Germany

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ABSTRACT

Dispersal is a fundamental trait influencing species' distribution patterns and metacommunity structure. Yet, for stream communities it remains unclear how communities differ in dispersal capacity. Due to the dendritic network structure of streams and the greater spatial variability in environmental conditions in headwaters than in mainstems, we asked three main questions: 1) Do benthic invertebrates inhabiting headwaters have lower community-wide dispersal capacities (*DCc*) on average than those living in mainstems? 2) In turn, does the degree of community dissimilarity among sites differ between the different locations in the river network? 3) Are these differences more pronounced in highland streams compared to lowland streams as a consequence of major landscape features (i.e. mountains)? To examine these questions, we compiled 1466 benthic invertebrate samples across the southern highland and northern lowland areas of Germany. Results showed that overall *DCc* increased with stream size in both highland and lowland streams. In highland streams, higher *DCc* in mainstems was associated with more homogeneous communities compared to headwater communities. However, this pattern did not occur in lowland streams. This suggests that both dispersal capacity and landscape structure interact to determine community structure in these networks. Our results therefore stress the importance of considering dispersal traits and landscape features, as well as habitat control (or environmental filtering) to better understand (meta-) community structure across various landscape types.

1. Introduction

Biogeographic patterns of communities result from the combined influences of habitat characteristics, landscape features, historical contingencies, and species interactions (Levin, 1992; Cottenie, 2005). To explore species' distribution and diversity patterns, the meta-community concept has been called upon in recent years (Leibold et al., 2004; Holyoak et al., 2005; Logue et al., 2011; Winegardner et al., 2012). The two most commonly evoked paradigms, species sorting and mass effects, primarily differ with regard to the relative importance of dispersal-driven processes (Cottenie, 2005; Beisner et al., 2006; Abbott, 2011; Altermatt et al., 2011). Species sorting often occurs in moderately connected habitats and assumes that communities are mainly structured by local environmental conditions (i.e. habitat control), depending on adequate dispersal capacity of species, a measure of the frequency and distance of an organism's movement among different habitats (Heino, 2013; Li et al., 2016), to track preferred conditions.

Mass effects, on the other hand, often apply in highly connected habitats, where dispersal-driven processes override habitat control (Mouquet and Loreau, 2003; Leibold et al., 2004).

Stream ecosystems depict relatively isolated habitats in the general landscape but they are highly connected longitudinally and are structured as hierarchical dendrites, providing a unique network structure for their inhabitants (Dunning et al., 1995; Campbell Grant et al., 2007; Swan and Brown, 2014). Such a network organization can strongly regulate and structure local communities by limiting dispersal routes for many taxa (Altermatt et al., 2013; Anderson and Hayes, 2018; Brown et al., 2018; Tonkin et al., 2018). For instance, the dispersal of benthic invertebrates is often constrained to the stream corridors; adults with a flight stage can disperse in the air after emergence, while others are limited to in-stream dispersal (Bilton et al., 2001; Shurin et al., 2009; Tonkin et al., 2018). As a result, metacommunity dynamics in dendritic stream systems may largely differ from those of the terrestrial realm (Campbell Grant et al., 2007; Munepeerakul et al., 2008;

* Corresponding author at: Senckenberg Research Institute and Natural History Museum Frankfurt, Department of River Ecology and Conservation, Clamecystrasse 12, Gelnhausen 63571, Germany.

E-mail address: qflee3@gmail.com (F. Li).

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Auerbach and Poff, 2011; Swan and Brown, 2014), and there is a growing body of empirical research that demonstrates this (Liu et al., 2013; Heino et al., 2015; Fourtune et al., 2016; Seymour et al., 2016a,b). Hierarchical dendritic stream systems therefore offer a unique perspective to examine the influence of habitat connectivity, dispersal modes and regional biodiversity structure (Brown and Swan, 2010; Altermatt et al., 2013; Göthe et al., 2013).

There is evidence to suggest that headwater communities are structured by local habitat conditions (species sorting paradigm), whereas mainstem communities are increasingly structured by geographic distance (inferring dispersal-driven control, i.e., mass effects) due to the higher level of connectivity between sites (Brown and Swan, 2010; Schmera et al., 2018). Well-connected sites located centrally in stream networks may also support greater local species richness compared to more isolated communities (Altermatt et al., 2013). Recent experimental work found population densities to be highest in nodes connected to headwaters, rather than central nodes or the headwaters themselves (Altermatt and Fronhofer, 2018). Although habitat control and connectivity are primary structuring agents of community composition, the different role that dispersal-driven processes play in headwaters and mainstems suggests that dispersal capacity of organisms will likely influence metacommunity dynamics. Studies investigating the difference in dispersal capacity of stream organisms between headwaters and mainstems are, however, limited (Brown and Swan, 2010; Göthe et al., 2013; Cañedo-Argüelles et al., 2015).

Weak dispersers are often specialist species that can out-compete strong dispersers (or generalist species) in their most favoured habitats (Verberk et al., 2010; Buchi and Vuilleumier, 2014). In headwaters, where environmental sorting is strong, one can expect more specialist species and thus most likely lower dispersal capacities. Given previous findings and the potentially strong role of dispersal capacity in shaping stream metacommunity dynamics, we addressed the following two questions at large spatial scales across Germany: 1) Does dispersal capacity of benthic invertebrate communities differ between headwaters and mainstems? 2) In turn, does the degree of community dissimilarity between sites differ between the different locations in the river network?

Previous stream metacommunity studies have mostly focused on low order stream networks (1st to 3rd order) in areas with moderate topographic relief (e.g. Brown and Swan, 2010; Swan and Brown, 2014). However, there has been a recent expansion in the exploration of metacommunity studies in stream networks at both large scales (Liu et al., 2013; Tonkin et al., 2015; Fourtune et al., 2016; Seymour et al., 2016a, b) and in regions with extreme topography (Tonkin et al., 2017). Here, in addition to taking a large-scale perspective on this question, including a wide range of topographic relief (highland vs. lowland areas), we also examined the importance of dispersal capacity, its relation to community structure, and dependence on overall landscape structure over a much greater gradient of stream sizes (up to 1000 km² in catchment area). The topographic structure of highland areas potentially poses greater barriers to dispersal for stream organisms than in lowland areas through both greater relief and a more hierarchical dendritic structure of the stream networks (Haddad, 1999). Indeed, Tonkin et al. (2017) showed that extreme topographic relief can represent a clear dispersal barrier to aerially dispersing insects in the Himalayas. These differences in landscape structure may also be reflected in the dispersal capacity of organisms from highland and lowland environments. The landscape of Germany provides a good platform to test this difference as the southern part is characterized by continuous mountains (highland region) and the northern part consists purely of floodplains (lowland region). Therefore, given the more hierarchical structure of highland stream networks compared to streams in lowland areas, we also examined whether overall landscape structure would affect the strength of the relationships between headwaters and mainstems. More specifically, we asked our final question: 3) Are changes in community dispersal capacity (*DCc*) and community

dissimilarity between headwaters and mainstems more pronounced in highland compared to lowland areas?

2. Materials and methods

2.1. Data collection and preparation

A collection of 7982 benthic invertebrate samples was obtained from standardized field surveys provided by the Umweltbundesamt (UBA) of Germany for the period 2006–2009. Four criteria were used with regard to the inclusion of samples. First, all samples from sites with poor habitat quality were eliminated and only samples labelled as “high” or “good” Ecological Quality Class (EQC) according to the EU Water Framework Directive (Bis and Usseglio-Polatera, 2004; Furze et al., 2006) were selected. Subsequently, samples from rivers with catchment areas greater than 1000 km² were eliminated. Following step two, only streams indexed as highland (stream type indices 2–19; alpine foothills and central highlands) or lowland (stream type indices 14–23; central plains) were selected for analysis (see Sommerhäuser and Pottgiesser, 2004 for an overview of stream type index in Germany). Finally, only one random sample was selected if temporally replicated samples were recorded at the same sampling site. After filtering, 1466 samples remained (Fig. 1; Appendix 1; 1261 and 205 samples were defined as highland and lowland, respectively), which covered 753 km in latitude, 603 km in longitude and 1117 m in elevation.

For each site, catchment area was extracted from digital elevation maps (U.S. National Aeronautics and Space Administration, <https://wist.echo.nasa.gov>, resolution: 30 m). Catchment area group (or stream section) was determined based on the category of catchment size which was defined by the EU Water Framework Directive (Sommerhäuser and Pottgiesser, 2004). Sampling sites from group 1 (0–10 km²) were defined as headwaters, sites from group 2 (10–100 km²) were classified as transitions, and sites from group 3 (100–1000 km²) were mainstems. The number of sampling sites in each group is available in Appendix 1.

Benthic invertebrates were collected and identified according to the protocol of Haase et al. (2004a, b). All the involved taxon lists were then filtered by the “Operational Taxalist” (Haase et al., 2006) to ensure comparable taxonomic resolution. Most taxa were identified at genus or species level, while Chironomidae, Naididae, and Tubificidae were determined only to the sub-family or family level, which resulted in 661 taxa from the filtered 1466 samples.

2.2. Dispersal capacity

To address our first and third questions regarding the differences in dispersal capacities of benthic invertebrate communities between headwaters and mainstems for highland and lowland streams, we calculated the overall community dispersal capacity (*DCc*) for each sample. To do so, we first obtained the species dispersal capacity (*DCs*) for all the selected 661 taxa according to Li et al. (2016). Based on four dispersal modes (aquatic active, aquatic passive, aerial active, and aerial passive) of benthic invertebrates provided by the Standardization of River Classifications (STAR; www.eu-star.at) project, Li et al. (2016) developed an integral *DCs* for 802 benthic invertebrate taxa, ranging between 0 and 1. For the majority of benthic invertebrate species, the aerial dispersal distance is greater than the aquatic dispersal distance (Minshall and Petersen, 1985). Therefore, it is necessary to assign more weight to the aerial dispersal mode to increase the accuracy of an overall dispersal metric. Li et al. (2016) defined the most suitable overall (standardized and weighted) *DCs* as follows (Eq.(A.1)):

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

where *DCs* refers to species dispersal capacity metric, *aqa_i* refers to the aquatic active dispersal mode of species *i*, *aqp_i* refers to the aquatic

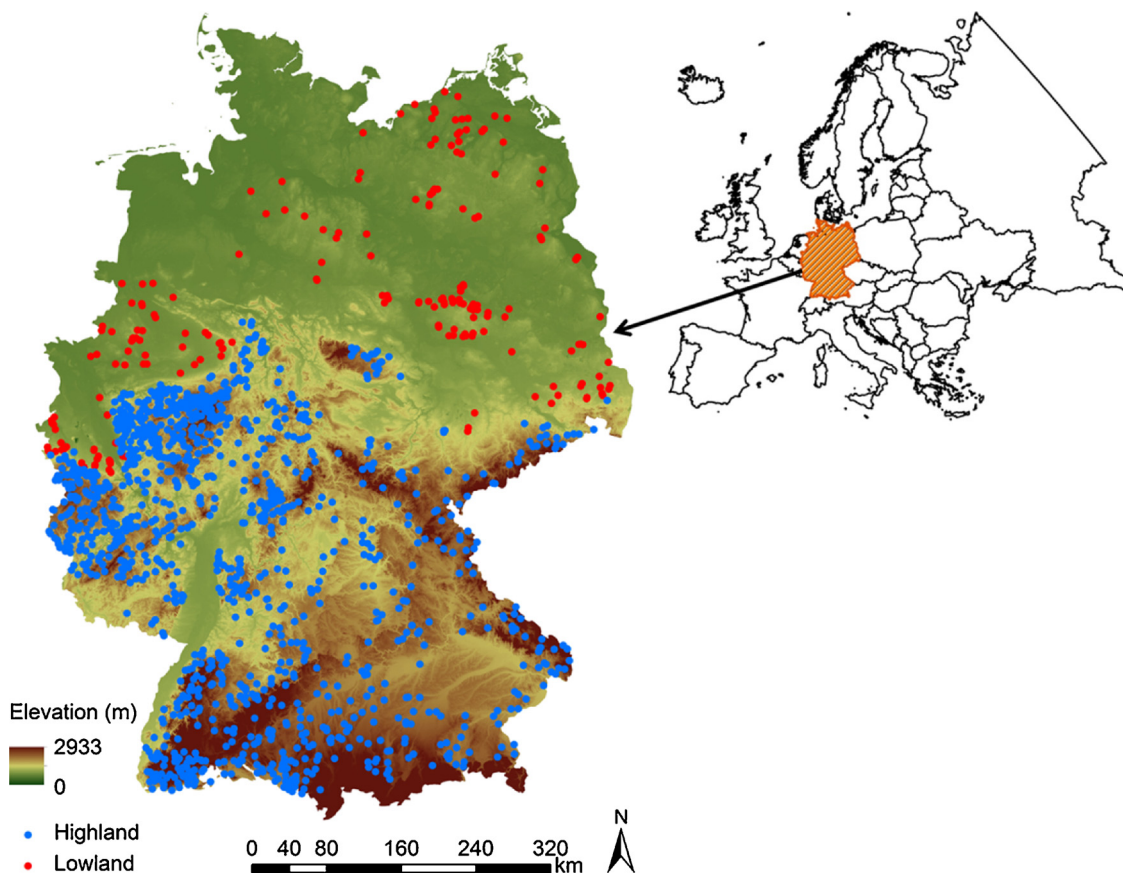


Fig. 1. Geographic locations of sampling sites in Germany. Highland refers to alpine foothills and central highlands, and Lowland refers to central plains.

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 ($n = 661$), respectively.

Second, a DCc of a given sample, reflecting the relative composition of weak and strong dispersers, was calculated as the average DCs weighted by species abundance. DCc is calculated as follows (Eq. (A.2)):

$$DCc_j = \frac{\sum_{i=1}^n DCs_i \times Abund_{ij}}{\sum_{i=1}^n Abund_{ij}} \quad (\text{A.2})$$

where DCc_j refers to community dispersal capacity at site j , DCs_i refers to dispersal capacity of species i , $Abund_{ij}$ refers to the abundance of species i at site j .

2.3. Statistical analysis

All statistical analyses were carried out in R 3.0.2 (R Core Team, 2015) using the “vegan” package (Oksanen et al., 2014).

To address our second question regarding the variability of community composition of benthic invertebrates, the degree of community dissimilarity between pair-wise samples was evaluated for each stream section across highland and lowland streams using Bray-Curtis distance. Prior to the calculation, the abundance community data was log-transformed to reduce the compound effect of extreme values. As dissimilarity values within each stream section were not independent of one another, a randomization-based permutational analysis of multivariate dispersion (PERMDISP) was used to discern whether stream sections differed in community dissimilarity (Anderson et al., 2006; Chase, 2010). Based on the Bray-Curtis distance matrix, beta-dispersion analysis produced an independent dissimilarity value for each sample by means of PERMDISP (999 permutations) – distance to group

centroid. Based on individual sampling sites, simple linear regressions were used to extract the relationships between DCc of sampling sites and independent dissimilarity index (distance to centroid) across highland and lowland streams.

For both lowlands and highlands, independent one-way analysis of variance (ANOVA) was performed to evaluate differences in DCc and community dissimilarity among the three stream sections used in our study. Tukey’s multiple comparison tests were then used in case of a significant ANOVA result ($\alpha = 0.05$).

3. Results

For both highlands and lowlands, the DCc of benthic invertebrates was significantly lower in headwaters than mainstems (Tukey’s test, $P < 0.05$; Table 1). In highland streams, DCc in transition sections was higher than in headwaters (Tukey’s test, $P < 0.05$; Table 1) but not different from mainstems. However, for lowland streams, DCc in transition sections was more similar to headwaters (Tukey’s test, $P > 0.05$; Table 1). Overall, DCc was higher in highland than lowland streams (Fig. 2A).

Significant differences in community dissimilarity (beta diversity) between headwaters and mainstems were found (Table 1). Most striking was that for highland sites, community dissimilarity decreased with stream size (ANOVA, $P < 0.05$; Table 1), whereas for the lowland streams, community dissimilarity was not linked to stream size and there was no difference between headwaters and mainstems (Tukey’s test, $P > 0.05$; Table 1, Fig. 2B).

DCc was significantly but weakly linked with community dissimilarity (distance to centroid based on PERMDISP) for highland streams (general linear regression, $P < 0.05$), whereas no significant relationship was observed for lowland streams (Fig. 3).

Table 1

One-way analysis of variance (ANOVA) and Tukey’s post hoc tests of community dispersal capacity (*DCc*) and community dissimilarity among three stream sections across highland and lowland streams in Germany. The community dissimilarity is calculated based on the distance to centroid using beta-dispersion analyses. The difference refers to mean pairwise difference between stream sections. No values are provided for community dissimilarity in lowland streams due to the non-significance of ANOVA.

Variable	Region	ANOVA			Tukey’s test		
		<i>df</i>	<i>F</i>	<i>P</i>	Comparison	Difference	<i>P</i>
<i>DCc</i>	Highland	2,1258	21.43	< 0.0001	Headwater-Transition	−0.05	0.0000
					Headwater-Mainstem	−0.05	0.0000
					Transition-Mainstem	0.00	0.9982
	Lowland	2,202	15.10	< 0.0001	Headwater-Transition	0.01	0.8112
					Headwater-Mainstem	−0.08	0.0016
					Transition-Mainstem	−0.09	0.0000
Community dissimilarity	Highland	2,1258	3.22	0.0403	Headwater-Transition	0.01	0.0365
					Headwater-Mainstem	0.01	0.0469
					Transition-Mainstem	0.00	0.7826
	Lowland	2, 202	0.67	0.5123	Headwater-Transition	–	–
					Headwater-Mainstem	–	–
					Transition-Mainstem	–	–

4. Discussion

While dispersal-driven processes play a key role in shaping benthic invertebrate community patterns along stream networks (Finn et al., 2011; Altermatt et al., 2013; Tonkin et al., 2018), the precise role of dispersal, and more specifically dispersal capacity, remains unclear. Observed shifts in metacommunity structure between headwaters and mainstems may not only be driven by habitat connectivity but by the actual capacity of organisms to disperse. In our study, we examined differences in dispersal capacity of stream benthic invertebrate communities and its role in shaping regional community structure across a large network of German streams and found clear patterns in community dispersal capacity (*DCc*) and community dissimilarity (the answer to question 1). The spatial extent of observation should influence the specific role of dispersal capacity in shaping biodiversity patterns in such studies. While previous work has indicated a shift in the relative roles of metacommunity paradigms from isolated headwaters to more connected mainstems in small streams (Brown and Swan, 2010), we examined these patterns across a much broader stream size gradient, and across larger spatial scales and elevational gradients.

4.1. Difference in *DCc* and community dissimilarity

We showed that dispersal capacity of benthic invertebrate communities is significantly lower in headwater streams than in mainstem sections. This answers our first question suggesting that mainstem species have a higher dispersal capacity compared to headwater

species. This may be a result of the greater average overland distance between two adjacent mainstems than between two adjacent headwaters across large catchment size gradients (up to 1000 km²) and spatial extents. We acknowledge that overland dispersal may be more difficult in headwaters in many instances because of complex topography (Bilton et al., 2001; Karna et al., 2015) but our argument that mainstems in large rivers tend to be more distant from their neighbours than headwater sites is supported by our results. These different observations mainly go back to differences in the study areas (i.e. catchment size and spatial extent). In our study, mainstems are defined as river sections with catchment sizes between 100 and 1000 km², differing from the previous studies of Brown and Swan (2010) and Swan and Brown (2014), who focused on low order stream sections. The differences in *DCc* between headwaters and mainstems in our study could be interpreted as either an evolutionary adaptation of mainstem species to the larger distances that need to be travelled between two larger mainstem sections and to allow for a sufficient gene flow, or alternatively the presence of a large number of generalist species with stronger dispersal capacity in mainstems compared to poorer dispersing specialists in headwaters. Recent genetic studies (Hughes, 2007; Geismar et al., 2015) reported that stream benthic invertebrates regularly disperse across catchment boundaries by either flying or crawling over land. The distances travelled is species specific, however. The headwater caddisfly *Drusus discolor*, for example, is limited in its dispersal to distances up to 20 km (Geismar et al., 2015).

The observed differences in *DCc* between headwater species and those inhabiting larger mainstems corresponds to the higher

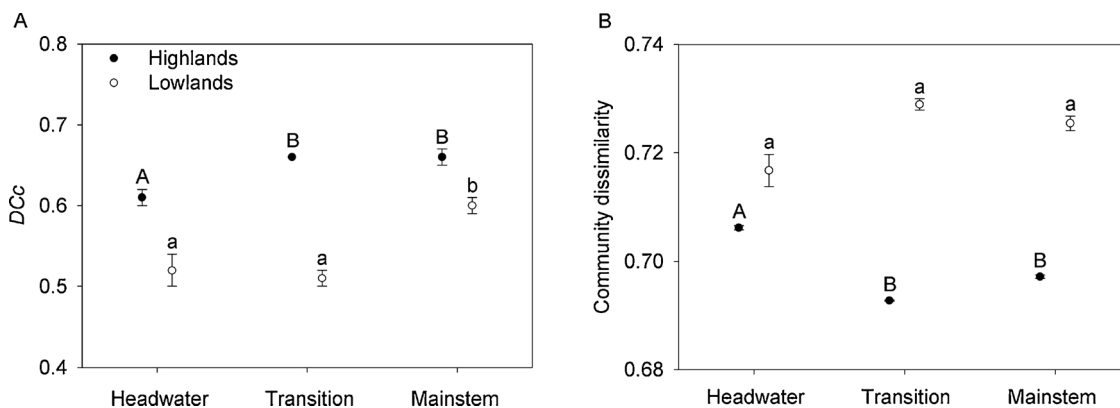


Fig. 2. (A) *DCc* (community dispersal capacity) and (B) community dissimilarity across highland and lowland streams in Germany. Points are mean and whiskers are standard error. Different letters indicate significant differences between stream sections (Tukey’s multiple comparison test, $P < 0.05$). The community dissimilarity is calculated based on the distance to centroid using beta-dispersion analyses.

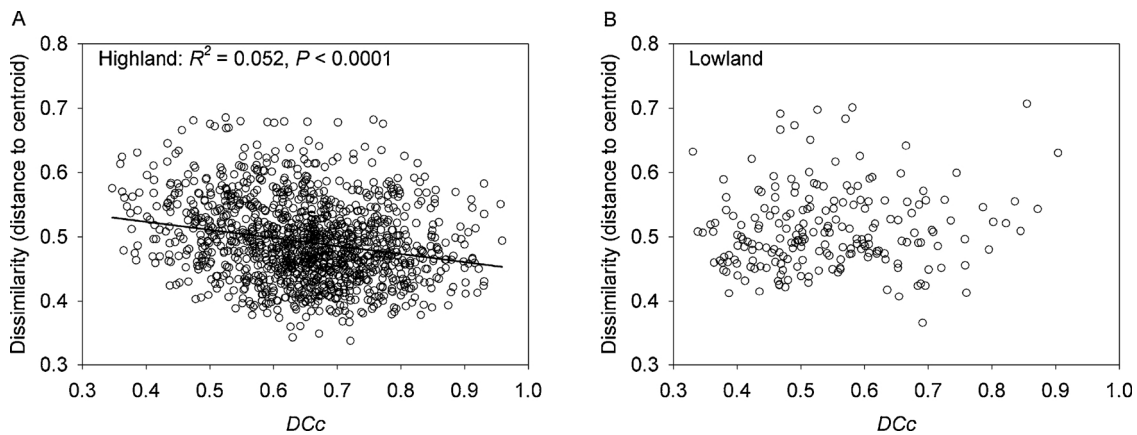


Fig. 3. Relationships between DCc (community dispersal capacity) and community dissimilarity across (A) highland and (B) lowland streams in Germany using general linear regressions. The community dissimilarity is calculated based on the distance to centroid using beta-dispersion analyses.

community dissimilarity in headwater sections than in mainstem sections in the highlands in our study (the answer to question 2). Previous studies have suggested that headwater communities should align with the species sorting paradigm, whereas dispersal-driven processes should override environmental control to shape mainstem communities, corresponding to the mass effects paradigm (Brown and Swan, 2010; Finn et al., 2011). In this sense, dispersal capacity should operate in unison with habitat connectivity gradients and, in turn, strongly influence the role of these various metacommunity paradigms in shaping local community structure. Essentially, a higher DCc should in turn lead to weaker habitat control, through source-sink dynamics, where organisms disperse into non-preferred habitats. Compared to Brown and Swan (2010) the different scale of observation is an important consideration to interpret our findings, as at these larger spatial extents and covering larger network gradients, other factors than connectivity alone likely play a much greater role in shaping community patterns and dispersal dynamics. Moreover, these factors are likely to differ depending on whether along-network or overland dispersal is considered (Cañedo-Argüelles et al., 2015; Karna et al., 2015; Tonkin et al., 2018), including differences in habitat gradients, topographic heterogeneity, and dispersal barriers between these sections. Thus an alternative explanation of the observed differences in community dissimilarity in our study is that other factors (e.g., physiochemical, morphological and hydrological factors) (Vannote et al., 1980; Verberk et al., 2010) than the observed differences in dispersal capacity are structuring communities. Among these factors, habitat heterogeneity and connectivity may play a more important role (Tonkin et al., 2018).

Indeed, while significant, dispersal capacity appeared to play a minor role in structuring these communities, explaining just 5.2% of variation (Fig. 3A). It is well understood that multiple factors (both niche and neutral processes) operate in unison to shape stream metacommunities, working at a range of spatial and temporal scales (Heino et al., 2015; Tonkin et al., 2016b). Thompson and Townsend (2006) found that both dispersal-driven effects and habitat control combined structured benthic invertebrate communities in New Zealand streams. While our study provides some insight into these metacommunity patterns, it is important to bear in mind that we addressed these patterns at large spatial scales, going beyond the typical metacommunity level of individual catchments and focusing on large regional-scale data. Therefore, we can only provide clear insight into the relative differences in DCc among larger stream networks, and whether there was a corresponding difference in variability in communities.

4.2. Highland versus lowland

Many stream metacommunity studies have focused on highland regions, where stream systems are strongly dendritic, and thus

bypassing potentially important differences between other landscape structures. Landscape type and associated geographic factors (e.g. geographic barriers) may act as a filter to shape specific dispersal dynamics and local communities (Poff, 1997; Chase and Ryberg, 2004). In our study, we found differences in overall DCc between highland and lowland streams with higher DCc in the highland region (Fig. 2A). Highland benthic invertebrate communities may need higher dispersal capacities to overcome the geographic barriers in their surroundings that may not exist in the lowlands. In addition, we found differences in community dissimilarity between headwaters and downstream sections in highland streams, but not in lowland streams (the answer to question 3). While in highland streams these differences may be explained by differences in DCc and/or geographic barriers, differences in DCc in lowland streams are not reflected in changes in community composition, indicating an overriding influence of landscape features (i.e. lack of geographic barriers).

Higher community dissimilarity of highland headwater streams compared to highland mainstem sections, with no corresponding differences between different lowland stream sections, probably reflects differences in the level of isolation apparent between these landscapes. Headwaters of highland streams are likely more isolated than headwaters in lowlands as the presence of geographic barriers such as steep valleys and mountains make it more difficult for organisms to disperse. The isolating effect of extreme topographic relief on the structure of aerially-dispersing stream insect metacommunities has been demonstrated in the Nepalese Himalaya (Tonkin et al., 2017). In highland regions the barrier effect decreases with increasing stream size. This in turn should promote beta diversity (community dissimilarity in our case) in highland headwaters (Swan and Brown, 2014), more so than in the lowlands. The importance of geographical barriers has been broadly documented as they are a major structuring forces in ecological and evolutionary organization, potentially leading to species extinctions or driving speciation (McCain, 2009; Larsen et al., 2011). In concordance with other studies (Poff, 1997; Haddad, 1999; Beisner et al., 2006; Hof et al., 2006), our results therefore further emphasize the importance of particular landscape settings on dispersal capacity, structuring large-scale biodiversity patterns, and at finer spatial scales, metacommunity structure. However, there are also other differences than topographic features between lowlands and highlands. For example, human pressures are probably stronger in lowlands potentially overriding topographic influences (Harrington et al., 2016; Tonkin et al., 2016a).

With our study, we highlight that using species dispersal traits can uncover important patterns to help understand the mechanisms underlying broad spatial patterns of community structure. The revealed patterns indicate that dispersal capacity can interact with regional landscape features to shape stream communities at large spatial scales. Understanding the way in which dispersal processes shape

biogeographic patterns in the context of major landscape features, particularly for stream ecosystems, also has strong applied implications. For instance, recent work has clearly indicated the importance of spatial processes in ensuring successful outcomes to river restoration projects in low mountain streams (Stoll et al., 2014; Tonkin et al., 2014; Stoll et al., 2016). A better understanding of benthic invertebrate dispersal capacity and the influence of landscape features on community variation within (longitudinal gradients, headwaters vs. mainstems) and between stream networks (landscape gradients, highland vs. lowland streams) is vital for understanding biogeographic patterns and meta-community structuring, and for promoting efficient landscape management.

Competing interests

The authors have declared that no competing interests exist.

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Appendix 1 Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.limno.2018.06.003>.

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