Metacommunity structuring in Himalayan streams over large elevational gradients: the role of dispersal routes and niche characteristics

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ABSTRACT

Aim To examine metacommunity structuring in stream communities over large elevational gradients by disentangling physical and environmental structuring and the importance of different dispersal routes and niche characteristics.

Location Headwater streams in three catchments in the Hindu-Kush Himalaya of central and eastern Nepal.

Methods We explored metacommunity structuring of stream invertebrates (including deconstructed assemblages by niche position and breadth) using a combination of approaches, including the elements of metacommunity structure and distance-decay relationships. We compared the importance of dispersal routes, elevation and local environmental conditions through five distance matrices: Euclidean, topographic, river network, elevational and environmental.

Results Communities were structured along the elevational gradient with clear turnover apparent in two catchments, with Clementsian (compartmentalized) and Gleasonian (individualistic) distributions. Local environment played a minor role, and the selected distance matrices (i.e. elevation, three physical distances and environment) varied between catchments and niche groups. Contrary to expectation, specialists were more spatially than environmentally controlled, potentially reflecting dispersal limitation.

Main conclusions In these physically dominated systems, local environment was overridden by dispersal limitation, particularly when considering specialists. Where barriers were not limiting dispersal, niche sorting along the elevational gradients represented the key structuring force. Overall, our findings reveal the importance of elevation and the spatial arrangement of sites in structuring metacommunities. We emphasize the value of considering physical structuring and spatial extent in modulating species sorting in metacommunities.

Keywords altitude, Clementsian, dispersal route, distance-decay, elements of metacommunity structure, invertebrate, nestedness, niche breadth, niche position, stream community

INTRODUCTION

Ecological communities are the product of the interaction between local and regional processes (Leibold et al., 2004; Holyoak et al., 2005). The relative role of these processes – local niche control and dispersal from the regional species pool – depends on the environmental setting and the organisms occupying the metacommunity. Differences in specialization of species may influence their response to local and regional processes. Following the species sorting metacommunity paradigm, habitat specialists reflect local environmental conditions more strongly and exhibit less spatial
structuring than generalists (Pandit et al., 2009). This reflects classical theory on the differentiation between common and rare species, where generalists are expected to occupy more sites and be more locally abundant than specialists (Brown, 1984). In contrast, specialists will be rare within a particular metacommunity, but abundant where environmental conditions suit (Brown et al., 1995).

In addition to niche filtering, dispersal is a fundamental component structuring metacommunities, regulating the role of species sorting (Leibold et al., 2004). Observed differentiation between metacommunity paradigms is often due to differential connectivity between locations. Mass effects and dispersal limitation (high and low dispersal, respectively) provide opposite ends of the dispersal spectrum in metacommunities (Heino et al., 2015a). Consequently, the structure of dispersal routes is central to controlling access to local communities, with stream networks providing a unique example (Cañedo-Argüelles et al., 2015; Kärnä et al., 2015). While environmental conditions are often more important than spatial structuring in stream invertebrate communities (Siqueira et al., 2012; Kärnä et al., 2015), the dendritic arrangement of river networks (Altermatt, 2013) plays a key role in organizing metacommunities (Brown & Swan, 2010). This structuring can elevate beta and decrease alpha diversity in headwaters compared with downstream sections (Finn et al., 2011).

Elevation also features strongly in structuring biodiversity (Rahbek, 1995; Lomolino, 2001), largely reflecting changing abiotic conditions, such as temperature and oxygen (Jacobsen, 2008). Studies in freshwater systems have found varied patterns in community structuring and turnover between different organisms along elevational gradients (e.g. Wang et al., 2011, 2012). Running water systems provide ideal testing grounds for exploring patterns and processes in metacommunity structuring along physical and environmental gradients for a variety of reasons, such as their high biodiversity, dendritic structure and isolated position embedded in a terrestrial matrix. Himalayan streams, in particular, comprise unique biodiversity (Allen et al., 2010) and large elevational gradients for testing metacommunity concepts. However, while there has been sporadic interest in stream communities of the Hindu-Kush Himalaya (e.g. Ormerod et al., 1994; Suren, 1994), comparatively little is known compared with other regions globally.

We examined metacommunity structure in Himalayan headwater streams in three catchments (Langtang, Yangri-Indrawati and Makalu) of central and eastern Nepal. We disentangled physical and environmental structuring and the importance of different dispersal routes (overland, topographic and along river) between different environmental settings spanning large elevational gradients using distance-decay relationships (DDR). We treat elevation as an environmental gradient in our study given its strong regulation of environmental conditions, but we also include a second data matrix of specific local habitat variables. We also applied the elements of metacommunity structure (EMS) framework to examine distributional patterns and compared patterns between deconstructed niche groups based on niche position and breadth, enabling an estimation of differences between specialist and generalist species. As demonstrated in a recent study on wetland microcrustaceans (Gascón et al., 2016), combining complementary techniques to examine metacommunity structure enables robust insights into the factors organizing metacommunities.

Given the large elevational gradients sampled and its central role in structuring biodiversity through altering abiotic conditions, we hypothesized (1) that elevation would be the strongest structuring force on these metacommunities (i.e. the most readily selected distance matrix in the DDR model selection approach), followed by spatial structuring between sites. The main difference between these three datasets was the arrangement of sampling sites along different branches of the river network (Fig. 1) allowing a clear look at the role of network structuring and dispersal barriers. Therefore, we hypothesized that (2) the different arrangement of sites would alter the importance of network compared to overland distances within catchments; large potential overland dispersal barriers (mountain ranges) were present between sites in two catchments (Fig. 1). Based on this, we expected river network distance would be more important in Langtang and Makalu, as sites were split between two river branches divided by high elevation mountain ranges resulting in limited overland dispersal between branches. (3) Metacommunities would display clear turnover in their structure, also due to the strong elevational gradient sampled (Gutiérrez-Cánovas et al., 2013). This would produce either Clementsian (clumped), Gleasonian (individualistic) or hyperdispersed (evenly spaced) gradients, but we did not formulate hypotheses about which of these patterns of turnover would emerge. Finally, based on the predictions of Pandit et al. (2009), we hypothesized (4) that deconstructed communities of generalist taxa would exhibit more evidence of spatial control than communities of specialists (tested using niche position and breadth).

MATERIALS AND METHODS

Study sites and sampling

Stream invertebrate assemblages were examined based on previously collected data (Shah et al., 2015) from three regions, representing separate catchments, in the Hindu-Kush Himalaya of central and eastern Nepal (Fig. 1). The Langtang catchment ($N = 22$) had the largest spatial extent, followed by Yangri-Indrawati ($N = 15$) and Makalu catchments ($N = 14$; see Appendix S1 in Supporting Information). We focused on each catchment as an independent metacommunity, rather than pooling the data, as there is clear evidence for strong structuring and isolation among the catchments (Hoppeler et al., 2016).

Sites were selected to cover a clear elevational gradient, with elevational ranges between 2492 and 2926 m for the
three catchments (Appendix S1). Thus, sites span from subtropical to alpine in condition in each catchment. Headwater stream (1st and 2nd order) sampling sites were selected at c. 200-m elevational intervals within each catchment. Benthic invertebrates and environmental variables were sampled along this gradient prior to the monsoon season from April to June 2012 and 2013. Each site was only sampled once. Previous research in these streams showed very little difference in the composition of an individual stream sampled over the 2 years (RDTS unpublished data). All sites were in near-pristine to semi-pristine conditions, being highly isolated and reachable only after several days of trekking.

Flow velocity was measured using a CP-1 Flow Probe (WTW, Weilheim, Germany) at three replicate riffle locations along the study reach. Water temperature (°C), conductivity (µS cm⁻¹) and pH were sampled using a Multi340i probe (WTW, Weilheim, Germany). Width, depth and % canopy cover over the stream were estimated visually along each study reach.

A multi-habitat sampling approach (Moog, 2007) was applied to collect benthic invertebrates. Microhabitat coverage was first assessed at 10 intervals over a 100-m reach, followed by subsamples being taken with kick samples (25 x 25 cm² D-net; 500 µm mesh) from among the available microhabitats (both mineral and organic). Organisms were sorted and identified to the lowest possible taxonomic level using available keys (Morse et al., 1994; Nesemann et al., 2011; unpublished keys of ASSESS-HKH project, www.assess-hkh.at); mostly genus level, but difficult taxa were often at lower resolution. For more details on sampling methods, see Shah et al. (2015).

Distance metrics

Pairwise direct-line distances were calculated using Euclidean distances between sites based on the site coordinates. River network distances were calculated manually using Google Earth (i.e. by tracing the river network between all site pairs), due to a lack of good GIS data for these small streams.

Topographic distances represented the full distance an organism would have to travel by taking the most direct path between pairs of sites, incorporating elevational gain and loss. Therefore, this accounts for both the direct ‘line of site’ distance and also the distance up and over any elevational barrier such as a mountain range (i.e. incorporating any undulations along the path). These distances were calculated using tools in the 3D Analyst extension of ArcMap 10.0 (ESRI Inc., Redlands, CA, USA). New line feature classes were first created with Z-values on the geometry between two sites over a digital elevation model, followed by calculating three-dimensional surface lengths using the ‘Add Surface Information’ tool.
Elevational distance was the pairwise difference in elevation between each site, regardless of the geographical distance. Environmental distance was the pairwise Euclidean distance in the full set of normalized environmental conditions between sites. Normalization was performed to set mean = 0 and SD = 1 using the ‘scale’ function in R.

**Statistical analyses**

All statistical analyses were performed in R 3.1.1 (R Core Team 2014). Unless presence–absence data were required (i.e. for the EMS analysis), analyses were based on log-transformed community abundance data. Details on environmental variables and their interrelationships and community structure can be found in Appendix S1.

**Niche group determination**

We calculated niche position and niche breadth using the outlying mean index (OMI) method of Doledec et al. (2000). This method calculates the marginality of habitat distribution of species. That is, the distance from the mean habitat conditions occupied by a species and the mean habitat conditions within a particular region. A given species’ position reflects its deviation from the distribution of an evenly distributed hypothetical species tolerating ‘average’ habitat conditions. Therefore, OMI represents the niche position of a species, where low OMI values represent non-marginal niches or high habitat availability and high OMI values represent marginal niches or low habitat availability. This method also calculates a metric of species tolerance, representing the niche breadth of a species, as it measures the distributional range of a species along the sampled environmental gradient. High tolerance values represent species that have a broad niche breadth (i.e. occur across large environmental gradient) and low tolerance values represent narrow niche breadth (Heino & Grönroos, 2014).

We ran the OMI analysis using the ‘niche’ function in the ‘ade4’ package (Dray et al., 2015), based on conductivity, temperature, pH, percent canopy cover, width, depth and velocity. We used local habitat niches as they represent the local conditions for which organisms are associated. We then grouped taxa into two equal groups for both niche position and niche breadth (i.e. we split the full dataset into two even groups for each niche measure). Evenly sized groups were used primarily to ensure that the following statistical analyses were not hampered by major differences in the degrees of freedom between the different datasets analysed. This is particularly important for the assessment of EMS as compartments are harder to detect with fewer species. While using other approaches, such as using rank abundance curves, may better group common versus rare species, this would lead to vastly different group sizes, reducing the ability to determine idealized metacommunity types following EMS.

We calculated the niche values based on the full set of 51 sites, rather than for each catchment individually as the low numbers of sites in each catchment would have created false niches for taxa.

**Elements of metacommunity structure**

The EMS framework takes a three-step approach to examining patterns in species range distributions: coherence, species turnover and range boundary clumping (Fig. 2; Leibold & Mikkelson, 2002; Presley et al., 2010). This uses ordination by reciprocal averaging (RA) to first maximize correspondence within a presence–absence matrix. Ordination axes then effectively represent a latent environmental gradient (Leibold & Mikkelson, 2002). The benefit of EMS is that it allows the concurrent examination of, and differentiation between, several different metacommunity types, rather than assessing each type individually.

The first step examines coherence where, for a metacommunity to be coherent, there must be significantly fewer embedded absences (species absences occurring within surrounding presences) in the matrix than expected by chance (i.e. compared to the null matrices using a z-test). If a metacommunity has significantly more embedded absences (i.e. 0–1 pairs) than chance ($z < 0$, $P < 0.5$), it is said to have a checkerboard distribution. Non-significant embedded absences represent a random distribution, where species distributions are independent of each other within the metacommunity. If the structure is positively coherent ($z > 0$, $P < 0.5$), turnover and range boundary clumping can then be assessed. We followed the approach of Presley et al. (2010), which includes quasi-structures, and boundary clumping values for nested structures, resulting in 14 possible idealized patterns (Fig. 2).

Turnover evaluates the number of times each species replaces another between two sites. Significantly negative turnover (i.e. fewer replacements than expected by chance; tested using a z-test) represents nestedness ($z > 0$, $P < 0.5$). Finally, boundary clumping, or how clumped the edges of species distributions are, can differentiate between three types of gradients with positive or negative turnover. Matrices with positive turnover can be differentiated into randomly distributed (Gleasonian), clumped (Clementsian) and hyperdispersed range boundaries. Matrices with negative turnover (i.e. nested subsets) can be subdivided into the same manner into hyperdispersed, random and clumped. Finally, matrices with non-significant turnover can be assigned quasi-structures (Presley et al., 2010), by examining range boundary clumping non-significant turnover or nestedness patterns.

We assessed the EMS using the R package ‘Metacom’ (Dallas, 2014), employing the ‘R1’ or ‘fixed incidence proportional’ null model, where the species richness of a site is maintained in the null model and the ranges of species are based on their marginal probabilities. We ran 1000 simulations of these null models to compare against our empirical matrix against. These models were run on presence-absence data where any taxa with only one occurrence in each catchment was removed, as such singletons are known to have
disproportionate influences on the outcome of EMS analyses, particularly coherence and boundary clumping (Presley et al., 2009). More detailed descriptions of the process of EMS can be found in previous articles (Leibold & Mikkelson, 2002; Presley et al., 2010; Tonkin et al., 2015).

We then extracted the primary RA axis as a representative of metacommunity organization within each catchment and correlated it with key environmental variables (elevation, temperature, conductivity and pH) using Pearson’s correlation (‘rcorr’ function in Hmisc).

**Distance–decay relationships**

We first correlated community distance matrices for all taxa combined and the four niche groups with each of the five physical or environmental distance matrices using Mantel tests based on Pearson’s product–moment correlation, using the ‘mantel’ function and 1000 permutations in the ‘ecodist’ package (Goslee & Urban, 2007). We plotted all DDRs for each of the five distances versus each of the five community dissimilarities for each catchment. We also examined relationships between the environmental and elevational distance matrices using Mantel tests.

To explore which distances were best at explaining community dissimilarity, we ran multiple regression on distance matrices (MRM) (Lichstein, 2007) using the ‘MRM’ function with 10,000 permutations in ‘ecodist’ (Goslee & Urban, 2007). This method uses permutation tests of significance for regression coefficients and $R^2$ values. We compared between physical, elevational and environmental distance. Therefore, prior to running the model, we selected the most strongly linked physical distance (i.e. Euclidean, river network or topographic) with community distance, based on the mantel $r$ value. We first ran the full model (Table S2.2) including the three distance matrices (physical, elevational and environmental). We then backwards-selected predictor matrices based on their significance in the model ($P < 0.05$) to sequentially eliminate non-significant coefficients from the models. We chose backwards-selection as alternatives, such as Akaike information criterion, cannot be applied using this
distance matrix approach where independence is not respected. See Rioux Paquette et al. (2014) for a similar approach.

RESULTS

Idealized metacommunity patterns

Gradients in metacommunity structure differed between each of the three catchments (Table 1). The full community in the Makalu catchment exhibited a Clementsian structure, where communities turned over in groups (i.e. significantly positive coherence and turnover and significant boundary clumping). Yangri-Indrawati communities were represented by Gleasonian distributions, where boundary clumping was non-significant, indicating individuals turning over in space. Langtang, however, exhibited a quasi-Clementsian structure, where turnover was non-significant, but otherwise similar to Clementsian distributions.

Niche groups exhibited highly variable structures, with no consistency in the patterns across catchments, but Gleasonian or Clementsian distributions (or their quasi-alternatives) were most prevalent (Table 1). Only one group exhibited evidence of nestedness (Langtang, non-marginal niche position), but this was largely due to a weak pattern (turnover z-score = 0.50).

Patterns in EMS were linked most strongly and consistently with elevation ($r = 0.84-0.94$; Table 2). Temperature was also strongly negatively linked due to a strong negative correlation with elevation. pH was correlated with the EMS axis in Langtang and Yangri-Indrawati catchments but not Makalu (Table 2).

Distance-decay relationships

Elevation and environmental distance matrices were significantly correlated in Yangri-Indrawati ($r = 0.38$, $P = 0.006$) and Langtang ($r = 0.37$, $P = 0.002$), but not Makalu ($r = 0.11$, $P = 0.24$). For the three physical distances, no distance matrix was consistently better linked with the community matrix between the different catchments and niche groups (Table S2.1 and Fig. S2.1). All DDRs confirmed that increasing distance (physical, elevational and topographic) led to decreasing similarity in communities (Fig. 3; Table 3; see Table S2.2). DDRs differed between the three catchments, with the MRM models selecting different distance matrices in each location. Predictions were lower in the Langtang (all $R^2 = 0.49$) and Makalu (all $R^2 = 0.51$) catchments than Yangri-Indrawati (all $R^2 = 0.58$). Likewise, the best described niche groups differed between catchments, with narrow niche breadth being the best model in Langtang, non-marginal niche position in Makalu, and both non-marginal niche position and narrow niche breadth in Yangri-Indrawati (Table 3). Considering all taxa together, the physical distance between sites was not important in Yangri-Indrawati, but was in Langtang and Makalu.

In the Langtang catchment, the important distance matrices varied across the five groups (all taxa and four niche groups; Fig. 3; Table 3). Topographic distance was always included in the model, except for the broad niche breadth group. Environmental conditions were important for non-marginal niche position and broad niche breadth (i.e. generalists with available habitat), whereas elevational distance was important for all taxa combined and specialists with lacking niches (narrow niche breadth and marginal niche position).

In the Makalu catchment, except for marginal niche position taxa (elevational distance selected) river network distance was the only distance significantly predicting community dissimilarity (Fig. 3; Table 3). Elevational distance was the sole significant distance in the Yangri-Indrawati catchment, except for the marginal niche position group, where a combination of elevational and environmental distance were selected in the MRM model (Fig. 3; Table 3).

DISCUSSION

Focusing on large elevational gradients over short geographical distances and incorporating multiple geographical and environmental distances enabled the disentanglement of true elevational, geographical and environmental gradients in our study. Our results revealed a clear distance-decay of community similarity with increasing spatial and environmental distance. Communities were structured along elevational gradients, with clear turnover present in two of the three catchments (Clementsian and Gleasonian gradients). However, there was considerable variability in the importance of different distance matrices, representative of environmental, elevational and physical structuring.

The influence of elevation

Given the large elevational gradients of each metacommunity and its central role in structuring biodiversity through altering abiotic conditions, we hypothesized that elevation would be the strongest structuring force, followed by spatial structuring between sites. While elevation was the most strongly correlated variable with the EMS axis, indicating communities were organized along this gradient, its importance varied between catchments. The same was true for the importance of elevational distance in the DDRs. Elevational distance was only consistently important (between full communities and deconstructed niche groups) in Yangri-Indrawati, whereas either environmental or physical distances were often more important in the other catchments. Elevation is a major organizational gradient of biodiversity in the Himalayas (Vetaas & Grytnes, 2002; Baniya et al., 2010) and elsewhere (Rahbek, 1995; Lomolino, 2001). Wang et al. (2012) found invertebrates, diatoms and bacteria were structured through a combination of environmental and spatial (including elevation and geographical distance) factors along a large elevational stream gradient. The clear importance of elevation in streams of this region
Table 1 Results of elements of metacommunity structure analysis examining the best-fit idealized metacommunity structure for all taxa combined, marginal and non-marginal niche position (NP), and narrow and broad niche breadth (NB) taxa in each catchment. Results shown are for the first axis of reciprocal averaging ordination on the taxa by site matrices testing for coherence, taxa range turnover and boundary clumping in each of the three catchments in Nepal: Langtang (LG), Makalu (MAK), and Yangri and Indrawati (YN_INDR). Abs = number of embedded absences, Re = number of replacements, MI = Morisita’s index, SD = standard deviation. Mean and SD values are those calculated from the 1000 generated null matrices.

Note: z-values are calculated by differentiating between the raw value (‘Abs’ or ‘Re’) and the value generated from the null model (‘Mean’). Fewer embedded absences and fewer replacements than chance gives a positive z value for coherence and turnover, respectively.

<table>
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<tr>
<th>Catchment</th>
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<th>Coherence</th>
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<th>Clumping</th>
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<td></td>
<td>df</td>
<td>Abs</td>
<td>z</td>
<td>P</td>
</tr>
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<td>27 130 2.33</td>
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</table>
has recently been supported at both population genetic (Hoppeler et al., 2016) and community (Shah et al., 2015) levels. It is important to recognize that elevation may not be the driver per se but the various chemical, physical and biotic parameters that change with elevation, including dissolved oxygen and temperature (e.g. Jacobsen, 2008). Hoppeler et al. (2016) found extremely high turnover and narrow elevational ranges in genetically identified operational taxonomic units of hydropsychid caddisflies in these streams. Our findings, along with those of Hoppeler et al. (2016) support the assertion that highland headwaters can support considerable beta diversity (Finn et al., 2011).

### Emergent metacommunity properties

Our findings support the hypothesis that metacommunities would exhibit clear compositional turnover (Clementsian and Gleasonian gradients), reflecting high specificity for sites along the large elevational gradients. This supports recent work on Himalayan stream invertebrates by Gutiérrez-Cánovas et al. (2013) and Shah et al. (2015). Willig et al. (2011) found gastropods followed a Clementsian gradient in mixed forest and quasi-Gleasonian in palm forest along 700-m tropical elevational gradients. The strong elevational turnover in our study reflects the concurrent turnover in niches through changes in chemical, physical and biotic conditions along these particularly large elevational gradients. Considerable biodiversity turnover, particularly at the regional scale between isolated compartments, is commonly observed for organisms in the Himalayas (Vetaas & Grytnes, 2002; Baniya et al., 2010), where the dynamic nature of this region has led to the evolution of unique faunas (Favre et al., 2015). Factors such as large elevational gradients can induce greater rates of adaptation over time, in turn promoting biodiversity at a regional scale (Bickford et al., 2007).

Our findings fit with those of Gutiérrez-Cánovas et al. (2013), who found elevational and other natural stressor gradients promoted beta diversity through turnover in organisms, rather than nestedness (associated with anthropogenic stress). Only the non-marginal niche position group in Langtang exhibited quasi-nestedness (i.e. a weak indication of nestedness). While we focused on higher taxonomic levels than species due to this being an understudied fauna, we found no evidence to indicate this hampered the results. Nestedness is more likely to occur at higher taxonomic groupings, due to a lower likelihood of taxonomic replacements between locations. Turnover at these taxonomic levels unambiguously indicates turnover at lower levels and, therefore, appears to have been a robust pattern in these metacommunities.

We focused on low-order tributaries of the main drainage, and thus the elevational patterns examined were not confounded by changes in stream characteristics along the catchment. Nevertheless, taxa typically have specific thermal niches (Finn et al., 2011). Therefore, despite the relatively small geographical extent of the three catchments, the large elevational gradients meant many taxa probably could not inhabit the full set of sites, producing the clear turnover patterns we observed. If this holds, one would expect a greater level of turnover for specialists (those with narrow niche breadth and marginal niche position). However, increased specialization only led to greater turnover signal in the Langtang catchment, where specialists (narrow niche breadth or marginal niche position) exhibited either Clementsian or Gleasonian distributions, compared with the quasi-nested and quasi-Gleasonian patterns of non-specialists.

When considering all taxa, weak turnover with compartmentalized distributions (quasi-Clementsian) and strong turnover with either compartments or individualistic responses to environmental gradients were found. Clementsian, which tend to predominate in studies of EMS (e.g. alpine grassland: Meynard et al., 2013; bats: Presley et al., 2009), and Gleasonian gradients are those most often observed in streams (Erős et al., 2013; Heino et al., 2015b; Tonkin et al., 2015, 2016b). The two compartmentalized distributions were observed in the two regions with split subcatchments (Langtang and Makalu), whereas individualistic turnover was observed where sites were more evenly distributed along the river network (Yangri-Indrawati). This fits with the findings of Tonkin et al. (2015) who argued the observed Clementsian gradient found in their study may have reflected the crossing of catchment boundaries, thereby incorporating different regional species pools in the process. Indeed, compartments emerging through Clementsian structures can reflect historical refugia and various past biogeographical processes (de la Sancha et al., 2014).

### Dispersal or niche mechanisms

As expected, the relative role of environmental structuring, through the measured local habitat variables, was rarely strong in our study compared with that of spatial structuring representing dispersal effects. While local habitat variables were important in two models on deconstructed groups in

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**Table 2** Pearson’s correlations between the first axis of metacommunity organization (RA 1) and key environmental variables within each catchment (LG: Langtang; MAK: Makalu; YN_INDR: Yangri and Indrawati) for all taxa combined.

<table>
<thead>
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<th>n</th>
<th>Variable</th>
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Figure 3 Distance-decay relationships for three catchments in central and eastern Nepal: Langtang (LG), Makalu (MAK), and Yangri and Indrawati (YN_INDR). Five distances were included: Euclidean or geographical, river network, topographic, elevational (i.e. pure difference in elevation) and environmental, based on selected variables. Relationships are plotted for five community groups: all taxa combined, marginal and non-marginal niche positions (NP), and narrow and broad niche breadths (NB). Significant mantel correlations are shown with a bold regression line and non-significant are lighter. The lines represent the fit of each of the MRM (multiple regression on distance matrices) models.
conjunction with spatial variables in the Langtang metacommunity, the variability explained was low. This likely reflects the strong physical structuring of the study catchments, with large elevational gradients and strong dispersal barriers in the steep valley sides overriding or masking the role of local conditions. Communities were dominated by Ephemeroptera, Plecoptera and Trichoptera (see Appendix S1), which are typically weaker dispersers than Odonata, Coleoptera and Hemiptera. Thus, the observed spatial structuring most likely represents dispersal limitation rather than mass effects (Heino et al., 2015a), particularly in Langtang where the sampling area extent was several times larger than in Makalu and Yangri-Indrawati. Nonetheless, elevational structuring also reflects the role of environmental filtering, as environmental conditions change predictably with elevation. Indeed, the weak association between the environmental and biotic matrices, but strong association between elevation and biota, in Makalu (see Table S2.1) indicates that unmeasured environmental variables that change with elevation played an important role along this environmental gradient.

Elevation was the dominant structuring force in Yangri-Indrawati, suggesting species sorting was the metacommunity paradigm at play in this catchment. This is not surprising given sites in this catchment were less spatially isolated compared with the other two catchments, particularly for overland dispersers. Local environmental conditions tend to predominate over spatial structuring in streams (Siqueira et al., 2012; Grønroos et al., 2013; Kärnä et al., 2015), but this depends on the level of connectivity and spatial extent of sites (Brown & Swan, 2010; Soininen, 2016; Tonkin et al., 2016a). The putatively limited connectivity observed in our study among high elevation and headwater streams also seems valid at lower levels of organization and may generally drive elevated beta diversity among headwater regions at the scale of species and intraspecific genetic variation (Finn et al., 2011; Geismar et al., 2015).

Contrary to our hypothesis, specialists exhibited more spatial than environmental control, but this varied between catchments. Pandit et al. (2009) highlighted that differences in specialization of species may influence their response to local versus regional processes. They found that habitat specialists responded mostly to environmental conditions, whereas generalists responded to spatial structuring. Our observed pattern probably reflected increased dispersal limitation for specialists, or non-widespread taxa, rather than specialists choosing their preferred environmental conditions in line with the species sorting model (Leibold et al., 2004).

The importance of dispersal route proxies varied between catchments and deconstructed groups, with topographic distance more important in Langtang and Yangri-Indrawati, and river network distance in Makalu. Interestingly, Langtang and Makalu both comprised sites split across two main branches, as shown in the network DDR (Fig. 3). These groups of sites were divided by high-elevation mountain ranges, which we expected to restrict overland movement and therefore limit dispersal to the river network, but this did not systematically influence the patterns. The lack of importance of river network distance may have been somewhat due to glacial runoff effects on instream conditions along the dispersal network, although there was no evidence that this differed between the catchments. Glacial runoff can

<table>
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alter the water chemistry, creating unfavourable conditions for certain taxa, thereby acting as a dispersal barrier for instream dispersers (Cauvy-Fraunie et al., 2015). Results on the most important dispersal routes for stream metacommunities inhabiting dendritic networks have been equivocal (Landeiro et al., 2011; Grönnroos et al., 2013; Cañedo-Arguelles et al., 2015; Kärnä et al., 2015), but this, of course, depends on the environmental context. Cañedo-Arguelles et al. (2015) found stream corridors were not the most important dispersal route compared to overland routes in arid-land stream networks subjected to flow fragmentation. Geismar et al. (2015) also demonstrated that dispersal outside the river network was most important in structuring population genetic variation in a highland caddisfly. Kärnä et al. (2015) found little difference in the importance of network, overland and cumulative cost distances in Finnish streams. Thus, finding good proxies for dispersal is proving a major challenge (Kärnä et al., 2015), but it is fundamental to the appropriate management and restoration of lotic ecosystems (Heino, 2013; Tonkin et al., 2014).

CONCLUSIONS

Our work has revealed the clear role of elevation in structuring stream metacommunities spanning large elevational gradients. Studies in the Himalayas, the largest elevational gradient globally, are rare, particularly for freshwater systems. In such physically dominated locations, local environment is likely overridden by dispersal limitation as our results indicate to some extent, particularly when considering specialist species. Nevertheless, niche sorting along the elevational gradient was prevalent where spatial extent and dispersal barriers were not limiting species sorting. Strong turnover, as we have found, is to be expected in the Himalayas (Vetaas & Grytnes, 2002; Baniya et al., 2010), with its dynamic history having promoted unique faunas (Favre et al., 2015). However, the way in which these organisms turned over did not occur consistently, with some evidence of grouped turnover and some individualistic. We comprehensively examined the importance of dispersal routes, elevation and local environmental conditions, and the relative roles of these factors differed between the three catchments. The importance of these did not emerge as we expected due to the structuring of the sites among subcatchments, which may have reflected some dispersal barriers emerging through the influence of glacial runoff. Our findings further emphasize the fundamental importance of considering physical structuring and spatial extent and their role in modulating species sorting, particularly when planning for conservation or restoration.

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REFERENCES


Himalayan stream invertebrate metacommunity structure


**SUPPORTING INFORMATION**

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

**Appendix S1** Characterization of the three regions and their fauna.

**Appendix S2** Additional results of distance-decay relationships.

**BIOSKETCH**

Jonathan Tonkin is a postdoctoral scholar with broad interests in community and metacommunity ecology through to macroecology. He is particularly interested in stream and river networks and the role of dispersal and connectivity in maintaining biodiversity. Website: jdtonkin.github.io

Author contributions: J.D.T. and S.U.P. conceived the ideas; R.D.T.S., D.N.S., F.H. and S.U.P. collected the data; J.D.T. and R.D.T.S. analysed the data; and J.D.T. led the writing with contributions from all other authors.

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