ORIGINAL ARTICLE

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

Jonathan D. Tonkin[1,2,3]*, Ram Devi Tachamo Shah[1,2], Deep Narayan Shah[1,2], Felicitas Hoppeler[2], Sonja C. Jähnig[4#] and Steffen U. Pauls[2#]

[1]*Department of River Ecology and Conservation, Senckenberg Research Institute and Natural History Museum Frankfurt, Clamecystrasse 12, 63571 Gelnhausen, Germany,* [2]*Senckenberg Biodiversity and Climate Research Centre (BiK-F), Senckenberganlage 25, Frankfurt am Main D-60325, Germany,* [3]*Department of Integrative Biology, Oregon State University, Corvallis, OR 97331, USA,* [4]*Department of Ecosystem Research, Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), Müggelseedamm 301, 12587 Berlin, Germany*

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.

*Correspondence: Jonathan D. Tonkin, Department of Integrative Biology, Oregon State University, Corvallis, OR 97331, USA.
E-mail: tonkinj@oregonstate.edu
#These authors contributed equally.

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-Arguelles *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
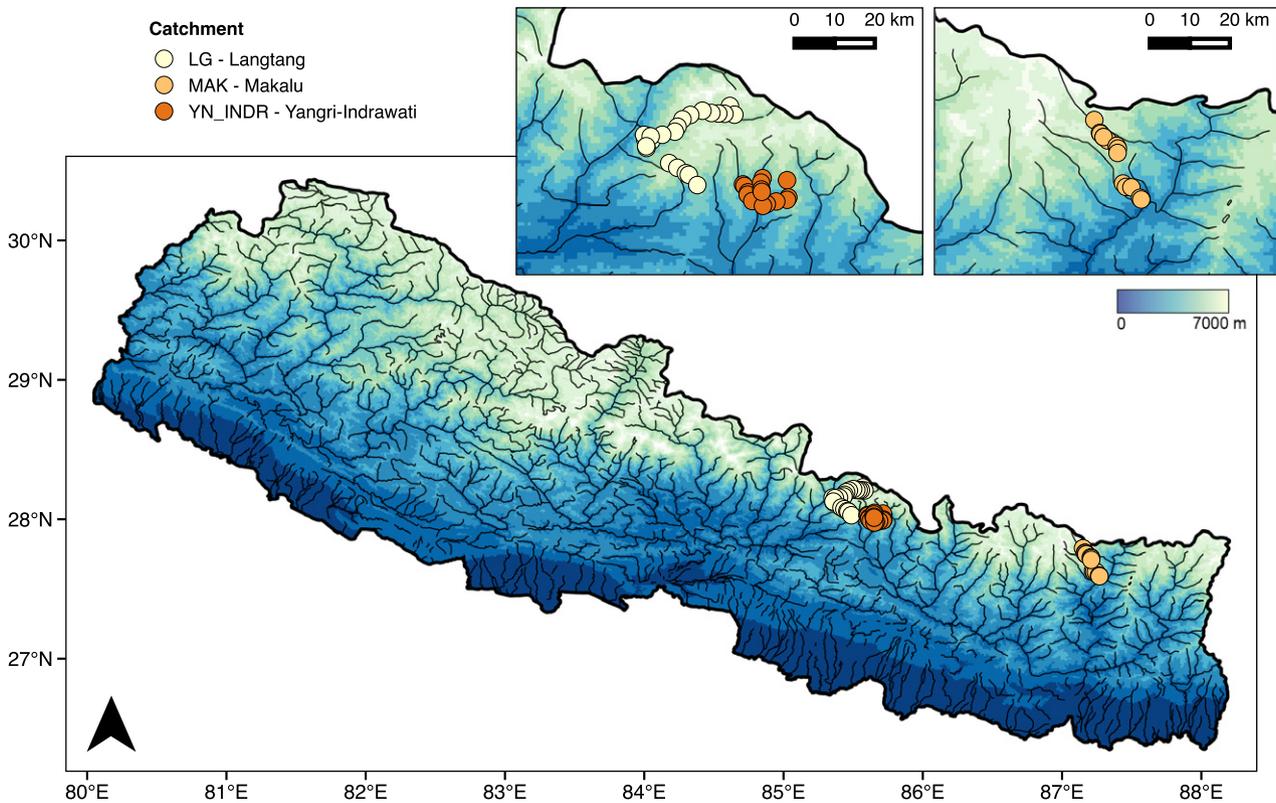
Figure 1 Location of the three study catchments in central and eastern Nepal: Langtang (LG; *n* = 22), Makalu (MAK; *n* = 14), and Yangri and Indrawati (YN_INDR; *n* = 15).

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 × 25 cm^2 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.
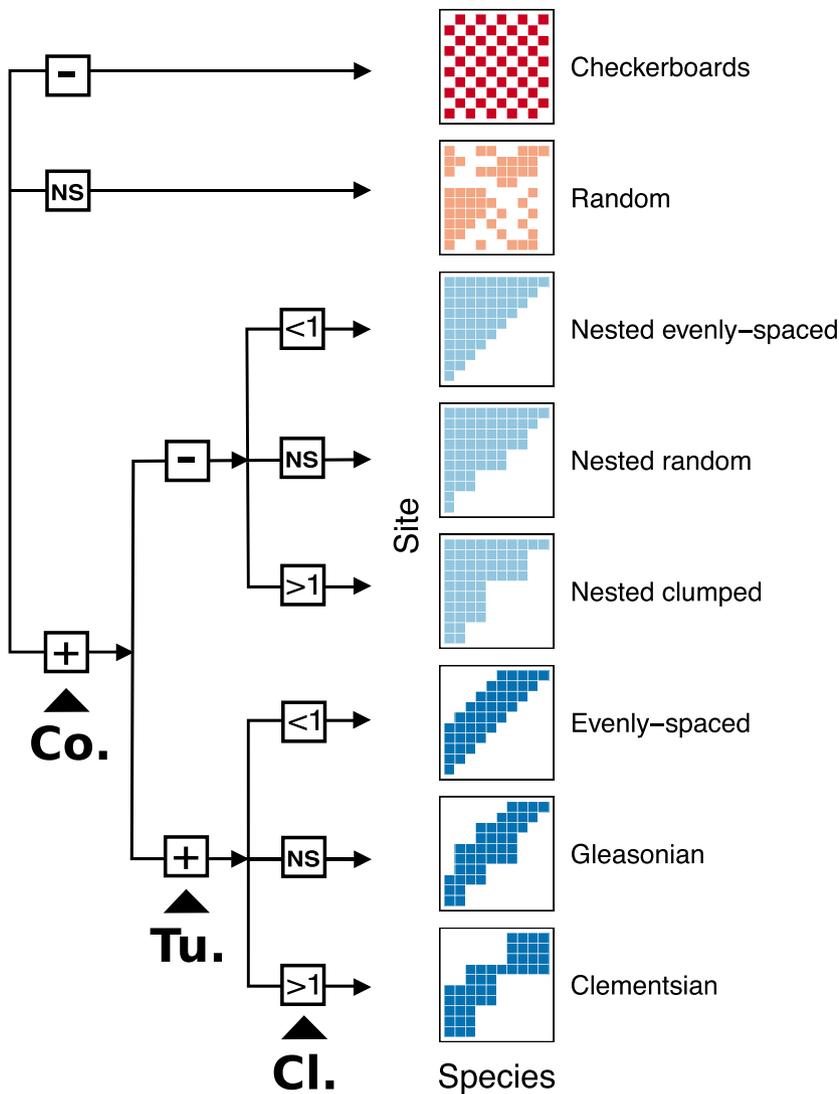
Elements of metacommunity structure

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

Figure 2 Schematic of the main eight metacommunity types examined following the elements of metacommunity structure framework of Leibold & Mikkelson (2002) and Presley *et al.* (2010). The boxes represent a typical pattern in a species-by-site incidence matrix for each metacommunity type. Solid colours represent species presences and blank cells represent absences. The other six quasi-structures are not depicted, but these are the resulting patterns where the turnover metric is not significant (quasi-turnover is a positive but non-significant turnover metric and quasi-nestedness is a negative but non-significant turnover metric). The schematic displays the three steps examined: Co. = coherence; Tu. = turnover; Cl. = boundary clumping. NS = non-significant. '+' represents significantly greater coherence ($z > 0$, $P < 0.5$) or turnover ($z < 0$, $P < 0.5$) than the null model (examined using a *z*-test), and '-' significantly less. Boundary clumping is examined using Morisita's index.

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.

Catchment	Group	df	Coherence			Turnover					Clumping				Structure
			Abs	z	P	Mean	SD	Re	z	P	Mean	SD	MI	P	
LG	All	54	396	7.03	< 0.0001	607.70	30.12	12,821	−1.31	0.1916	9226.58	2752.61	1.56	0.0296	Quasi-Clementsian
LG	Non-marginal NP	33	252	4.62	< 0.0001	341.42	19.37	3234	0.50	0.6137	3867.36	1254.85	1.35	0.0763	Quasi-Nested (random)
LG	Marginal NP	18	55	4.87	< 0.0001	109.97	11.29	3338	−2.77	0.0056	2002.62	482.12	0.97	0.4997	Gleasonian
LG	Narrow NB	19	112	3.93	< 0.0001	164.47	13.36	4726	−2.80	0.0051	2730.86	712.59	1.57	0.0085	Clementsian
LG	Broad NB	32	213	5.63	< 0.0001	329.90	20.75	6960	−1.60	0.1087	4621.49	1457.81	1.34	0.0663	Quasi-Gleasonian
MAK	All	50	175	6.37	< 0.0001	323.60	23.35	13,230	−4.01	< 0.0001	6066.62	1784.28	2.22	0.0088	Clementsian
MAK	Non-marginal NP	29	91	5.72	< 0.0001	174.05	14.52	3710	−1.93	0.054	2386.73	686.73	1.43	0.1322	Quasi-Gleasonian
MAK	Marginal NP	18	28	3.52	0.0004	60.74	9.31	1843	−1.31	0.189	1469.92	284.06	0.9	0.4144	Quasi-Gleasonian
MAK	Narrow NB	23	40	4.47	< 0.0001	86.29	10.36	2798	−3.22	0.0013	1593.07	373.71	1.6	0.1001	Gleasonian
MAK	Broad NB	24	77	4.59	< 0.0001	136.83	13.02	3130	−2.39	0.0168	1878.33	523.25	2.17	0.0015	Clementsian
YN_INDR	All	55	303	3.00	0.0027	363.56	20.18	9096	−4.76	< 0.0001	3690.53	1134.66	0.81	0.3592	Gleasonian
YN_INDR	Non-marginal NP	34	166	2.33	0.0197	195.36	12.59	3083	−3.62	0.0003	1449.60	450.92	2.41	0.0007	Clementsian
YN_INDR	Marginal NP	18	73	1.95	0.0509	92.83	10.15	2405	−2.00	0.0453	1659.46	372.48	1.24	0.1721	Random
YN_INDR	Narrow NB	25	115	3.09	0.002	155.35	13.08	3377	−2.93	0.0034	1801.31	538.31	1.04	0.4076	Gleasonian
YN_INDR	Broad NB	27	130	2.33	0.0199	158.27	12.14	1618	−0.63	0.5313	1356.9	417.08	1.72	0.016	Quasi-Clementsian

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.

Catchment	n	Variable	r	P
LG	22	Elevation	0.839	< 0.0001
LG	22	Temp	−0.799	< 0.0001
LG	22	Cond	−0.165	0.4623
LG	22	pH	0.451	0.0352
MAK	14	Elevation	0.94	< 0.0001
MAK	14	Temp	−0.859	< 0.0001
MAK	14	Cond	0.192	0.5109
MAK	14	pH	−0.036	0.9025
YN_INDR	15	Elevation	0.898	< 0.0001
YN_INDR	15	Temp	−0.775	0.0007
YN_INDR	15	Cond	−0.279	0.3139
YN_INDR	15	pH	−0.608	0.0161

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 (Graf *et al.*, 2008). 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
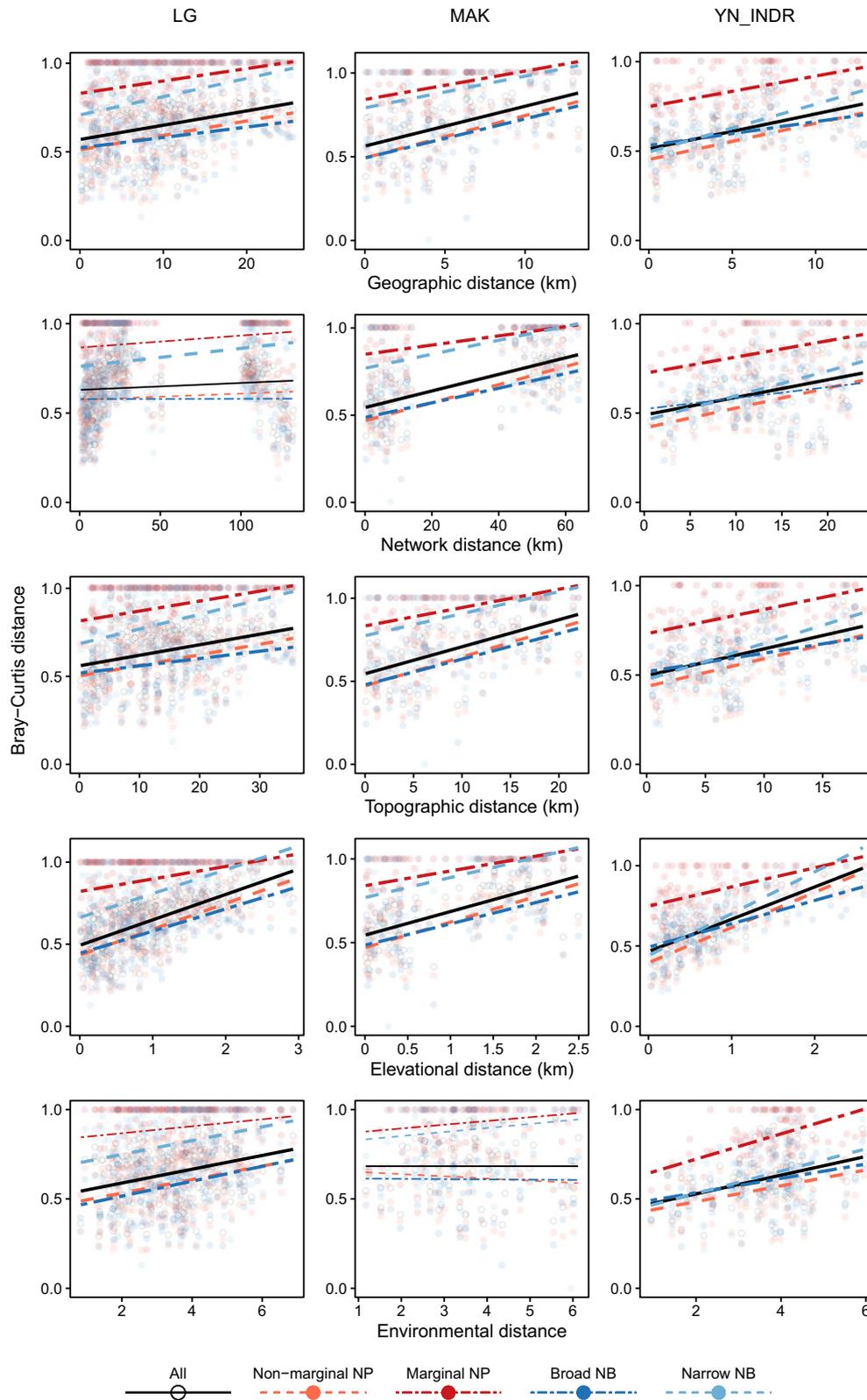
Figure 3 Distance–decay relationships for three catchments in central and eastern Nepal: Langtang (LG), Makalu (MAK), and Yangri and Indrawati (YN_INDR). Five distances were included: Euclidean or geographical, river network, topographic, elevational (i.e. pure difference in elevation) and environmental, 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.

Table 3 Final model results of multiple regression of distance matrices (MRM), based on 10,000 permutations. These models are based on backwards selection of coefficients, based on significance of coefficients. Physical distance measures were first selected for each community group and catchment using the highest mantel r value of the three distance measures (Euclidean, river network and topographic). Where '–' indicates that variable/matrix was not included in the final model. Five community groups were examined: all taxa combined, marginal and non-marginal niche positions (NP), and narrow and broad niche breadths (NB). Catchments: Langtang (LG), Makalu (MAK), and Yangri and Indrawati (YN_INDR). Full results can be found in the supplementary information. ns = non-significant. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.0001$.

Catchment	Group	Distance metric	Intercept		Distance		Elevation		Environ.		R^2	F	P
			Coefficients								Full model		
LG	All	Topographic	4.76E-01	ns	1.85E-06	*	1.46E-04	***	–	–	0.485	107.50	0.0001
LG	Non-marginal NP	Topographic	3.87E-01	ns	5.59E-06	***	–	–	3.44E-02	***	0.194	27.43	0.0001
LG	Marginal NP	Topographic	7.82E-01	ns	4.06E-06	*	5.62E-05	*	–	–	0.137	18.06	0.0003
LG	Narrow NB	Topographic	6.15E-01	ns	4.90E-06	**	1.21E-04	***	–	–	0.254	38.76	0.0001
LG	Broad NB	Euclidean	3.94E-01	ns	5.02E-06	**	–	–	3.88E-02	***	0.172	23.66	0.0002
MAK	All	River network	5.44E-01	***	4.75E-06	***	–	–	–	–	0.507	91.59	0.0005
MAK	Non-marginal NP	River network	4.69E-01	ns	5.17E-06	***	–	–	–	–	0.489	85.21	0.0003
MAK	Marginal NP	–	8.40E-01	**	–	–	8.84E-05	***	–	–	0.268	32.52	0.0002
MAK	Narrow NB	River network	7.70E-01	ns	4.01E-06	***	–	–	–	–	0.262	31.55	0.0002
MAK	Broad NB	River network	4.87E-01	ns	4.20E-06	***	–	–	–	–	0.347	47.26	0.0003
YN_INDR	All	–	4.66E-01	**	–	–	2.01E-04	***	–	–	0.579	141.90	0.0001
YN_INDR	Non-marginal NP	–	3.96E-01	ns	–	–	2.19E-04	***	–	–	0.583	144.00	0.0001
YN_INDR	Marginal NP	–	5.83E-01	ns	–	–	8.28E-05	*	5.33E-02	**	0.329	24.99	0.0001
YN_INDR	Narrow NB	–	4.41E-01	ns	–	–	2.60E-04	***	–	–	0.617	165.90	0.0001
YN_INDR	Broad NB	–	4.93E-01	ns	–	–	1.45E-04	***	–	–	0.354	56.42	0.0001

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 structure 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; Grönroos *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 selecting 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

alter the water chemistry, creating unfavourable conditions for certain taxa, thereby acting as a dispersal barrier for instream dispersers (Cauvy-Fraunié *et al.*, 2015). Results on the most important dispersal routes for stream metacommunities inhabiting dendritic networks have been equivocal (Landeiro *et al.*, 2011; Grönroos *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.

ACKNOWLEDGEMENTS

REFERENCES

Allen, D.J., Molur, S. & Daniel, B.A. (2010) *The status and distribution of freshwater biodiversity in the eastern Himalaya*. IUCN, Cambridge, UK; Gland, Switzerland: Zoo Outreach Organisation, Coimbatore, India.

Altermatt, F. (2013) Diversity in riverine metacommunities: a network perspective. *Aquatic Ecology*, **47**, 365–377.

Baniya, C.B., Solhøy, T., Gauslaa, Y. & Palmer, M.W. (2010) The elevation gradient of lichen species richness in Nepal. *The Lichenologist*, **42**, 83.

Bickford, D., Lohman, D.J., Sodhi, N.S., Ng, P.K., Meier, R., Winker, K., Ingram, K.K. & Das, I. (2007) Cryptic species as a window on diversity and conservation. *Trends in Ecology and Evolution*, **22**, 148–155.

Brown, B.L. & Swan, C.M. (2010) Dendritic network structure constrains metacommunity properties in riverine ecosystems. *Journal of Animal Ecology*, **79**, 571–580.

Brown, J. (1984) On the relationship between abundance and distribution of species. *The American Naturalist*, **124**, 255–279.

Brown, J.H., Mehlman, D.W. & Stevens, G.C. (1995) Spatial variation in abundance. *Ecology*, **76**, 2028–2043.

Cañedo-Arguelles, M., Boersma, K.S., Bogan, M.T., Olden, J.D., Phillipsen, I., Schriever, T.A. & Lytle, D.A. (2015) Dispersal strength determines meta-community structure in a dendritic riverine network. *Journal of Biogeography*, **42**, 778–790.

Cauvy-Fraunié, S., Espinosa, R., Andino, P., Jacobsen, D. & Dangles, O. (2015) Invertebrate metacommunity structure and dynamics in an Andean glacial stream network facing climate change. *PLoS ONE*, **10**, e0136793.

Dallas, T. (2014) metacom: an R package for the analysis of metacommunity structure. *Ecography*, **37**, 402–405.

de la Sancha, N.U., Higgins, C.L., Presley, S.J. & Strauss, R.E. (2014) Metacommunity structure in a highly fragmented forest: has deforestation in the Atlantic Forest altered historic biogeographic patterns? *Diversity and Distributions*, **20**, 1058–1070.

Doledec, S., Chessel, D. & Clementine, G.-C. (2000) Niche separation in community analysis: a new method. *Ecology*, **81**, 2914–2927.

Dray, S., Dufour, A.B., Thioulouse, J., Jombart, T., Pavoine, S., Lobry, J.R., Ollier, S., Siberchicot, A. & Chessel, D. (2015) *Ade4: analysis of ecological data: exploratory and Euclidean methods in environmental sciences*. R package version 1.7-4.

Erős, T., Sály, P., Takács, P., Higgins, C.L., Bíró, P. & Schmera, D. (2013) Quantifying temporal variability in the metacommunity structure of stream fishes: the influence of non-native species and environmental drivers. *Hydrobiologia*, **722**, 31–43.

Favre, A., Päckert, M., Pauls, S.U., Jähnig, S.C., Uhl, D., Michalak, I. & Muellner-Riehl, A.N. (2015) The role of the uplift of the Qinghai-Tibetan Plateau for the evolution of Tibetan biotas. *Biological Reviews*, **90**, 236–253.

Finn, D.S., Bonada, N., Múrria, C. & Hughes, J.M. (2011) Small but mighty: headwaters are vital to stream network biodiversity at two levels of organization. *Journal of the North American Benthological Society*, **30**, 963–980.

Gascón, S., Arranz, I., Cañedo-Argüelles, M., Nebra, A., Ruhí, A., Rieradevall, M., Caiola, N., Sala, J., Ibàñez, C., Quintana, X.D. & Boix, D. (2016) Environmental filtering determines metacommunity structure in wetland microcrustaceans. *Oecologia*, **181**, 193–205.

Geismar, J., Haase, P., Nowak, C., Sauer, J. & Pauls, S.U. (2015) Local population genetic structure of the montane caddisfly *Drusus discolor* is driven by overland dispersal and spatial scaling. *Freshwater Biology*, **60**, 209–221.

Goslee, S.C. & Urban, D.L. (2007) The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software*, **22**, 1–19.

Graf, W., Murphy, J., Dahl, J., Zamora-Munoz, C. & Lopez-Rodriguez, M.J. (2008) *Distribution and ecological preferences of European freshwater organisms. Volume 1. Trichoptera*. Pensoft Publishing, Sofia-Moscow.

Grönroos, M., Heino, J., Siqueira, T., Landeiro, V.L., Kotanen, J. & Bini, L.M. (2013) Metacommunity structuring in stream networks: roles of dispersal mode, distance type, and regional environmental context. *Ecology and Evolution*, **3**, 4473–4487.

Gutiérrez-Cánovas, C., Millán, A., Velasco, J., Vaughan, I.P. & Ormerod, S.J. (2013) Contrasting effects of natural and anthropogenic stressors on beta diversity in river organisms. *Global Ecology and Biogeography*, **22**, 796–805.

Heino, J. (2013) The importance of metacommunity ecology for environmental assessment research in the freshwater realm. *Biological Reviews of the Cambridge Philosophical Society*, **88**, 166–178.

Heino, J. & Grönroos, M. (2014) Untangling the relationships among regional occupancy, species traits, and niche characteristics in stream invertebrates. *Ecology and Evolution*, **4**, 1931–1942.

Heino, J., Melo, A.S., Siqueira, T., Soininen, J., Valanko, S. & Bini, L.M. (2015a) Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. *Freshwater Biology*, **60**, 845–869.

Heino, J., Nokela, T., Soininen, J., Tolkkinen, M., Virtanen, L. & Virtanen, R. (2015b) Elements of metacommunity structure and community-environment relationships in stream organisms. *Freshwater Biology*, **60**, 973–988.

Holyoak, M., Leibold, M.A. & Holt, R.D. (2005) *Metacommunities: spatial dynamics and ecological communities*. University of Chicago Press, Chicago, IL, USA.

Hoppeler, F., Shah, R.D.T., Shah, D.N., Jähnig, S.C., Tonkin, J.D., Sharma, S. & Pauls, S.U. (2016) Environmental and spatial characterisation of an unknown fauna using DNA sequencing – an example with Himalayan Hydropsychidae (Insecta: Trichoptera). *Freshwater Biology*, doi:10.1111/fwb.12824.

Jacobsen, D. (2008) Low oxygen pressure as a driving factor for the altitudinal decline in taxon richness of stream macroinvertebrates. *Oecologia*, **154**, 795–807.

Kärnä, O.-M., Grönroos, M., Antikainen, H., Hjort, J., Ilmonen, J., Paasivirta, L. & Heino, J. (2015) Inferring the effects of potential dispersal routes on the metacommunity structure of stream insects: as the crow flies, as the fish swims or as the fox runs? *Journal of Animal Ecology*, **84**, 1342–1353.

Landeiro, V.L., Magnusson, W.E., Melo, A.S., Espírito-Santo, H.M.V. & Bini, L.M. (2011) Spatial eigenfunction analyses in stream networks: do watercourse and overland distances produce different results? *Freshwater Biology*, **56**, 1184–1192.

Leibold, M.A. & Mikkelson, G.M. (2002) Coherence, species turnover, and boundary clumping: elements of meta-community structure. *Oikos*, **97**, 237–250.

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M. & Gonzalez, A. (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, **7**, 601–613.

Lichstein, J.W. (2007) Multiple regression on distance matrices: a multivariate spatial analysis tool. *Plant Ecology*, **188**, 117–131.

Lomolino, M. (2001) Elevation gradients of species-density: historical and prospective views. *Global Ecology and Biogeography*, **10**, 3–13.

Meynard, C.N., Lavergne, S., Boulangeat, I., Garraud, L., Van Es, J., Mouquet, N. & Thuiller, W. (2013) Disentangling the drivers of metacommunity structure across spatial scales. *Journal of Biogeography*, **40**, 1560–1571.

Moog, O. (2007) *Manual on pro-rata multi-habitat-sampling of benthic invertebrates from wadeable rivers in the HKH-region*. Deliverable 8, part 1 for ASSESS-HKH, European Commission, 29 pp.

Morse, J.C., Yang, L. & Tian, L. (1994) *Aquatic insects of China useful for monitoring water quality*, 1st edn. Hohai University Press, Nanjing, 570 pp.

Nesemann, H., Devi, R., Shah, T. & Shah, D.N. (2011) Key to the larval stages of common Odonata of Hindu Kush

Himalaya, with short notes on habitats and ecology. *Journal of Threatened Taxa*, **3**, 2045–2060.

Ormerod, S.J., Rundle, S.D., Wilkinson, S.M., Daly, G.P., Dale, K.M. & Juttner, I. (1994) Altitudinal trends in the diatoms, bryophytes, macroinvertebrates and fish of a Nepalese river system. *Freshwater Biology*, **32**, 309–322.

Pandit, S.N., Kolasa, J. & Cottenie, K. (2009) Contrasts between habitat generalists and specialists: an empirical extension to the basic metacommunity framework. *Ecology*, **90**, 2253–2262.

Presley, S.J., Higgins, C.L., López-González, C. & Stevens, R.D. (2009) Elements of metacommunity structure of Paraguayan bats: multiple gradients require analysis of multiple ordination axes. *Oecologia*, **160**, 781–793.

Presley, S.J., Higgins, C.L. & Willig, M.R. (2010) A comprehensive framework for the evaluation of metacommunity structure. *Oikos*, **119**, 908–917.

R Core Team (2014) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rahbek, C. (1995) The elevational gradient of species richness: a uniform pattern? *Ecography*, **2**, 200–205.

Rioux Paquette, S., Talbot, B., Garant, D., Mainguy, J. & Pelletier, F. (2014) Modelling the dispersal of the two main hosts of the raccoon rabies variant in heterogeneous environments with landscape genetics. *Evolutionary Applications*, **7**, 734–749.

Shah, R.D.T., Sharma, S., Haase, P., Jähnig, S.C. & Pauls, S.U. (2015) The climate sensitive zone along an altitudinal gradient in central Himalayan rivers: a useful concept to monitor climate change impacts in mountain regions. *Climatic Change*, **132**, 265–278.

Siqueira, T., Bini, L.M., Roque, F.O. & Cottenie, K. (2012) A metacommunity framework for enhancing the effectiveness of biological monitoring strategies. *PLoS ONE*, **7**, e43626.

Soininen, J. (2016) Spatial structure in ecological communities – a quantitative analysis. *Oikos*, **125**, 160–166.

Suren, A.M. (1994) Macroinvertebrate communities of streams in western Nepal – effects of altitude and land-use. *Freshwater Biology*, **32**, 323–336.

Tonkin, J.D., Stoll, S., Sundermann, A. & Haase, P. (2014) Dispersal distance and the pool of taxa, but not barriers, determine the colonisation of restored river reaches by benthic invertebrates. *Freshwater Biology*, **59**, 1843–1855.

Tonkin, J.D., Sundermann, A., Jähnig, S.C. & Haase, P. (2015) Environmental controls on river assemblages at the regional scale: an application of the Elements of Metacommunity Structure framework. *PLoS ONE*, **10**, e0135450.

Tonkin, J.D., Stoll, S., Jähnig, S.C. & Haase, P. (2016a) Contrasting metacommunity structure and beta diversity in an aquatic-floodplain system. *Oikos*, **125**, 686–697.

Tonkin, J.D., Stoll, S., Jähnig, S.C. & Haase, P. (2016b) Elements of metacommunity structure of river and riparian assemblages: communities, taxonomic groups and deconstructed trait groups. *Ecological Complexity*, **25**, 35–43.

Vetaas, O.R. & Grytnes, J.A. (2002) Distribution of vascular plant species richness and endemic richness along the Himalayan elevation gradient in Nepal. *Global Ecology and Biogeography*, **11**, 291–301.

Wang, J., Soininen, J., Zhang, Y., Wang, B., Yang, X. & Shen, J. (2011) Contrasting patterns in elevational diversity between microorganisms and macroorganisms. *Journal of Biogeography*, **38**, 595–603.

Wang, J., Soininen, J., Zhang, Y., Wang, B., Yang, X. & Shen, J. (2012) Patterns of elevational beta diversity in micro- and macroorganisms. *Global Ecology and Biogeography*, **21**, 743–750.

Willig, M.R., Presley, S.J., Bloch, C.P., Castro-Arellano, I., Cisneros, L.M., Higgins, C.L. & Klingbeil, B.T. (2011) Tropical metacommunities along elevational gradients: effects of forest type and other environmental factors. *Oikos*, **120**, 1497–1508.

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.

Editor: Richard Pearson