Distance decay of benthic macroinvertebrate communities in a mountain river network: Do dispersal routes and dispersal ability matter?

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HIGHLIGHTS

- We tested DDRs between beta diversity and environmental/physical distances.
- Environmental heterogeneity was the major driver of total beta diversity and replacement component.
- Overland distance was more influential for beta diversity than watercourse and cost distances
- Dispersal ability determined how communities responded to environmental and physical distances.
- Maintaining environmental heterogeneity and natural connectivity are important to conserve stream biodiversity.

GRAPHICAL ABSTRACT
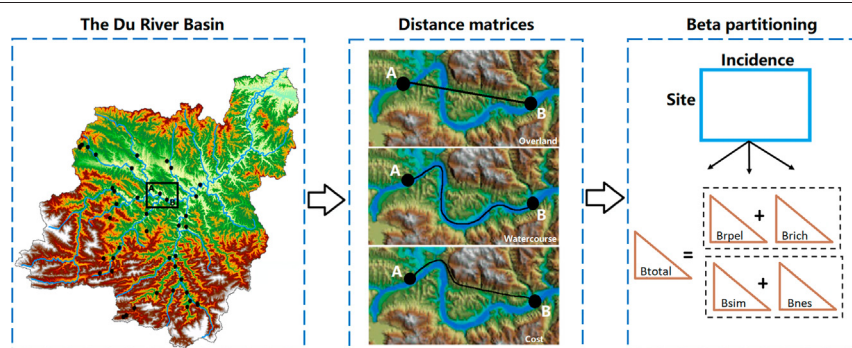
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ABSTRACT

Environmental heterogeneity and dispersal limitation are important drivers of beta diversity; however, their relative influence on the two fundamental components of beta diversity (i.e., species replacement and richness difference) has not been fully examined in montane streams. Here, we examined the relative importance of local environmental gradients and three physical distance matrices (i.e., overland, watercourse and cost distances) on beta diversity and its two components for a macroinvertebrate metacommunity in a stream network. To provide additional insights into community assembly, we also analysed variation in two deconstructed subcommunities based on dispersal ability (i.e., weak and strong dispersers). Both environmental filters and physical distances (dispersal limitation) drove patterns of overall beta diversity, with the former generally prevailing over the latter. Species replacement components showed stronger correlations with environmental gradients than physical distances, while the opposite is true for the richness difference components. Overland distances were generally more important than cost and watercourse distances for community dissimilarity of stream macroinvertebrates, implying that lateral dispersal out of stream corridors through flight was the major dispersal route in the studied steam network. As expected, community dissimilarity of strong dispersers was primarily shaped by environmental filtering, while community dissimilarity of weak dispersers was associated with the joint effects of environmental filtering and dispersal limitation. Our findings demonstrate that partitioning overall dissimilarity into species replacement and richness difference provides more insights into the processes driving

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spatial variability in biological communities compared with the utilization of total beta diversity alone. Our results support the notion that maintaining environmental heterogeneity and natural connectivity of stream networks should be effective measures to conserve regional biodiversity.

1. Introduction

Understanding key mechanisms shaping species diversity at different spatial and temporal scales is a long-standing issue in community ecology (Chesson, 2000). Species diversity can be depicted by three aspects depending on spatial scales: alpha diversity measures species richness at a site; gamma diversity quantifies the total species richness within a region unit; and beta diversity describes variation in species composition between localities (Whittaker, 1960). Beta diversity derives from two distinct processes: species replacement and species loss (or gain), each with a specific meaning in ecology (Podani and Schmera, 2011). Species replacement refers to the substitution of certain taxa by others, which may arise from deterministic processes, including environmental filtering or interspecific interactions (Legendre and De Caceres, 2013). Species loss (or gain) may result from stochastic processes (e.g., random dispersal and extinction), environmental change or competitive exclusion, and it would lead to richness differences between sites (Carvalho et al., 2012; Novotny and Weiblen, 2005; Ricklefs and He, 2016). Compared to research on alpha and gamma diversities, ecologists have shown considerable interest in beta diversity over the last two decades, owing to its importance for unraveling the mechanisms of community assembly (Baselga and Orme, 2012; Mori et al., 2018; Soininen et al., 2018).

Among the processes affecting beta diversity, environmental factors at the local scale have traditionally been regarded to be of considerable importance (Heino et al., 2015a; López-Delgado et al., 2020). In the freshwater realm, key environmental factors include habitat conditions (e.g., water depth, stream width, aquatic plants, substrates and current velocity) and water chemistry (e.g., nitrogen, phosphorus and calcium) which act as filters, eliminating certain taxa and favoring others (Li et al., 2012; Mykrä et al., 2007). This filtering effects induced by environmental gradients matches with the species sorting paradigm in metacommunity ecology (Leibold et al., 2004). On the other hand, beta diversity patterns are also strongly associated with dispersal-driven processes, such as mass effects and dispersal limitation (Chase and Bengtsson, 2010; Leibold et al., 2004). Dispersal can regulate the relative importance of environmental filtering, since either very high (e.g., mass effects) or very low (e.g., dispersal limitation) dispersal rates are likely to decouple the potentially strong associations between beta diversity and local environments (Heino et al., 2017; Jamoneau et al., 2018). For example, insufficient dispersal may prevent species from tracking environmental gradients, thus weakening the influence of local environments on community variation (Gianuca et al., 2017; Hill et al., 2017). In this scenario, beta diversity of strongly dispersing taxa may show stronger environmental control and weaker spatial structuring (via dispersal limitation), whereas beta diversity of weakly dispersing species may display stronger spatial structuring and lessened control by environmental filters (Kärnä et al., 2015).

Dispersal is also one of the most complicated natural phenomena to measure, and ecologists thus model the potential dispersal routes of organisms indirectly by using various proxies, such as pairwise physical distances between sites (Tonkin et al., 2018a). In freshwater ecosystems, the most commonly used proxies for dispersal are overland (i.e., straight-line distance) and watercourse distance (the shortest distance between two sites along river channel) matrices (Bottin et al., 2014; Tonkin et al., 2014). Overland distances may be appropriate for organisms that can disperse overland, such as some wind-borne plants and the adults of winged aquatic insects (Heino et al., 2015c). In contrast, many exclusively aquatic organisms, like fishes, bivalves, and some aquatic insects have to rely on routes via watercourses to spread (Warfe et al., 2013). While the two types of distances are regarded as effective proxies for dispersal and have been widely used previously, recent studies highlighted the importance of considering landscape resistance to the dispersal of organisms among sites (Graves et al., 2014; He et al., 2020). In this vein, the cost distance presumes that dispersal occurs along concave corridors (e.g., river valley and saddle points along mountain ridges), and uses a resistance map to calculate the least-cost route between sites in a landscape (Mozzaquattro et al., 2020; Phillipsen and Lytle, 2013; Razeng et al., 2016). Since cost distance takes complicated topographic (e.g., elevation and slop) and environmental conditions (e.g., vegetation cover and constructions) into consideration, it may be a promising proxy for dispersal of freshwater organisms (Razeng et al., 2016; Tonkin et al., 2018a).

Mountain streams provide ideal testing grounds for examining different ecological drivers of beta diversity, since they often exhibit high levels of environmental heterogeneity and complex topographical conditions (Tonkin et al., 2017; Wang et al., 2020). Mountain streams are also characterized by high biodiversity, especially for benthic macroinvertebrates (Kim et al., 2018; Wang and Tan, 2017). Macroinvertebrates have diversified dispersal modes (e.g., passive and/or active movements along river corridor or flying in the air) and a wide range of dispersal abilities, making them ideal study organisms to understand the processes governing beta diversity (Heino and Peckarsky, 2014; McCauley, 2006).

Here, we tested the relative importance of environmental conditions and physical distance matrices on beta diversity and the two components of macroinvertebrates in a subtropical mountain river network by analyzing the distance decay relationships (DDRs). We hypothesized that: (1) Beta diversity of macroinvertebrates would significantly correlate with both environmental and physical distances (Soininen et al., 2007), but that environmental distance would be more influential than physical distances in shaping beta diversity patterns (Kärnä et al., 2015). (2) Watercourse distance would be more important than overland and cost distance matrices in determining beta diversity (Landeiro et al., 2011). This is because the dispersal of most stream organisms is likely to be concentrated within stream corridors (Petersen et al., 2004). (3) The replacement components would be more strongly determined by environmental filters, while the richness difference components would be better explained by dispersal-driven processes (Peláez and Pavanelli, 2019). (4) Beta diversity of strongly dispersing taxa would be primarily shaped by environmental filters, as these taxa can track environmental variation more effectively (Padial et al., 2014; Razeng et al., 2016). In contrast, beta diversity of weakly dispersing species would be explained by the joint effects of environmental filters and dispersal-driven processes via dispersal limitation (Hill et al., 2017).

2. Material and methods

2.1. Study area

This study was conducted in the Du River which is the largest tributary of the Hanjiang River, China (Yao et al., 2010). The Du River network covers a drainage area of 11,140 km^2, with a total length of 354 km (Fig. 1). Located in a transitional area of the temperate and subtropical zones, the weather is moderately warm (annual mean air temperature: 12–15 °C) and the rainfall is abundant (average annual precipitation: 800-1000 mm) (Yao et al., 2010). The topography of the region is diverse and complex, with mountains and low-elevation hills
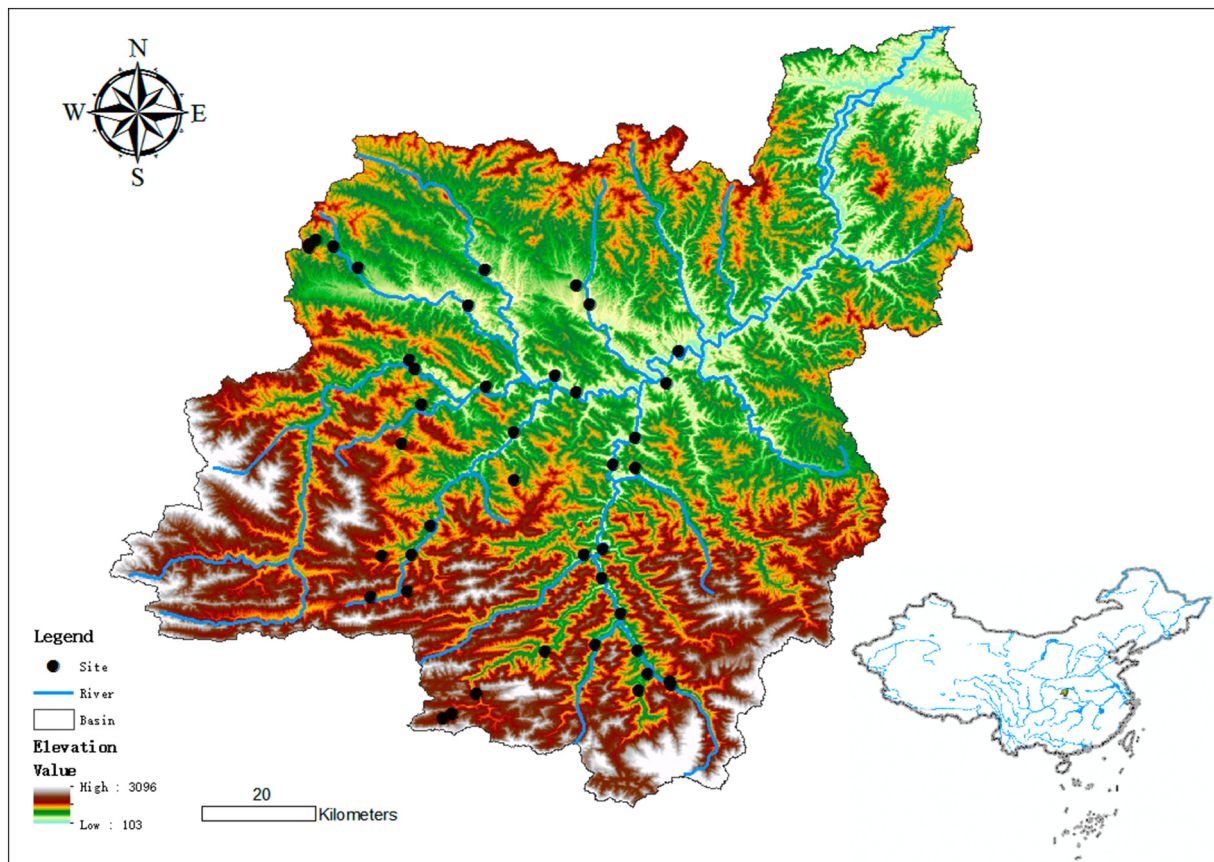
Fig. 1. The 42 sampling sites in the Du River Basin, China.

(altitudinal ranges from 201 to 2984 m) the main landform types. The Du River network has also been recorded to harbor a high level of freshwater biodiversity, particularly for benthic macroinvertebrates (Jiang et al., 2017; Jiang et al., 2014). However, research findings on beta diversity and its determinants in macroinvertebrate communities in this important river basin is far from adequate compared to those in lowland waters.

2.2. Macroinvertebrate data

Benthic macroinvertebrates were collected from 42 stream sites in the Du River network during March and April 2011; the period when most benthic macroinvertebrates in central China are in their larval stage (Yan and Li, 2008). Using a Surber net (500 μm mesh), five replicate samples were taken from the typical habitats along a 100 m stream reach at each site. Samples were kept in a car fridge and were carried to the field monitoring station for further treatment. Benthic animals were carefully picked from sediments and were preserved with 75% alcohol. All animals were identified to genus level by consulting related reference books and articles (Brinkhurst et al., 1990; Epler, 2001; Mccafferty and Cladistics, 2008; Morse et al., 1984). The five replicate samples at each site were then merged and averaged to represent local community structure.

To understand the role of dispersal capacity in determining community structure, the entire metacommunity was classified into weak and strong dispersal ability groups. Thus, we analysed three datasets: the entire metacommunity and each of the two dispersal groups. Considering that macroinvertebrates typically employ different dispersal modes throughout their life stages, we applied a grouping method based on a recently proposed dispersal capacity metric (DCMc) (Li et al., 2016). DCMc is a comprehensive index that incorporates all the four dispersal

modes (i.e., aquatic passive, aquatic active, terrestrial passive and terrestrial active) of a species by summing the dispersal capacity value of each dispersal mode. As we currently do not have detailed information on dispersal modes of macroinvertebrates in central China, we obtained genus-level information of dispersal capacity by referring to Li et al. (2016). Macroinvertebrate taxa with DCMc values larger than five were assigned as strong dispersers, and those with less than five as weak dispersers (Supplementary file: Table S1).

2.3. Environmental factors

Following macroinvertebrate sampling, we measured local scale environmental factors that have previously been reported important for macroinvertebrate assemblages in this basin (Jiang et al., 2014). Water depth, river width and current velocity were averaged from 10 random locations in each sampling site. Conductivity, water temperature, dissolved oxygen, pH and turbidity were measured with a Multi-Parameter Water Quality Probe (YSI EXO2). Bottom substrates were classified into five categories: boulder (>256 mm), cobble (64–256 mm), pebbles (16–64 mm), gravel (2–16 mm) and sand and clay (0.1–2 mm). Afterwards, water samples were collected at each site and analysed in the laboratory for the following seven chemical parameters: nitrite, nitrate, ammonia, total nitrogen, orthophosphate, total phosphorus and chemical oxygen demand. Chemical parameters were measured based on standard methods in China (Huang et al., 1999).

2.4. Distance metrics

To quantify the potential dispersal routes, we calculated three distance metrics: overland, cost and watercourse distances. Overland

distance refers to the straight-line (Euclidean) distance between sites in two-dimensional space; landscape cost distance represents the pairwise resistance between sites based on low resistance of map pixels with concave topography; and watercourse distance denotes the pairwise minimum pathway between sites along the stream network.

We used Point Distance Analyst Tool of ArcGIS to calculate Euclidean distance as proxy of overland straight-line dispersal. We quantified watercourse distance between sites with the Network Analyst Tool of ArcGIS. To calculate landscape cost distance, we assumed that the cost of overland movement is dependent on surface relief, which allows the slope and elevation of terrain to be used as a direction-dependent factor, i.e. resistance influencing the cost of movement across landscape. Therefore, based on a digital elevation model, we used resistance maps to calculate the best route between two locations in the Linkage Mapper Tool 2.0.0 of ArcGIS. All three types of between-site distances were measured with ArcGIS 10.3 (ESRI Inc., Redlands, CA, U.S.A.).

2.5. Data analysis

2.5.1. Biological dissimilarity matrices

To calculate beta diversity metrics, we used two different approaches that were commonly used to decompose overall dissimilarity. (1) Podani and Schmera's (2011) partitioning framework: We produced three dissimilarity matrices using Sørensen family of beta diversity measures based on presence–absence data. This analysis was run with the function "beta" in the package BAT (Cardoso et al., 2015). We got three dissimilarity matrices that describe overall compositional differences (β_{total}), beta diversity explained by replacement of species alone (β_{repl}) and beta diversity explained by species loss/gain (richness differences) alone (β_{rich}).

(2) Baselga's (2010) partitioning framework: We used presence–absence data to get three dissimilarity matrices with the function "beta.pair" in the R package betapart (Baselga et al., 2013). For comparison, Sørensen dissimilarity were also used to partition overall beta diversity. Simpson dissimilarity (β_{sim}) measures replacement independent of richness difference; Nestedness-resultant fraction (β_{nes}) measures nestedness component deriving from nestedness-related richness difference. It should be noted that nestedness is just a particular case (i.e., smaller assemblages become subsets of larger ones) of an ordered pattern of differences in species richness (Carvalho et al., 2012).

2.5.2. Correlations between biological and environmental/spatial matrices

We tested the relative role of local environmental and physical distance matrices on beta diversity and its two components by analyzing the distance decay relationships (DDRs). DDRs depict the biogeographic phenomenon that the compositional similarity between local communities decays as the environmental or physical distances increase (Nekola and White, 1999). This phenomenon has attracted a lot of interest by ecologists and biogeographers in recent years, but remains poorly understood for freshwater communities (Astorga et al., 2012; Brown and Swan, 2010; Rocha et al., 2019).

Prior to the main statistical analysis, bio-env analysis was conducted with the "bioenv" function to select the best combination of environmental distance matrices for each biological dissimilarity matrix (beta diversity indices for the whole metacommunity and each dispersal ability group) (Clarke and Ainsworth, 1993). Based upon standardized environmental factors, this analysis tests all the potential combinations of environmental factors and finds out the combination that shows the strongest correlation coefficient with biological dissimilarity. Furthermore, we performed Mantel test using the function "mantel" to examine the correlations between biological dissimilarity matrices and environmental (based on Euclidean distance matrices) and spatial (overland, watercourse and cost) distance matrices, respectively (Mantel, 1967). Finally, we applied partial Mantel test with the function "partial.mantel" to explore the effects of standardized environmental

Euclidean distances on dissimilarity metrics when controlling for each physical distance matrix, and vice versa. We used a Moran spectral randomization (MSR; Wagner and Dray, 2015) to address the potential bias introduced by spatial autocorrelation in the Mantel and partial Mantel tests. The MSR aims at producing random replicates that preserves the spatial structures of the original variables so that spatial autocorrelation is taken into account in the testing procedure (Crabot et al., 2019).

All analyses were conducted in the R environment (R Core Team, 2019). Bio-env, Mantel test and partial Mantel test analyses were run in the R package vegan (Oksanen et al., 2019), while MSR procedure was performed using the adespatial package (Dray et al., 2017). All analyses were conducted for the whole metacommunity, weak and strong dispersers, respectively.

3. Results

3.1. Environmental factors and macroinvertebrate community features

Both environmental factors (e.g., physical habitats and water chemistry) and physical distances (i.e., overland, watercourse and cost) showed considerable variation among the 42 stream sites (Table 1). We identified a total of 145 genera of macroinvertebrates from seven classes, 14 orders and 64 families (Table S1). These taxa were further divided into weak (84 taxa) and strong (61) dispersal ability groups (Table S1). The average taxon richness of the entire community, weak dispersers and strong dispersers at each site were 24 (8–40), 9 (2–16) and 16 (2–25), respectively.

Total beta diversity ($\beta_{total} = 0.596$) of the entire metacommunity could be explained almost exclusively by the replacement ($\beta_{repl} = 0.415$; $\beta_{sim} = 0.500$) rather than the richness difference component ($\beta_{rich} = 0.181$; $\beta_{nes} = 0.096$) (Table S2; Fig. 2). For the two dispersal groups, the magnitude of total beta diversity for weak dispersers ($\beta_{total} = 0.694$) was larger than that for strong dispersers ($\beta_{total} = 0.542$) (Table S2). Similar to case of the whole metacommunity, total beta diversity of both weak and strong dispersers was mainly driven by replacement. Moreover, for both entire and the two deconstructed communities, β_{repl} was always lower than β_{sim}, while β_{rich} was almost twice the value of β_{nes} (Table S2; Fig. 2).

3.2. Relationships between beta diversity and environmental and spatial distances

The bio-env procedures selected different sets of environmental factors as the best combinations that showed the strongest association with beta diversity matrices (Tables 2, 3 and 4). In general, conductivity (EC, 10 times), dissolved oxygen (DO, 9 times), channel width (Width, 8 times), current velocity (CV, 8 times) and percentage of Cobble (% Cobble, 8 times) were the most commonly selected environmental variables in the models (Fig. S1). Correlations between beta diversity and environmental and physical distances varied considerably among the beta diversity components, beta partitioning frameworks (Baselga's or Podani & Schmera's methods) and dispersal ability groups (weak or strong dispersers).

3.2.1. Environmental vs. physical distances

For the entire metacommunity and the two dispersal groups, both environmental and physical distances correlated significantly to beta diversity matrices. However, the associations between beta diversity and environmental distances were generally stronger than those between beta diversity and physical distances (Tables 2, 3 and 4).

3.2.2. Overland vs. cost vs. watercourse distance

As for physical distance matrices, overland distance always displayed stronger correlations with beta diversity components compared to cost and watercourse distances (Tables 2, 3 and 4). Cost

Table 1
Descriptive statistics showing the maximum (Max), minimum (Min), median and mean values and standard deviation (SD) of local environmental factors and physical distances (overland, cost and watercourse distances) across the 42 sampling sites in the Du River Basin.

	Abbreviation	Max	Min	Median	Mean	SD
Environmental factors						
Water temperature (°C)	WT	21.70	3.09	10.95	10.88	3.09
Conductivity (µs/cm)	EC	326.30	54.10	171.75	179.46	66.10
Total dissolved solids (mg/L)	TDS	0.262	0.096	0.153	0.158	0.053
Dissolved oxygen (mg/L)	DO	13.48	9.38	11.70	11.73	0.84
pH	pH	8.83	7.45	8.31	8.28	0.26
Channel width (m)	Width	56.00	0.45	13.50	18.93	16.24
Water depth (m)	Depth	0.80	0.04	0.25	0.33	0.20
Current velocity (m/s)	CV	0.90	0.07	0.52	0.53	0.19
Percentage of boulder	% Boulder	0.70	0.00	0.20	0.26	0.19
Percentage of cobble	% Cobble	0.60	0.10	0.38	0.36	0.12
Percentage of pebble	% Pebble	0.40	0.05	0.10	0.14	0.09
Percentage of gravel	% Gravel	0.40	0.05	0.15	0.16	0.08
Percentage of sand	% Sand	0.25	0.00	0.05	0.07	0.05
Total nitrogen (mg/L)	TN	3.288	0.254	0.760	1.142	0.845
Nitrate (mg/L)	NO_3	2.767	0.017	0.630	0.862	0.693
Nitrite (mg/L)	NO_2	0.014	0.000	0.001	0.001	0.002
Ammonium nitrogen (mg/L)	NH_4	0.861	0.000	0.000	0.055	0.165
Total phosphorus (mg/L)	TP	0.153	0.024	0.052	0.059	0.024
Phosphate (mg/L)	SRP	0.108	0.009	0.023	0.029	0.017
Chemical oxygen demand (mg/L)	COD	4.263	0.589	1.356	1.468	0.682
Physical distances						
Overland distance (km)	OD	100.62	0.63	41.15	43.08	21.67
Cumulative cost distance	CD	395.00	2.00	173.00	179.81	91.51
Watercourse distance (km)	WD	196.69	0.50	95.27	93.55	46.97

distance also correlated significantly to beta diversity matrices in some cases. However, watercourse distance was only significantly correlated with the β_{total} and β_{sim} of weak dispersers, and the correlation coefficients were relatively low (Table 3).

3.2.3. Species replacement vs. richness difference component

The replacement components (β_{repl} and β_{sim}) correlated more strongly and significantly with environmental distances, in spite of the methods used for partitioning beta diversity. The correlations between the replacement components and physical distances were either relatively weak or completely non-significant (Tables 2, 3 and 4).

On the other hand, β_{rich} showed non-significant correlations with environmental distances, but correlated significantly to physical distances when the whole metacommunity and weak dispersers were

considered (Tables 2 and 3). However, β_{nes} showed non-significant correlations with either physical or environmental distance matrices.

3.2.4. Weak vs. strong dispersers

For weak dispersers, total beta diversity, species replacement (β_{repl} and β_{sim}) and richness difference (β_{rich}) were significantly associated with environmental gradients as well as physical distance matrices (Table 3a). Even after controlling for environmental distances, physical distance matrices also showed significant correlations with these beta diversity matrices (Table 3b).

For strong dispersers, environmental distances correlated strongly and significantly with total beta diversity and the replacement component matrices (Table 4a). Overland distance was also weakly correlated with total beta diversity. However, after accounting for environmental
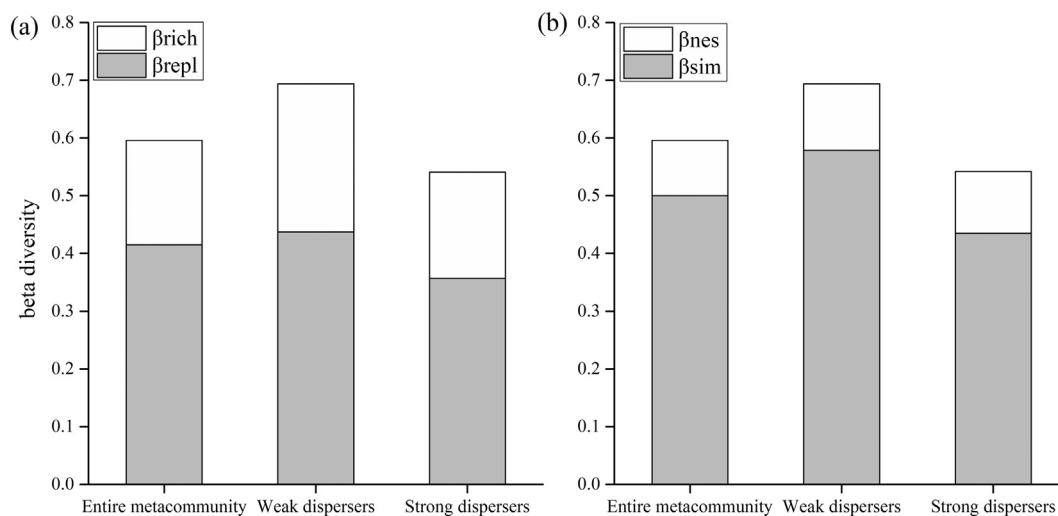
Fig. 2. Relative contributions of replacement and richness difference to total beta diversity of the entire metacommunity, weak and strong dispersers. (a) Beta diversity measures based on Podani and Schmera's (2011) approach; (b) Beta diversity measures calculated using Baselga's (2010) method. For more details, see Table S2 in the Supplementary file.

Table 2
Results of bio-env, Mantel test and partial Mantel test for beta diversity and its components of the whole metacommunity. Shown are (a) the correlations (Mantel statistic r) between beta diversity and physical distances (overland, watercourse and cost) or environmental distance (env), and the environmental factors selected by bio-env; (b) the correlations between beta diversity and physical distances controlling for environmental distances and between beta diversity and environmental distance controlling for physical distances.

(a)	Overland	Watercourse	Cost	Env	Environmental factors selected by bio-env
β_{total}	0.2209***	0.0653	0.2018***	0.2646***	EC, DO, pH, width, CV, cobble, pebble, gravel, sand, NO_2
β_{repl}	0.0204	0.0386	0.0191	0.2651***	EC, CV, cobble
β_{rich}	0.1505**	0.0143	0.1333*	0.1106	DO, pH, width, pebble, gravel, TN, $N0_2$
β_{sim}	0.1529**	0.0725	0.1431**	0.3274***	EC, DO, width, CV, depth, cobble
β_{nes}	0.0239	−0.0524	0.0131	0.0573	DO, pH, pebble, gravel, TN, NO_2

(b)	Over|Env	Water|Env	Cost|Env	Env|Over	Env|Water	Env|Cost
β_{total}	0.1756**	0.0436	0.1736**	0.229**	0.2604**	0.2444**
β_{repl}	0.0021	0.0143	−0.0099	0.2643...	0.2628***	0.2646***
β_{rich}	0.1166*	−0.0232	0.1026*	0.0553	0.1121	0.0704
β_{sim}	0.1402*	0.0478	0.1175*	0.3221***	0.3233***	0.3179***
β_{nes}	0.0157	−0.0634	0.0054	0.0186	0.0441	0.0229

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

distances, none of the physical distance matrices showed significant correlations with beta diversity matrices (Table 4b).

4. Discussion

We examined the DDRs of a macroinvertebrate metacommunity by integrating local environmental filters and various dispersal routes in a montane stream network. We found that both environmental and physical distances correlated significantly with dissimilarity matrices, suggesting that variation in macroinvertebrate communities was determined jointly by environmental filtering and dispersal-driven processes (supporting the first hypothesis) (Leibold et al., 2004). However, our results indicated that environmental filtering was more important than physical distances (i.e., proxies for dispersal), which is in line with previous findings for stream organisms using both distance-based (Cañedo-Argüelles et al., 2015; Kärnä et al., 2015; Soininen et al., 2007) and ordination-based approaches (Chaparro et al., 2018; García-Girón et al., 2019; Hill et al., 2019; Mykrä et al., 2007). The relative contribution of local environmental factors on community dissimilarity largely depends on the length of environmental gradients across the study region (Grönroos et al., 2013; Heino et al., 2015b). Although we only focused on a single catchment, local environmental features in this mountainous region displayed considerable variation. This variation, induced by natural factors and human activities acting at various temporal and spatial scales (Jiang et al., 2014; Li et al., 2020), can

serve as a strong filter on community assembly, hence increasing the observed strength of environmental control.

Physical distances also correlated significantly to dissimilarity matrices in some cases, suggesting the potential effects of either high (i.e., mass effects) or low (dispersal limitation) rates of dispersal (Brown and Swan, 2010). Considering the fact that our study was conducted in a mountain river network with relatively large spatial extent, and that the sampling sites were not closely adjacent, we conjectured the significant association with physical distances mainly resulted from limited dispersal (Heino et al., 2015c; Li et al., 2019a). However, our second hypothesis was not supported as overland distance appeared to be the most influential for community dissimilarity followed by cost and watercourse distances after controlling for local environmental factors. This result was somewhat counter-intuitive at first glance, since most stream organisms are traditionally assumed to use the stream corridor as their primary dispersal pathway (Kärnä et al., 2015; Tonkin et al., 2018b). Nevertheless, similar findings were also recorded in previous studies conducted in streams with large spatial extent (Sarremejane et al., 2017), high topographic variability (Tonkin et al., 2017), or with poor hydrological connectivity (Cañedo-Argüelles et al., 2015; He et al., 2020; Razeng et al., 2016).

Several causes for the predominance of overland distance in this study are possible. First, in the Du River network, over 90% of the macroinvertebrate taxa were aquatic insects with a winged adult stage that can fly in the air (Table S1). Although highly variable, many aquatic

Table 3
Results of bio-env, Mantel test and partial Mantel test for beta diversity and its components of the weak dispersers. Shown are (a) the correlations between beta diversity and physical distances (overland, watercourse and cost) or environmental distance (env), and the environmental factors selected by bio-env; (b) the correlations between beta diversity and physical distances controlling for environmental distances and between beta diversity and environmental distance controlling for physical distances.

(a)	Overland	Watercourse	Cost	Env	Environmental factors selected by bio-env
β_{total}	0.2428***	0.1799**	0.2214***	0.2745***	EC, DO, pH, width, depth, cobble, gravel, sand
β_{repl}	0.1191*	0.0564	0.0285	0.1985**	EC, DO, CV, cobble, sand
β_{rich}	0.1498**	0.0154	0.1364**	0.0595	EC, width, cobble, gravel
β_{sim}	0.1737**	0.1480**	0.1703**	0.2560**	EC, pH, width, depth, boulder, cobble, sand
β_{nes}	−0.0674	−0.012	−0.0272	0.0134	WT, TN

(b)	Over|Env	Water|Env	Cost|Env	Env|Over	Env|Water	Env|Cost
β_{total}	0.1820**	0.1158*	0.1534**	0.2235**	0.2392**	0.2249**
β_{repl}	0.1191*	0.0448	0.0090	0.1905**	0.1956**	0.1967**
β_{rich}	0.1402**	0.0032	0.1245*	0.0270	0.0576	0.0198
β_{sim}	0.1130*	0.079	0.1090*	0.2208**	0.2215**	0.2250**
β_{nes}	−0.0662	−0.0102	−0.0263	−0.0167	−0.0201	−0.0198

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

Table 4

Results of bio-env, Mantel test and partial Mantel test for beta diversity and its components of the strong dispersers. Shown are (a) the correlations between beta diversity and physical distances (overland, watercourse and cost) or environmental distance (env), and the environmental factors selected by bio-env; (b) the correlations between beta diversity and physical distances controlling for environmental distances and between beta diversity and environmental distance controlling for physical distances.

(a)	Overland	Watercourse	Cost	Env	Environmental factors selected by bio-env
β_{total}	0.1327[*]	−0.0377	0.1132[*]	0.2532[**]	EC, DO, pH, width, CV, depth, pebble, gravel, NO_2
β_{repl}	0.0156	−0.0137	0.0385	0.2104[***]	EC, CV, depth, pebble
β_{rich}	0.0823	−0.0164	0.0438	0.1572	DO, pH, CV, pebble, gravel, NO_2
β_{sim}	0.0581	−0.0421	0.0614	0.2039[***]	EC, CV, depth, cobble
β_{nes}	0.0369	−0.0669	0.0014	0.0763	DO, width, pebble, sand, NO_2

(b)	Over|Env	Water|Env	Cost|Env	Env|Over	Env|Water	Env|Cost
β_{total}	0.0783	−0.0705	0.0756	0.2307[**]	0.2597[**]	0.2396[**]
β_{repl}	−0.0233	−0.0584	−0.0047	0.2110[***]	0.2176[***]	0.2070[***]
β_{rich}	0.0895	0.0006	0.0554	0.1610	0.1564	0.1607
β_{sim}	0.0091	−0.0699	0.0259	0.1960[***]	0.2111[***]	0.1965[***]
β_{nes}	0.0229	−0.0764	−0.0086	0.0489	0.0678	0.0575

[*] $p < 0.05$.
[**] $p < 0.01$.
[***] $p < 0.001$.

insects can disperse more efficiently during their aerial phase than their aquatic phase (Li et al., 2016; Minshall and Petersen, 1985). For instance, previous studies showed that filter-feeding caddis larvae (*Hydropsyche* sp.) can only drift 11.5 m on average when flow velocity was ca. 0.5 m/s (Elliott, 1971), while their adults can disperse, on average, 1.8 km by flying (Kovats et al., 1996). Recent research based on genetic methods has also suggested that the dispersal of some aquatic insects between catchments via overland dispersal might be more common than previously thought (Geismar et al., 2015; Razeng et al., 2017). These findings imply that aerial flying in the adult stage is likely to be a more efficient dispersal mode than crawling along concave corridors or swimming within stream networks. However, the strength of different dispersal routes implied in the context of DDRs may reflect the specific topographic relief of the system (Tonkin et al., 2017). Second, the movement of aquatic insects along stream networks generally includes much longer distances and more barriers (e.g., resistance of flow to upstream movement) than overland straight-line distances between sites (Grant et al., 2007; He et al., 2020; Heino et al., 2015c). Several water retaining dams and reservoirs have been built recently in this river (Jiang et al., 2017), both of which may interrupt the dispersal of organisms along the network (Zhang et al., 2019). Thus, aquatic insects may have to disperse laterally out of networks to seek habitats suitable for survival and reproduction.

Similar to previous studies on beta diversity partitioning of freshwater organisms, total dissimilarity was explained mainly by species replacement (Jamoneau et al., 2018; López-Delgado et al., 2020; Tonkin et al., 2016). In line with our third hypothesis, species replacement (both β_{repl} and β_{sim}) correlated more strongly with environmental distances, which suggests that environmental gradients drive variation in community structure mainly by replacing species from one site to another (Baselga and Orme, 2012; Hill et al., 2017; Legendre and De Caceres, 2013). On the other hand, β_{rich} was mainly associated with physical distances, indicating that limited dispersal engendered species richness difference (species loss or gain) between sites (Carvalho et al., 2012). These findings further support the idea that partitioning overall dissimilarity into replacement and richness difference would enhance the understanding of community assembly, as the two components are generally structured by distinct ecological factors (Carvalho et al., 2012; Legendre, 2014; Podani and Schmera, 2011).

Surprisingly, neither environmental nor physical distances were associated with the nestedness components (β_{nes}), implying that certain ecological processes other than environmental filtering or dispersal limitation drove nestedness patterns. This result might be attributed to the method used for beta partitioning, as Baselga's approach has been reported to underestimate richness differences and overestimate the

replacement component (Carvalho et al., 2012). Indeed, suitable predictor variables that can efficiently explain the pattern of nestedness may not be included in the dataset, since it generally accounted for only a small fraction of the overall dissimilarity (Hill et al., 2017; Jiang et al., 2019; Rocha et al., 2019). This result might also owe to the fact that we used genus-level community data for analysis, which may keep us from getting the 'real' species nestedness-resultant dissimilarity.

In line with our fourth hypothesis, the community dissimilarity of strong dispersers was primarily determined by environmental factors, while variation in weak dispersers was explained by the joint effects of environmental and dispersal-driven processes. The exclusive role of environmental control on strong dispersers suggests that these organisms were primarily structured by species sorting via sufficient dispersal (Leibold et al., 2004). In the present study, strong dispersers mainly included taxa with strong wings and an active aerial dispersal mode, such as dragonflies and some caddisflies (Li et al., 2019b). These taxa can track environmental gradients effectively to seek their optimal habitats despite potential dispersal barriers or large physical distances between sites (i.e., dispersal limitation) (Razeng et al., 2016; Thompson and Townsend, 2006). At the same time, their dispersal is not sufficiently strong to overwhelm species sorting, and thereby display mass effects (Grönroos et al., 2013; Heino, 2011; Leibold et al., 2004). As expected, physical distances were more influential for the community dissimilarity of weak dispersers than strong dispersers, suggesting a role of dispersal limitation (Brown and Swan, 2010; Cañedo-Argüelles et al., 2015). Weakly dispersing taxa in this study mainly comprised oligochaetes and weakly-flying aquatic insects (e.g., stoneflies and some non-biting midges), with instream drift or passive aerial dispersal (aided by water flow, wind, or animal vectors) being the major dispersal mechanisms (Bilton et al., 2001). Limited by their low dispersal capacity, long-distance movement may be uncommon for these taxa; thus, dispersal limitation would exert strong controls on their beta diversity (Phillipsen and Lytle, 2013). Our results also showed that total beta diversity for weak dispersers was larger than that for strong dispersers, suggesting that restricted dispersal would result in high dissimilarity in species composition (Cañedo-Argüelles et al., 2015; Shurin et al., 2009).

Our study can help to inform applied fields such as environmental management and conservation biology. For instance, given the strength of environmental distances in shaping community dissimilarity, it may be advisable for conservation biologists and environmental managers to focus on improving the quality of the local environment (e.g., water chemistry and substrates) and maintaining catchment-wide environmental heterogeneity (Heino and Tolonen, 2017; Hill et al., 2019). Considering that watercourse distance was not important to explain DDRs,

natural connectivity of stream networks should be preferably increased. This physical distance may be not necessary for aquatic insects (as they can disperse overland through flying) in this region, but should be vitally important for obligate aquatic dispersers, such as fishes and bivalves (Liu et al., 2020; Zhang et al., 2019). Therefore, future studies should give further emphasis to evaluating the availability of various dispersal proxies for multiple organism groups dispersing in stream networks (Grönroos et al., 2013; Heino et al., 2017).

CRediT authorship contribution statement

Zhengfei Li: conceptualization, methodology, writing- original draft preparation; Xiao Chen: visualization, investigation, measuring distance matrices; Xiaoming Jiang: sampling, species identification, environmental factors; Jonathan D. Tonkin: commenting on the original draft; Jani Heino: revising the original draft and providing suggestions; Zhicai Xie: providing research ideas, supervising, reviewing and editing.

Declaration of competing interest

The authors declare that they have no conflicts of interest to this work.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2020.143630.

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