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Temperature drives local contributions to beta diversity in mountain streams: Stochastic and deterministic processes

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Abstract

Aim: Community variation (i.e. beta diversity) along geographical gradients is of substantial interest in ecology and biodiversity reserves in the face of global changes. However, the generality in beta diversity patterns and underlying processes remains less studied across trophic levels and geographical regions. We documented beta diversity patterns and underlying ecological processes of stream bacteria, diatoms and macroinvertebrates along six elevational gradients.

Locations: Asia and Europe.

Methods: We examined stream communities using molecular and morphological methods. We characterised community uniqueness with local contributions to beta diversity (LCBD), and investigated the drivers of its geographic patterns using Mid-Domain Effect (MDE), coenocline simulation, Raup-Crick null model approach, and through comparisons to environmental factors. MDE is a stochastic model by considering species elevational range, while coenocline simulation is a deterministic model by considering species niche optima and tolerance. The null model provides possible underlying mechanisms of community assembly with the degree to which deterministic processes create communities deviating from those of null expectations.

Results: Across all taxa, we revealed a general U-shaped LCBD-elevation relationship, suggesting higher uniqueness of community composition at both elevational ends. This pattern was confirmed and could be explained by both stochastic and deterministic models, that is, MDE and coenocline simulation, respectively, and was supported by the dominance of species replacement. Temperature was the main environmental factor underlying elevational patterns in LCBD. The generalists with broad niche breadths were key in maintaining community uniqueness, and the higher relative importance of deterministic processes resulted in stronger U-shaped patterns regardless of taxonomic group.

Conclusions: Our synthesis across both mountains and taxonomic groups clearly shows that there are consistent elevational patterns in LCBD among taxonomic groups, and that these patterns are explained by similar ecological mechanisms, producing a more complete picture for understanding and bridging the spatial variation in biodiversity under changing climate.

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KEYWORDS

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1 | INTRODUCTION

Geographical transects on the Earth, for example, elevation and water depth, usually cover biological communities and environmental factors in a gradient of ecosystems (called 'ecocline' by Clements, 1936). The corresponding community gradients, called 'coenocline' (Whittaker, 1960, 1967), have been documented for over two centuries by Linnaeus and his contemporaries (cf. Lomolino, 2001). Their studies show that along elevational gradients there is a compressed and very orderly succession of climate, vegetation zones, animal communities (Grytnes & McCain, 2007; Lomolino, Sax, & Brown, 2004; McCain, 2009; Morueta-Holme et al., 2015; Rahbek, 2005), and more recently, also of microbial communities with a clear zonation (e.g. Wang, Pan, Soininen, Heino, & Shen, 2016). The characteristics of biodiversity along geographical coenoclines are of substantial interest as they shed light on the identification of the underlying mechanisms of biodiversity distributions, the development of ecological theories, and the examination of biodiversity response in the face of global changes (Clarke, Mac Nally, Bond, & Lake, 2008; Fukami & Wardle, 2005; Legendre & De Cáceres, 2013; Martiny et al., 2006). Thus, the generality in biodiversity patterns is important to be examined along geographical gradients, such as elevation (Rahbek, 2005; Rahbek et al., 2019; Wang et al., 2017).

Changes in species composition through space, that is, beta diversity, are as important as alpha diversity for ecological applications and theory, and have also long been of great interest to ecologists (Whittaker, 1960, 1967). The concept of beta diversity was first proposed by Robert Whittaker (1960) to be quantified with non-directional beta diversity, namely the ratio between the number of species in a region (i.e. gamma diversity) and the mean number of species at the study sites (i.e. alpha diversity). Beta diversity can also be measured non-directionally as community similarity among studied sites (Whittaker, 1972), and as the slope of similarity decay in species composition with geographical distance (Harte, McCarthy, Taylor, Kinzig, & Fischer, 1999; Soininen, McDonald, & Hillebrand, 2007). In general, these approaches to estimating beta diversity are, however, inevitably numerically related to alpha and gamma diversity (Kraft et al., 2011).

By adopting the total variance of community data as an estimate of beta diversity, Legendre and De Cáceres (2013) proposed a new approach, computationally independent of alpha and gamma diversity. This approach allows researchers to partition beta diversity into local contributions to beta diversity (LCBD). Local contributions to beta diversity can be used to quantify the relative contributions of individual sites to total beta diversity, and to test whether individual sites have an exceptionally high contribution to overall beta diversity. When beta diversity is measured as the total variance captured by dissimilarity measures (e.g. Jaccard, Sørensen indices), total beta diversity can be decomposed into local contributions to replacement ($Repl_{LCBD}$) and richness differences ($RichDiff_{LCBD}$) (Legendre, 2014). Lower species richness or higher dissimilarity of community composition thus may cause higher LCBD. These new developments enable ecologists to answer precise ecological questions and to test hypotheses about the origin and maintenance of beta diversity in ecosystems; they also allow to identify the sites with unique environmental conditions and communities, the sites plagued by invasive species or those with high conservation values (Legendre & De Cáceres, 2013).

Beta diversity along coenoclines on mountainsides has long been extensively examined among macroorganisms (e.g. higher plants and animals). Elevational beta diversity is often used to infer variation in the processes structuring communities and the results obtained are comparable with those of latitudinal gradients (e.g. Kraft et al., 2011). For plants, beta diversity showed monotonically decreasing (Kraft et al., 2011) and hump-shaped (Tello et al., 2015) patterns towards high elevations. However, elevational beta diversity for microorganisms has been receiving increasing attentions only recently (e.g. Wang et al., 2012). Stochastic processes (i.e. dispersal, ecological drift) have been shown to be less likely dominant in structuring spatial variations in bacterial assemblages in various habitats ranging from subsurface environments, soil, stream, to lake (Wang et al., 2013). The mid-domain effect (MDE), a stochastic model considering only geometric constraints on species geographic ranges, could generate a mid-domain peak or plateau in species richness (Colwell & Lees, 2000), and further affect the geographic patterns in beta diversity. The focal question to be answered is whether general elevational patterns in beta diversity for microbes exist – and if so, what are the main drivers behind elevational patterns in beta diversity? Moreover, a fruitful approach would be to compare the elevational patterns in beta diversity of microorganisms with those of macroorganisms from the same ecosystems and spatial scales.

Here, we examined the elevational patterns in beta diversity along the coenoclines of stream micro- and macroorganisms at the same sites of six mountains from Europe and Asia continents, and investigated the underlying drivers for the observed elevational patterns. Streams represent important aquatic ecosystems embedded within the terrestrial landscape in mountain regions, and provide a great variety of habitat types and disproportionately high biodiversity (Vörösmarty et al., 2010). For the streams of each

mountain, we used LCBD and its relative metrics (i.e. $Repl_{LCBD}$ and $RichDiff_{LCBD}$) to quantify beta diversity. Our main questions were: (a) Are there general elevational patterns in LCBD across the three taxonomic groups? (b) Can the observed LCBD patterns be repeated and supported with MDE and simulated coenoclines, for example, based on the observed communities along elevations? (c) What are the dominant ecological processes and important environmental variables affecting LCBD? Such experiment design with the true replication across taxonomic groups and mountains over a large spatial scale enables the generality of the findings on the approached research questions for the elevational patterns of community composition.

2 | MATERIAL AND METHODS

2.1 | Study area and field sampling

We sampled six streams along mountainsides in three regions: (1) one stream in the Balggesvarri Mountain in Norway in July 2012, (2) one stream in Pyrenees Mountain in Spain in October 2012, and (3) four streams in Hengduan Mountain region in China (Wang et al., 2017). For the latter, we used the stream samples from Laojun Mountain collected in October 2009 (Wang et al., 2011), complemented by three streams in Haba, Meili and Yulong Mountains in October 2013 (Wang et al., 2017), all in Yunnan Province, China. These six different mountains covered great climatic variations (Table S1) and thus the generality in the observed patterns in beta diversity may be expected. By following the same protocols as in Wang et al. (2011), each study site was divided into five or 10 cross-sections, depending on the stream width. For diatoms and bacteria, 10 stones were selected randomly from riffle/run habitats along these sections. Biofilm was scraped off the stones for subsamples from a predefined area (9 cm^2) using a toothbrush (for diatoms) or a sterilized sponge (for bacteria). We collected four kicknet samples of macroinvertebrates from stony riffle/run habitats. Biofilm bacteria and diatoms were obtained from all six mountains, whereas macroinvertebrates were sampled in the four mountains of China. We measured environmental characteristics in situ, such as latitude, longitude, elevation, shading (% canopy cover), water depth, current velocity, width, substratum particle size, water conductivity, pH and temperature. More details on field sampling could be found in previous reports (Wang et al., 2017, 2011).

2.2 | Physical, chemical and climatic variables

Total phosphorus (TP) was analysed by peroxodisulphate oxidation and spectrophotometric method (Wang et al., 2017). Chromophoric dissolved organic matter (cDOM) abundance was measured by the absorption coefficient of cDOM at wavelength 355 nm (m^{-1}) (Wang et al., 2017). To indicate spatial patterns in temperature, we used mean annual temperature (MAT) obtained from WorldClim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). We did not include nitrogen variables, such nitrate, because they were below detection limit for the water in Norway.

2.3 | Biological communities

Macroinvertebrates were identified to the lowest category level (e.g., species) when possible using standard keys (Morse, Yang, & Tian, 1994) as in our previous studies (Wang et al., 2011, 2017). The diatom and bacterial communities were obtained following our previous studies (Wang et al., 2011, 2017). Briefly, for diatoms, a total of 500 frustules per sample were identified to species level using phase-contrast light microscopy (magnification 1000×). For bacteria, 16S rRNA genes were amplified using bacterial primers (515F and 806R) (Wang et al., 2017), and were sequenced with Illumina MiSeq (Illumina, San Diego, CA, USA). The sequences were clustered into OTUs at 97% pairwise identity with uclust algorithm (Edgar, 2010). We randomly subsampled 10,000 sequences per sample, and the relative abundance of each species was calculated for each sample.

2.4 | Statistical analyses

We quantified biological community differences with beta diversity following Legendre and De Cáceres (Legendre & De Cáceres, 2013). The total beta diversity for each mountain (BD_{Total}) was estimated as the variance of the Hellinger-transformed community data matrix, and was decomposed into the relative contributions of individual elevations, called LCBD (Legendre & De Cáceres, 2013). The Hellinger transformation is suitable for abundance data because it gives low weights to species with low counts and many zeros (Legendre & Gallagher, 2001), which is especially true for microbial data. The LCBD indices were calculated as the row sums of the squared deviations from the species means in the abundance matrix, divided by the total sum of squares. LCBDs were tested for significance with 999 permutations (Legendre & De Cáceres, 2013). Significant LCBD values indicate the sites that have different community compositions from the other sites on each mountain. Different from traditional pairwise beta diversity metrics, such as Sorensen and Bray-Curtis, LCBD, based on the site level, quantifies the relative contributions of individual sites to total beta diversity, and allows us to test whether each site has an exceptionally high contribution to overall beta diversity.

To examine the relative proportion of species replacement ($Repl_{Prop}$) and richness difference ($RichDiff_{Prop}$) to BD_{Total}, we partitioned BD_{Total} into species replacement and richness difference based on replacement and richness difference matrix, respectively, with Sørensen dissimilarity in Podani family for both quantitative and qualitative communities (Legendre, 2014; Podani, Ricotta, & Schmera, 2013; Podani & Schmera, 2011). These two metrics were well described in previous studies (e.g. Legendre, 2014). For instance, species replacement refers to the fact that species tend to replace each other along ecological gradients that are sufficiently

long; the replacement rate is also a function of the ecological tolerance, or niche breadth, of the species (Baselga, 2010; Legendre, 2014; Podani & Schmera, 2011). Richness difference refers to the fact that one community may include a larger number of species than another, and may reflect the diversity of niches available at different locations along the sampling axis or throughout the study area (Legendre, 2014). Because the replacement components were extremely dominant for quantitative bacteria and diatom community data, we only considered $Repl_{LCBD}$ and $RichDiff_{LCBD}$ for qualitative data (that is, binary data; Fig. S1). There were no significant differences for $RichDiff_{LCBD}$ whether or not the species replacement components derived from the Baselga's and Podani's frameworks (Baselga & Leprieur, 2015) are independent of richness difference because the species replacement was usually dominant as shown in the following results (Fig. S1) and there were strong correlations for either component between these two frameworks (Fig. S2). These LCBD analyses were done using adespatial package in R (Dray et al., 2017).

To explore the LCBD-elevation relationships (LCBDer), we used linear and quadratic models with the better goodness of fit model selected based on lower value of Akaike information criterion (AIC) (Yamaoka, Nakagawa, & Uno, 1978).

We further confirmed the geographic patterns in LCBD and investigated the drivers using MDE (Colwell & Lees, 2000), coenocline simulations, Paup-Crick null model approach (Chase, Kraft, Smith, Vellend, & Inouye, 2011), and through comparisons to environmental drivers. The framework of our data analyses is shown in Fig. S3, and the details of these statistical analyses are as follows.

First, to support the observed LCBDer or explore possible ecological processes underlying the beta diversity patterns, we asked whether the observed LCBDer could reproduced and supported by MDE (Colwell & Lees, 2000) and coenocline simulation. MDE is a pure stochastic model by considering species elevational range size only. Generally, MDE will produce a mid-domain richness peak with elevational geometric constraints even without environmental gradients (Colwell & Lees, 2000). We however expect that MDE will result in higher LCBDs towards elevational edges where MDE produce lower species richness and higher dissimilarities of community composition. For each species, we considered its maximum elevational range size. If the elevational range size was zero (which indicates that species occurred in only one site), we replaced the elevational range size by half of the shortest elevation difference among sites in each mountain.

Compared to MDE, coenocline simulation is a more deterministic model by considering species niche optima and tolerance along the main environmental gradient, that is, the elevational gradient (Fig. S4). For each species, we estimated the species weighted elevational optimum by averaging the product of the species elevation values and their abundances across all samples (Wang et al., 2013), and calculated each species' environmental tolerance as its maximum elevational range size. Then, we simulated coenoclines with the obtained weighted elevational optimum and elevational range size for each species along an elevational gradient with the Gaussian response model in R package *coenocliner* (Simpson, 2016). We would like to note that we did not examine the fundamental niches for optima or tolerance, which is a challenge so far for these diverse taxonomic groups examined, for example, for thousands of bacterial species. We also did not simulate species counts or occurrences with error from the parameterized species response curves, and thus the values of the parametrized response curves evaluated at the gradient locations were returned. The coenocline simulations were carried out for each mountain and taxonomic group, and we calculated the simulated LCBDs based on each coenocline. We further partitioned the variations of observed LCBDs into MDE and coenocline simulation by the modelled or simulated LCBDs using linear model across mountains and taxonomic groups (Borcard, Legendre, & Drapeau, 1992).

We also simulated coenoclines using generated communities to study, for species with fairly similar niche breadths, the extent to which species replacement affects the U-shaped LCBD pattern that we discovered (Figure 1). We generated communities of 20 species at 30 equally spaced locations along a hypothetical spatial gradient. The abundance of each species was set to a maximum of 20. For each simulation, the niche optima of 20 species was an arithmetic progression from 0 to 30. The niche breadth of all 20 species was a fixed value selected from an arithmetic progression from 0.2 to 2.6 by a constant quantity of 0.05, which indicates the change in species replacement. We then calculated the LCBD for each simulation, and the trends of LCBD along the spatial gradient were fitted with quadratic models. With the species of similar niche breadths, we could tease out whether specialist or generalist species are more associated with the U-shaped pattern.

Second, for each mountain, we explored the linear relationships between beta diversity (i.e. LCBD, $Repl_{LCBD}$ and $RichDiff_{LCBD}$) and environmental variables with an information theoretical approach (Burnham & Anderson, 2002; Nakamura et al., 2015). Briefly, we selected 11 environmental variables with low collinearity by excluding variables with Pearson $r > 0.75$): MAT, squared MAT, stream depth, substratum, shading, streamwater width, velocity, pH, conductivity, TP and cDOM. We first fitted models of all combinations of the *z*-transformed variables (2^{11} models), using linear models for beta diversity. We ordered all fitted models from most to least plausible based on the corrected AIC values (AIC_c, developed to handle situations where the sample size is small relative to the number of predictor variables) (Burnham & Anderson, 2002). AIC_c 'penalizes' over-parameterized models and hence these models with a large number of predictor variables did not attain high Akaike weights (Burnham & Anderson, 2002; Wagenmakers & Farrell, 2004). The relative importance of each predictor variable was then calculated by summing the Akaike weights of all models in which that predictor variable was included. The sum of the Akaike weights indicates the importance of a variable in explaining variation in a given dataset, relative to other predictor variables included in the analysis. We selected 'plausible' predictor variables by testing whether the sum of the Akaike weights of each predictor variable was significantly greater than the summed Akaike weights obtained from a

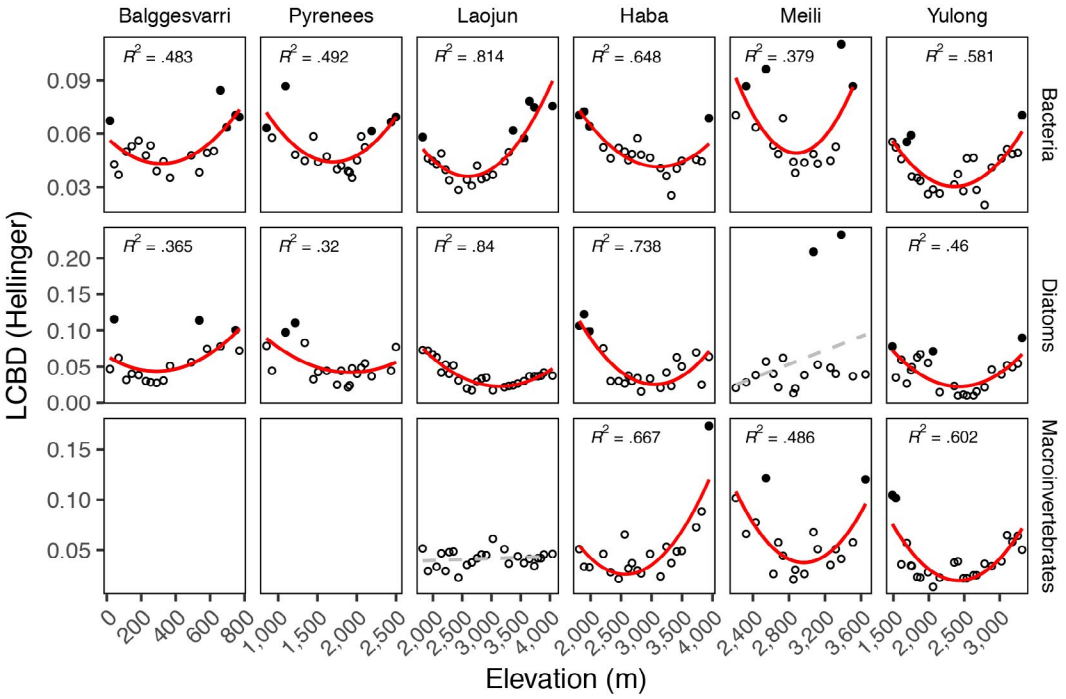

FIGURE 1 Local contributions to beta diversity (LCBD) along multiple elevational gradients. LCBDs were calculated for each mountain based on a Hellinger-transformed species abundance matrix. Solid dots indicate the significant ($p \leq .05$) LCBD with permutation test. These trends along elevations were fitted with linear and quadratic models. The best model, shown as a solid line, was selected based on the lower value of Akaike's information criterion. The values of R^2 were shown for each significant regression. Non-significant trends for both models are shown by dotted grey lines of linear model. The upper, middle and lower panels are for bacteria, diatoms and macroinvertebrates, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

null distribution of sites (999 permutations) with custom *R* scripts (Nakamura et al., 2015).

We also asked what environmental variables affect the magnitude of LCBDer in a meta-analysis context. Because most LCBDers were best fitted with quadratic models, we quantified the LCBDer in each mountain with the coefficient of determination (R^2) of a quadratic model as effect size, and further to explore the potential factors (i.e. MAT and heterogeneity in environmental variables) in explaining R^2 of LCBDers across mountains and taxonomic groups. We considered the mean value of MAT in each mountain as an explanatory variable for LCBDer R^2. We also included the environmental heterogeneities in explaining LCBDer R^2, which were first classified into four different variable groups: (1) stream morphology (stream width, shading, substratum size, depth and current velocity), (2) chemistry (pH and conductivity), (3) nutrients (TP and cDOM), and (4) MAT. Second, for the first three groups, environmental heterogeneity was calculated as the mean environmental Euclidean distance of standardized variables (mean = 0; *SD* = 1) among sites for each mountain, while for MAT, the heterogeneity was calculated as the standard deviation of MAT for each mountain. Among the above five explanatory variables, the Pearson coefficients of determination were smaller than 0.60. The relationships between LCBDer R^2 and potential explanatory variables were analysed using beta regression of the logit link with the *betareg* R package (Cribari-Neto & Zeileis, 2010). The non-significant LCBDer R^2 values were excluded from the meta-analyses, and we note that more comprehensive meta-analyses are wanted in future studies by including both significant and non-significant LCBDers from more mountains and taxonomic groups. Such meta-analysis would show us how the environmental conditions, such as stream morphology and chemical variables, will affect the relationships between LCBD and elevation.

We further investigated to what extent the LCBDer pattern would be affected by generalist and specialist species by removing the species with large and small niche breadth (i.e. species elevational range size), respectively. This is because generalist and specialist species may contribute differently to LCBD values and thus affect the generality of the relationships between LCBD and elevation. For each mountain and taxonomic group, we classified the species into 20 range-size categories according to their elevational range size. For generalist species, for instance, we removed the species starting from the category of the largest elevational range size for the observed community, and then recalculated LCBD. The relationship between the recalculated LCBD and elevation for each category was determined with a quadratic model, and the change in the coefficient of determination (R^2) was used to quantify the effects of species removal of generalists or specialists on the LCBDer. Such experimental removal of generalists or specialists could identify the threshold for non-detectable U-shaped elevational patterns in LCBD.

Finally, in order to understand how LCBDer R^2 is affected by ecological community assembly processes (that is, deterministic or stochastic processes), we used a null model approach based

on the Raup-Crick metric of beta diversity (β_{RC}) following Chase et al. (2011) method for the observed communities and also the sub-communities with the generalist species gradually removed. We did not distinguish detailed ecological processes combining both phylogenetic beta diversity and β_{RC} (Chase et al., 2011; Stegen, Lin, Fredrickson, & Konopka, 2015) because we lacked phylogenic information for diatoms and macroinvertebrates. β_{RC} values, ranging from −1 to 1, were calculated for each pair of local communities after a total of 1000 iterations of null communities with random species distribution among samples. To identify the deterministic and stochastic processes affecting the community assembly, the β_{RC} metric was converted to a binary number after analyzing three possibilities: the binary value was 1 when β_{RC} was more similar (i.e. $-0.95 > \beta_{RC} > -1$) or less similar (i.e. $0.95 < \beta_{RC} < 1$) than by chance, and 0 when β_{RC} was inside the interval (i.e. $-0.95 < \beta_{RC} < 0.95$). The proportions of dominant assembly processes were estimated as the ratio between the sum of all positive pairwise tests (comparisons with values equal to 1) and the total number of possible pairwise comparisons. It is worth noting that the influence of environmental filtering and dispersal limitation on β_{RC} (or any β-diversity metric) will depend on the sampling scale (Chase et al., 2011). β_{RC} could be significant due to either low or high rates of dispersal, and can also be significant due to environmental filtering (Chase et al., 2011; Stegen et al., 2015). For instance, β_{RC} can also be closer to 1 when dispersal among sites is very low, leading to dispersal limitation (Chase et al., 2011). This, however, is less likely dominant for our study with fairly short spatial distances and continuously running water for each mountain. We thus did not decompose deterministic processes into significantly positive and negative deviations. As the sampling scale was consistent for both the observed communities and the sub-communities with the generalist gradually removed, the obtained deterministic or stochastic processes using β_{RC} should be comparable within each mountain.

3 | RESULTS

3.1 | Elevational patterns of observed and modelled LCBDs

We observed consistent, significant ($p < .05$) U-shaped patterns for almost all LCBD-elevation relationships, except for the diatoms in Meili Mountain and the macroinvertebrates in Laojun Mountain (Figure 1). The LCBDs of coenocline simulations (Fig. S4) and MDE (Fig. S5) also showed consistent U-shaped elevational patterns for all mountains and taxonomic groups (Fig. S6). We further used partial linear regression to partition the variation of observed LCBDs between the modelled values of MDE and coenocline simulations, and found both models could contribute substantially to observe LCBDs across mountains and taxonomic groups (Figure 2).

U-shaped patterns were also observed in coenocline simulations along a hypothetical spatial gradient, but the strength of the U-shaped patterns decreased towards smaller species niche breadth, and became non-significant ($p > .05$) when a species replacement percentage was lower than 89.6% and the species niche breadth was below than a threshold of 0.5 (Fig. S7).

Significant ($p < .05$) LCBD-richness relationships were observed on all six mountains for bacteria, five mountains for diatoms, and only one mountain for macroinvertebrates (Fig. S8); however, the LCBD-richness patterns were contrasting across mountains. For instance, the patterns were significantly ($p < .05$) declining in eight cases, but five of them were better modelled by quadratic models (Fig. S8).

3.2 | Replacement and richness difference components of LCBD

The replacement component was dominant in beta diversity (Fig. S1). The dominance of the replacement component was much stronger

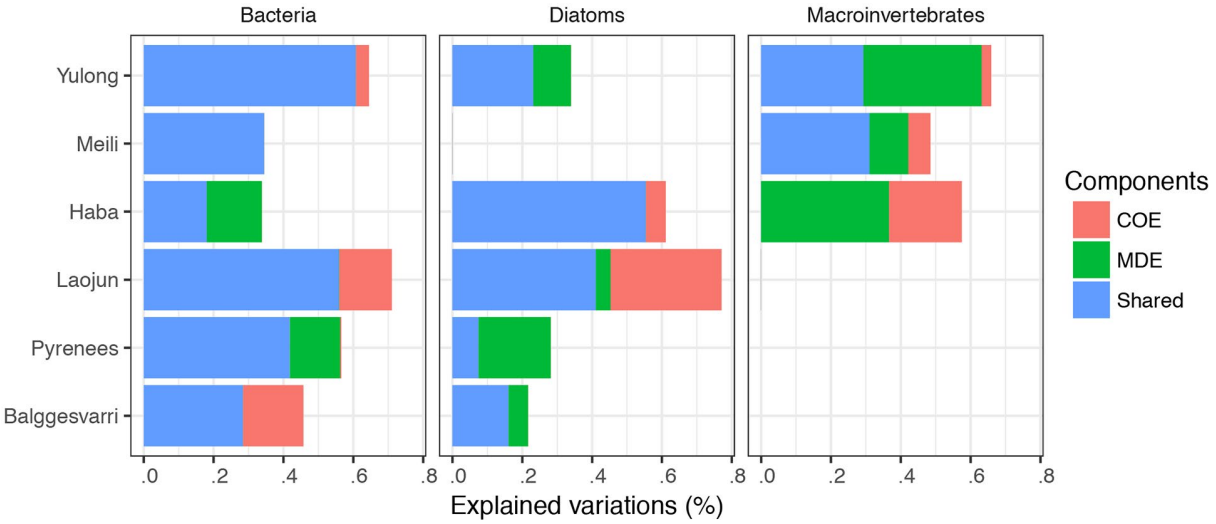

FIGURE 2 The variations of observed LCBDs explained by Mid-Domain Effect (MDE) and coenocline simulation (COE) across mountains and taxonomic groups [Colour figure can be viewed at wileyonlinelibrary.com]

when we considered the abundance-based communities, compared with the presence-absence analyses for bacteria and diatoms (Fig. S1).

$Repl_{LCBD}$ showed significant ($p < .05$) elevational patterns for one mountain for bacteria, five for diatoms and three for macroinvertebrates, but the outcomes were contrasting: U-shaped (4), hump-shaped (1), increasing (3) and decreasing (1) patterns (Fig. S9). Similarly, no consistent elevational patterns were observed for $RichDiff_{LCBD}$, which showed significant ($p < .05$) U-shaped elevational patterns for two mountains for bacteria, two for diatoms and two for macroinvertebrates (Fig. S10).

3.3 | Ecological explanations of LCBD and its relatives

For each mountain, both climatic and local environmental variables were frequently considered for explaining the elevational patterns of LCBD (Figure 3), $Repl_{LCBD}$ (Fig. S11), and $RichDiff_{LCBD}$ (Fig. S12). For instance, MAT and its squared values were key variables for LCBD (Figure 3), $Repl_{LCBD}$ (Fig. S11) and $RichDiff_{LCBD}$ (Fig. S12) of the three taxonomic groups. Other environmental variables, such as conductivity, substratum and pH, were also important for $Repl_{LCBD}$ (Fig. S11).

The R^2 of quadratic LCBDer (Figure 1) did not show significant differences among taxonomic groups ($F_{2,29} = 0.603$, $p = .550$, two-way ANOVA), while there were significant differences among mountains ($F_{5,26} = 2.639$, $p = .047$). When potential explanatory variables were considered, the R^2 values were significantly ($p < .05$) negatively related to the heterogeneity of stream morphology, but positively related to the heterogeneities of MAT, and were also marginally significantly ($p = .06$) positively related to the mean values of MAT in each mountain (Fig. S13). The heterogeneity of stream morphology ($p < .01$) was most important, followed by the heterogeneities of MAT ($p = .07$).

When generalist species were removed gradually, the significant U-shaped elevational patterns in LCBD were persistent with moderate removal of species of larger elevational range sizes, but became non-significant for almost all mountains and taxonomic groups after the removal of species over specific elevational range sizes (Figure 4). For instance, in Laojun Mountain, U-shaped LCBDers became non-significant for all taxonomic groups when the species with elevational range sizes larger than 1000 m were removed (Figure 4). However, the removal of specialists did not affect the observation of significant U-shaped LCBDers for 11 out of 16 cases (Fig. S14).

Raup-Crick beta diversity showed that community assembly was dominantly structured by deterministic processes for bacteria (62.5 ± 11.0%), but not for diatoms (21.0 ± 10.3%) and macroinvertebrates (16.3 ± 9.2%) (Figure 5). For all taxonomic groups, the removal of generalists decreased deterministic processes for community assembly (Fig. S15), and further resulted in a significantly ($p < .05$) positive relationship between deterministic processes and the R^2 of quadratic LCBDers for most mountains and taxonomic groups, except for the diatoms of three mountains (Figure 5).

4 | DISCUSSION

To the best of our knowledge, this is the first study to extensively reveal a universal pattern in beta diversity along elevational gradients across micro- and macroorganisms using the total variance of community composition and the LCBD metric family. Briefly, we revealed a general U-shaped elevational pattern for LCBD, despite striking differences in organism taxonomy, geographical locations of mountains, and elevational patterns in species richness. This pattern was supported by the dominance of species replacement in total beta diversity and was further demonstrated by both stochastic and deterministic models, that is, Mid-Domain Effect and coenocline simulations. The climatic variable, temperature, as the main environmental gradient, was dominant in explaining beta diversity and its metric relatives for the three taxa, followed by local environmental variables. U-shaped elevational patterns in LCBD were favoured by the occurrence of generalist species, and increasing deterministic processes of community assembly strengthened the higher uniqueness of community composition at both ends of the gradients.

4.1 | Universal elevational patterns in LCBD

Our results revealed that the U-shaped elevational pattern for LCBD on mountainsides is not only consistent across mountains, but also did not show significant differences between micro- and macroorganisms. The pattern could not be caused by the presence of fewer species towards the ends of the gradient because the elevational patterns in species richness were different across taxonomic groups and even among mountains (Wang et al., 2017, 2011), and there were no consistent relationships between LCBD and species richness (Fig. S8). Our finding is also consistent with the elevational patterns in LCBD for microbial communities in arctic ponds (Teittinen, Wang, Strömgård, & Soininen, 2017; Yeh, Soininen, Teittinen, & Wang, 2019). Thus, this general finding in the U-shaped pattern suggests that the higher uniqueness of community compositions at both ends of elevational gradients is a general ecological pattern across taxa. For instance, if the species abundances vary in a unimodal manner with the elevational gradient and species replacement is dominant in coenoclines, we can expect the sampling units near the centre of the gradient to have small LCBD values because the species abundances are near the column means of the Site-by-Species matrix, whereas the sampling units (streams in this study) at the ends of the gradient have the largest deviations from the mean.

4.2 | Underlying mechanisms for elevational pattern in LCBD

To support this coenocline hypothesis, we first referred to the predictions in the context of classical ecological hypotheses about how gradients and edge effect can affect community composition, such as MDE and coenocline simulation, because simulated data can be

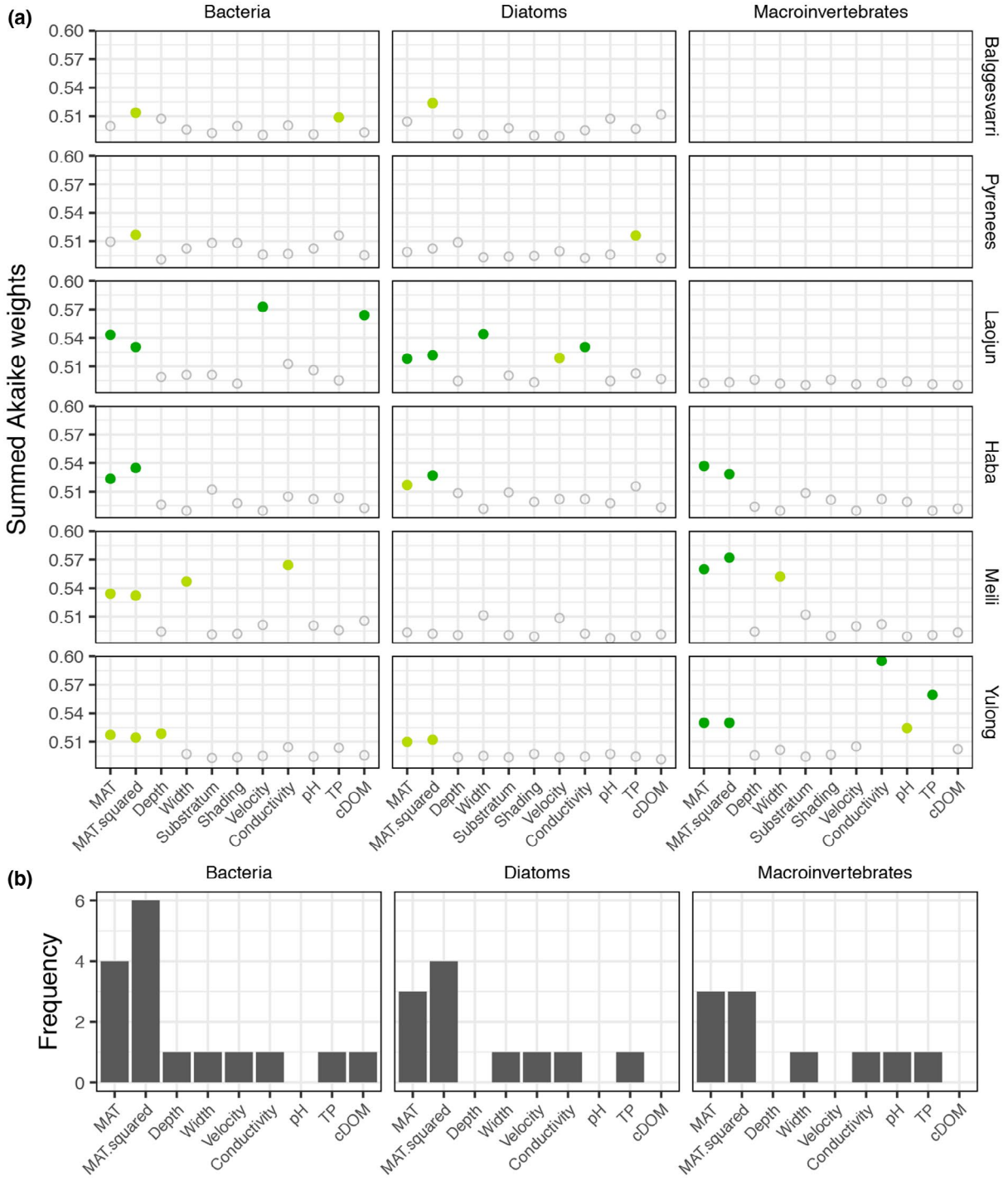

FIGURE 3 Environmental factors related to local contributions to beta diversity (LCBD). For all taxonomic groups, the explanatory factors were identified by an information theoretical approach, and the significance was tested by asking whether the sum of the Akaike weights of each predictor variable was significantly greater than the summed Akaike weights obtained from a null distribution of sites. (A) For each mountain or taxonomic group, non-significant variables are shown by grey open circles, and the significant variables by black and grey filled circles for $p < .01$ and $p < .05$, respectively. (B) Frequency of environmental variables which significantly ($p < .05$) explained LCBD for each taxonomic group. MAT: mean annual temperature. MAT.squared: squared MAT. Depth: streamwater depth. Width: stream width. Velocity: current velocity. TP: total phosphorus. cDOM: chromophoric dissolved organic matter [Colour figure can be viewed at wileyonlinelibrary.com]

compared with field data to see how realistic the underlying model of the simulation is. The interplay between theoretical model and field data can yield insights into the community and coenocline structures (Gauch & Whittaker, 1972). The simulated coenoclines showed that there were species with narrow niche breadths in elevation and others with very broad niche breadths (Fig. S4).

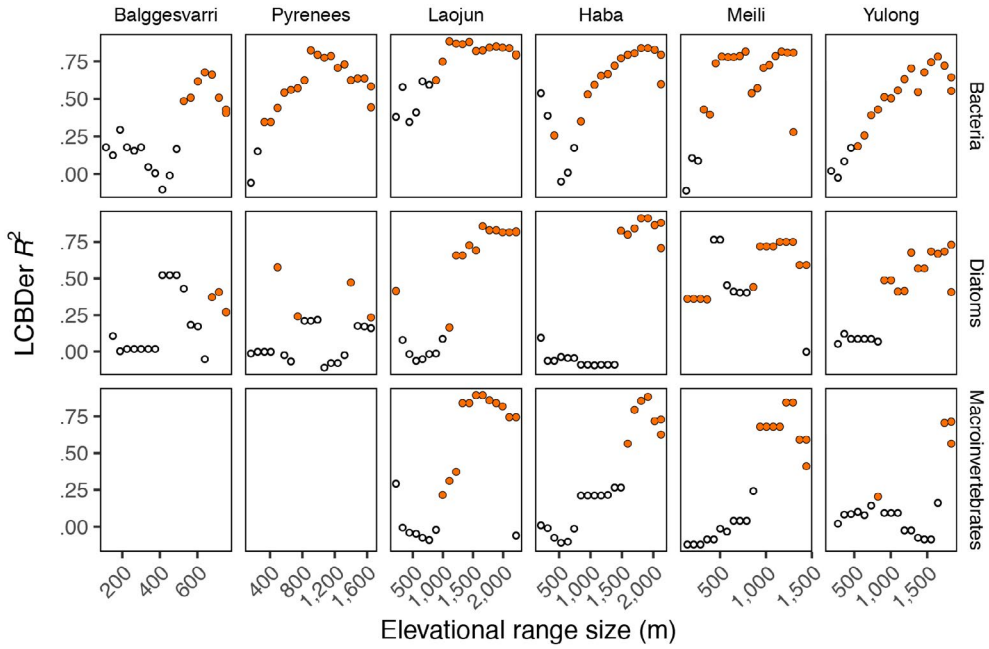

FIGURE 4 Effects of species elevational range size on the local contributions to beta diversity (LCBD) and elevation relationships (LCBDer). Beta diversity was decomposed into LCBD. All species having larger elevational range size than specific cut-offs (x-axes) were removed from the observed community matrix and then LCBD were recalculated for each mountain and taxonomic group. The relationship of LCBD and elevation for each cutoff was quantified with a quadratic model and the significant ($p < .05$) and non-significant ($p > .05$) relationships are shown by filled and open circles for adjusted R^2, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

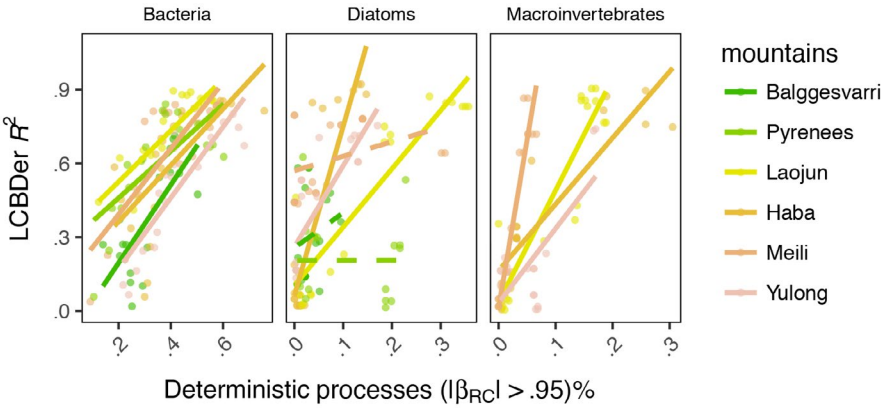

FIGURE 5 Effects of deterministic processes on the local contributions to beta diversity (LCBD) and elevation relationships (LCBDer). The relative importance of deterministic processes was quantified with Raup-Crick metric of beta diversity as the ratio between the sum of all positive pairwise tests (i.e. $|\beta_{RC}| > 0.95$) and the total number of possible pairwise comparisons. All species having larger elevational range size than specific cut-offs were removed from the observed community matrix and then the proportions of deterministic processes were calculated for the sub-communities of each mountain and taxonomic group (Fig. S15). The relationship between LCBD R^2 and the relative importance of deterministic processes was evaluated with linear model and the significant ($p < .05$) and non-significant ($p > .05$) relationships are shown by solid and dashed lines, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

The modelled LCBDs from both MDE and coenocline simulation revealed a stronger U-shaped elevational pattern across taxonomic groups and mountains than the observed LCBDs and also left largely unexplained the variations of observed LCBDs, suggesting that the observed LCBD can be partly explained by these two null models, but is also affected by local environmental variables. It should be noted that because no particular ecological variable or process of range limitation is specified, these two models are potentially very general for elevational LCBD, but their predictive and explanatory power is severely limited as they provide little basis for interpreting how specific ecological variables limit elevational ranges of species or the uniqueness of community compositions in different parts of the gradient (Brown, 2001).

Second, species replacement was dominant in total beta diversity for all six mountains, especially when the abundance information was considered for bacteria and diatoms. The dominance of species replacements in total beta diversity confirmed that the community uniqueness based on LCBD was mainly driven by species

replacement and also partly abundance-based replacement, indicating that species abundance changes along environmental gradients were stronger than species shifts. This also partly supports the importance of coenocline simulation in explaining the observed LCBD.

Third, coenocline simulations were further used to explore, for species with fairly similar niche breadths, how much community replacement there can be while the U-shaped pattern is still detected in LCBD indices. Along the hypothetical spatial gradient with 20 species at 30 equally spaced locations, for instance, the U-shaped pattern in LCBD disappears if the species replacement percentage is lower than 89.6%, where the species niche breadth is 0.5 (Fig. S7). This result indicates that for biological communities along a long environmental gradient with strong species replacement, the significant U-shaped pattern in LCBD should emerge.

To test the above thresholds in species replacement or niche breadth, we experimentally removed the species with large niche breadths from the observed communities and recalculated LCBD, and found that there were thresholds for non-detectable U-shaped patterns for almost all mountains and taxonomic groups. These results clearly show that the generalist species with broad niche breadths are key in maintaining community uniqueness for each environmental gradient. This conclusion was further confirmed by starting to remove the species with small niche breadths from the observed communities, which shows that the removal of such specialist species affected less the U-shaped patterns in LCBD than the removal of generalist species (Fig. S14). Thus, we think that the pattern in community uniqueness is a general paradigm for elevational gradients, and the U-shaped LCBD should be seen in all systems in which there are species capable of existing across a large portion of the main associated environmental gradients. We expect that such a pattern should also be found in other environmental gradients, such as water depth and latitudinal gradients.

Fourth, we explicitly considered the relative importance of deterministic and stochastic processes in explaining the U-shaped patterns by using β_{RC} diversity with null models, and found positive relationships between deterministic processes and the R^2 of quadratic LCBDers. This result indicates that increasing deterministic processes favoured higher uniqueness of community composition at the two ends of the gradients regardless of the taxonomic groups and regions. The deterministic processes may be caused by environmental filtering, such as temperature and local environmental variables, and also dispersal limitation (Chase et al., 2011; Leibold et al., 2004), which is less likely dominant in running waters of small spatial scales as in this study, especially for unicellular species due to its small size, strong adaptation, and high abundance and dispersal ability (Lennon & Jones, 2011).

Finally, we found that the variations in these relationships were related to environmental heterogeneity in each mountain, such as the heterogeneities of stream morphology and MAT. For instance, the mountainsides with higher heterogeneity in climate variables, that is, with greater elevational gradient, will show stronger relationships between elevation and LCBD. However, the contributions of MAT heterogeneity were compromised by the heterogeneity in stream morphology, showing higher homogenization in stream morphology resulting in weaker relationships between elevation and LCBD. This finding revealed the different effects of local environment and climate on elevational beta diversity patterns. For instance, the elevational gradient and associated climatic variables usually promote the higher uniqueness of communities at both ends of elevational gradients. However, the local environment differentiates the community compositions at local scales, and thus masks the corresponding climatic effects. This might be the reason for the observed non-significant relationships between elevation and LCBD for macroinvertebrates in Laojun Mountain or diatoms in Meili Mountain (Figure 1). In Meili Mountains, the substantial increase in nutrients due to the input of domestic sewage from the Yubeng Village (elevation ~ 3100 m) (Wang et al., 2017) may cause the unexpected high uniqueness in diatom communities. Thus, such trade-off between local and climatic effects on community uniqueness would have important implications to guide future studies dealing with climate gradients but with strong local environmental homogenization, for example, caused by human activities.

4.3 | Species richness and environmental variables in explaining LCBD

Using comprehensive data sets across mountains and taxonomic groups, we support the observation that the negative relationship between LCBD and species richness is not universal, which is also indicated by Legendre and De Cáceres (2013). For instance, we observed various patterns in LCBD along the gradients of species richness, including decreasing, U-shaped and non-significant patterns. This is unexpected because negative correlations between LCBD and species richness are frequently, but not always, as reported by previous studies (Heino & Grönroos, 2016; Legendre & De Cáceres, 2013; da Silva & Hernández, 2014; Tonkin, Heino, Sundermann, Haase, & Jähnig, 2016). This indicates that high uniqueness of species composition was often (but not always) related to low numbers of species, and that sites with high LCBD were occupied by specialized species tolerant of harsh conditions (Legendre & De Cáceres, 2013). The LCBD based on binary community data (Fig. S16) also did not show clear improvement in the LCBD and species richness relations compared to those based on abundance community data (Fig. S8). Furthermore, coenocline simulations confirm that there is no general pattern between LCBD and species richness (data not shown), and our findings suggest that the rare species have less influence on the overall elevational patterns of LCBD than the generalist species (Figure 4, S14). Thus, our study suggests that the uniqueness in community composition is possibly explained by different underlying factors than species richness.

Regarding the U-shaped elevational patterns in LCBD, MAT and its squared values were the key variables. This is not surprising because temperature is usually the main environmental gradient on mountainsides (Lomolino, 2001; Wang et al., 2016), resulting in orderly successions of climates and ecotones of plants (Korner & Spehn,

2019; Lomolino, 2001; Lomolino et al., 2004), animals (Lomolino, 2001; Lomolino et al., 2004) and microbes (Wang et al., 2016). For species richness, water chemistry variables such as TP and pH were the dominant drivers for bacteria and diatoms (Wang et al., 2017). For LCBD, however, the dominant driver was the main environmental gradient, that is, temperature. Therefore, LCBD is probably more efficient than species richness in reflecting the most dominant underlying driver of community changes in environments (e.g. water depth in oceans and lakes, temperature variation on mountainsides).

5 | CONCLUSIONS

We comprehensively showed a generality in the U-shaped elevational patterns in LCBD across mountains and taxonomic groups. The U-shaped patterns were affected by the dominance of species replacement in total beta diversity, and could be strengthened by the generalist species with large elevational range size, while being less affected by the rare species with small elevational range size. These patterns were highly constrained by deterministic processes, and were mainly explained by annual mean temperature but were also mediated by local environmental variables. Compared to natural gradients studied here, anthropogenic stressors may show different effects on species replacement and nestedness components of beta diversity (e.g. Gutiérrez-Cánovas, Millán, Velasco, Vaughan, & Ormerod, 2013). Thus, the universal patterns and pivotal roles of climatic variables enable a more complete picture for the understanding and further bridging of the spatial variation in biodiversity under global change.

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AUTHOR CONTRIBUTIONS

JW conceived the idea. JW, JSo and EC performed the field experiments, or provided the environmental and biological data. JW performed the data analyses, with the contributions from PL and JSo. JW led the writing, with the contributions from co-authors. All authors approved the final version of the manuscript.

CONFLICT OF INTEREST

The authors declare no conflict of interests.

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DATA AVAILABILITY STATEMENT

The sequences were deposited in MG-RAST under accession number 90968.

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BIOSKETCH

Jianjun Wang is a professor at Chinese Academy of Sciences. He is interested in the natural and anthropogenic causes for aquatic microbial distributions and in the relationships between microbial biodiversity and ecosystem functioning.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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