Elevation, aspect, and local environment jointly determine diatom and macroinvertebrate diversity in the Cangshan Mountain, Southwest China

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Elevation, aspect, and local environment jointly determine diatom and macroinvertebrate diversity in the Cangshan Mountain, Southwest China

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Abstract

Freshwater ecosystems in high-mountain regions are subject to emerging threats such as global warming and expanding human activities. Stream diatoms and macroinvertebrates form an essential component of freshwater ecosystems in high-mountain regions. Although these organisms are sensitive to environmental changes, knowledge regarding their elevational diversity patterns remains limited. Opposite aspects (e.g., north-facing vs south-facing, east-facing vs west-facing) usually receive different amounts of solar radiation and precipitation, leading to distinct in-stream characteristics such as discharge, flow regime, and water temperature. Despite the suggested strong influence of aspect on biodiversity patterns in mountains, its effect on stream diatoms and macroinvertebrates has been largely overlooked. The aims of our study were to 1) investigate whether macroinvertebrate and diatom taxon richness follows the same pattern along an elevational gradient; 2) test the effect of aspect on the elevational diversity (i.e., taxon richness and assemblage dissimilarity) patterns of macroinvertebrate and diatom assemblages; and 3) examine the relative importance of elevation, aspect, and the local environment (e.g., in-stream physicochemical variables) in shaping macroinvertebrate and diatom assemblages. We investigated macroinvertebrate and diatom assemblages in six nearly parallel streams (three streams on the east aspect and three on the west) in the Hengduan Mountains region. We found that the taxon richness of both macroinvertebrates and diatoms showed a monotonic increase with elevation (1623-2905 m a.s.l.) when aspect was not accounted for. In addition, taxon richness of macroinvertebrates may also follow a potential unimodal pattern. When aspect was taken into consideration, macroinvertebrate taxon richness still showed a monotonically increasing elevational pattern on both the east and west aspects, but with significantly different model slopes, while a monotonical pattern for diatoms only remained on the west aspect. The distance-decay relationships followed the same patterns as taxon richness, suggesting that the influence of aspect on diatom and macroinvertebrate assemblages was not negligible. Our results suggested that the diversity of both diatoms and macroinvertebrates was jointly determined by elevation, aspect and local environment. Compared to macroinvertebrates, the diatom assemblages were more strongly influenced by the local environment. To gain a better understanding of the underlying mechanisms driving elevational patterns of stream biodiversity in high-mountain regions, comparative studies that involve multiple organisms, streams, and mountains across a large elevational range are needed.

Keywords: species richness; distance-decay relationship; topography; high mountain stream; altitude; Hengduan Mountains.

1. Introduction

The variation in the spatial patterns of biodiversity and the underlying mechanisms are key issues in biogeography since spatial and topographic factors play vital roles in species distribution and evolution (Gaston, 2000; Sundqvist et al., 2013; Szewczyk and McCain, 2016; Willig et al., 2003). Elevation is among the most powerful of these factors. Many environmental factors are associated with elevational change, including temperature, atmospheric pressure, and solar radiation, which in turn shape biological communities (Körner, 2007). During the last century, elevational diversity patterns have been examined for various groups, such as mammals, birds, plants, fungi and soil bacteria (Guo et al., 2013). Instead of showing a universal pattern, as suspected (i.e., a linear decrease in biodiversity with increasing elevation, similar to latitudinal patterns; MacArthur, 1984; Stevens, 1992), elevational diversity patterns vary across taxonomic groups and regions (Nogues-Bravo et al., 2008; Quintero and Jetz, 2018; Rahbek, 2005; Shen et al., 2014; Sundqvist et al., 2013). A unimodal pattern is the most commonly documented, followed by a monotonically decreasing pattern, though others (e.g., monotonically increasing, bimodal, or no pattern) have also been observed in previous studies (Guo et al., 2013). Several hypotheses have been proposed to explain these patterns, which can be categorized into four groups (i.e., climatic, spatial, historical, and biotic) according to the main driving factors (Grytnes and McCain, 2007; Lomolino, 2001). Although the role of elevation in shaping biodiversity has been intensively studied, there is a lack of generalization of the underlying mechanisms of elevational diversity patterns.

Mountain regions encompass steep environmental gradients across narrow geographic areas and provide unique environments in which to examine species' observed responses to elevational gradients (Körner, 2007). The humped shape of mountains results in multi-aspect environments where opposite aspects (e.g., north-facing vs south-facing, east-facing vs west-facing) of the same mountain usually receive different amounts of energy, resulting in different rates of precipitation, snow ablation, evaporation, and water cycling (Broxton et al., 2009; Geroy et al., 2011), or even human disturbance (Mendez-Toribio et al., 2016). These different conditions in turn influence biological communities. Indeed, it has been documented that terrestrial species (e.g., plants, mammals) show different elevational diversity patterns on opposite aspects of the same mountain (Shuai et al., 2017; Zhao et al., 2005).

Streams and the organisms that inhabit them are an essential component of mountain ecosystems and are strongly influenced by physicochemical factors within the catchment (Allan and Castillo, 2007). In addition, the differences in terrestrial organisms, such as soil bacteria, vegetation, and animals, driven

by aspect could have a considerable influence on the fluxes of biogeochemistry, energy, and organisms (e.g., macroinvertebrates and diatoms) within a catchment (Badano et al., 2005; Yirdaw et al., 2015). Given the strong terrestrial-freshwater linkage and the sensitivity of stream organisms to environmental change (Allan and Castillo, 2007), the effects of terrain heterogeneity, expressed through aspect and geodiversity including geomorphological characteristics and soil structure, on stream biodiversity are not negligible (Kärnä et al., 2018; Toivanen et al., 2019). Hence, aspect should be considered an important variable in biogeographic studies when examining the relationships between biodiversity and elevation and environmental factors. Nevertheless, the influence of aspect has been largely overlooked in previous freshwater research, which could hamper our further understanding of actual elevational diversity patterns and their underlying mechanisms.

An increasing number of studies have focused on the elevational diversity patterns of freshwater organisms during the last decade (Harrington et al., 2016; Teittinen et al., 2017; Wang et al., 2017; Wang et al., 2011). However, the effects of aspect on the elevational diversity patterns of stream organisms such as diatoms and macroinvertebrates have been rarely explored. Due to differences in their trophic levels and dispersal capacities (Grenouillet et al., 2008; Schmera et al., 2018), diatoms and macroinvertebrates might not respond to topographic factors (e.g., elevation and aspect) in the same way. Indeed, it has been reported that macroinvertebrates and diatoms in the same stream do not follow the same elevational diversity pattern but do show similar distance-decay relationships (Wang et al., 2011, 2012). Opposite aspects of the same mountain have been indicated to be characterized by different climatic conditions and intensities of human activity (Broxton et al., 2009; Geroy et al., 2011; Mendez-Toribio et al., 2016). Performing comparative studies examining the influence of aspect on elevational diversity patterns could enhance our understanding of future potential species distribution shifts due to global changes, such as climate change and expanding human activities, which is urgently required to establish proactive strategies aimed at biodiversity conservation.

In this study, we investigate stream macroinvertebrate and diatom assemblages along an elevational gradient in the Hengduan Mountains region, a global biodiversity hotspot (Boufford, 2014). Our aims are threefold: 1) assessing whether macroinvertebrate and diatom taxon richness follows the same pattern along an elevation gradient; 2) testing the degree to which aspect has an effect on the elevational diversity (i.e., taxon richness and assemblage dissimilarity) patterns of macroinvertebrate and diatom assemblages; and 3) examining the relative importance of elevation, aspect, and local environmental factors (e.g., in-stream physicochemical variables) in shaping macroinvertebrate and

diatom assemblages.

2. Materials and Methods

2.1 Study area

The study area (25.64–25.85°N, 99.95–100.20°E) is located in the Cangshan Mountain-Erhai Lake National Nature Reserve, Southwest China (Fig. 1). As a part of the Hengduan Mountains, Cangshan Mountain is located in the transition zone from the Qinghai-Tibetan plateau to the Indo-Malayan lowland regions. The summit of Cangshan Mountain reaches 4122 m a.s.l., with 18 almost parallel mountainous ridges. Due to its unique topographic structure, many nearly parallel streams run through valleys on both the east and west aspects of the mountain. The regional climate is influenced by monsoons, being characterized by wet (May to October) and dry (November to April) seasons. Due to the wide elevation range of 1370 to 4122 m, there are several vertical climate zones along the elevation gradient. The mean annual precipitation is 1683 mm, which is the major source of stream flow, with additional supplementation by snow melt in the dry seasons (Sun, 2008). The sampling area is mainly covered by forest, and most of the sampling sites are considered almost pristine, with a low level of anthropogenic influence in low-elevation areas (e.g., below 2100 m a.s.l. on the east aspect and 1900 m on the west aspect).

2.2 Field sampling and lab analysis

Forty-eight sites were investigated along six streams on both east and west aspects (Fig. 1). All the sampled streams are small, shallow, and embedded with stones, with a maximum width of 4.9 m. Field samples were collected between November 13th and December 10th, 2012, during the dry season. Field data were collected within river reaches of 50-100 m in length. Our aims were to sample all the stream reaches without heavy influence from human activities, covering middle-low parts to headwaters. However, it was impossible to reach headwater sections for some streams due to the steep slope and barrier in valleys (e.g. water falls). So we tried to sample all the reachable stream sections with an approximate elevational interval of 100 m (Table S1). The elevation and geographical location of each sampling site were determined with a GPS unit (Magellan Triton 500, USA). Land-use data for the upstream area of each site were calculated using the methods described in Dong et al. (2016). Physicochemical variables, including water temperature, conductivity, total dissolved solids (TDS), dissolved oxygen (DO), and pH, were measured *in situ* with a YSI Professional Plus handheld

multiparameter meter (YSI Incorporated, USA). For other physicochemical variables, water samples were collected in precleaned polyethylene bottles and acidified to a pH below 2 with sulfuric acid. In the laboratory, a segmented flow analyzer (Skalar San++, Netherlands) was used to determine the concentrations of nutrients, including total phosphorus (TP), orthophosphate (PO_4-P), total nitrogen (TN), nitrate (NO_3-N), ammonium (NH_4-N), and dissolved silicon (SiO_2-Si).

At each site, 12 pebble/cobble-sized rocks were randomly selected from the riverbed. Diatom samples were collected by scrubbing the rocks with a nylon brush. Prior to collecting the diatoms, a corer (27 mm in radius) was placed on the upper surface of the rock. The area around the corer was thoroughly scrubbed and flushed with stream water. Then, the diatoms beneath the corer were scrubbed and washed into the container (355 ml) with distilled water and preserved in 4% buffered formaldehyde. A portion of the remaining periphyton sample (80 – 120 ml, depending on the periphyton concentration) was filtered through a glass fiber filter (Whatman, GF/F), which was kept at -20 °C for ash-free dry mass (AFDM) measurement in the lab. The periphyton biomass was calculated based on the weight loss of the glass fiber after incineration following Biggs and Kilroy (2000). Diatoms were identified at the species level and counted under oil immersion after acid digestion (see Dong et al., 2016). We aimed to count at least 500 diatom valves at each site if possible. For sites where diatom density was quite low, it was still difficult to reach 500 diatom valves after four-hour screening with microscope. Thus, a minimum of 300 valves were counted at these sites. On average, 497 diatom valves were counted for one site.

Macroinvertebrates were collected using a Surber net (30*30 cm, mesh size 500 μm) and preserved in 70% alcohol. Five replications were conducted at each site, covering multiple habitats. In the lab, macroinvertebrates were sorted and identified following Morse et al. (1994). All collected macroinvertebrates were sorted and identified, with at least 600 individuals counted in each site. At 38 out of 48 sites, more than 1000 individuals were counted. The average of counted macroinvertebrate individuals was 1676. Aquatic insects were identified to the genus level except for Chironomidae, which were identified to the subfamily level. Oligochaeta and Turbellaria were identified only to the class level.

2.3 Data analysis

All analyses were conducted in R (R Core Team, 2016). Environmental data on the east and west aspect were summarized in Table S2. Environmental data were log transformed (i.e. TN, PO_4-P, TN:TP ratio, water depth, water temperature, and land-use data) or square-root transformed (SiO_2 and velocity) before analysis (detailed summary of environmental data has been described in Dong et al., (2016). Spearman's rank correlation was conducted to examine the correlations between local physicochemical

variables and elevation on east and west aspects as well as for overall sites with the *Hmisc* package (Harrell and Dupont, 2008). Principal Component Analysis (PCA) was performed to examine the environmental differences between the east and west aspect. We used taxon richness as a measure of assemblage diversity. The Jaccard and Bray-Curtis indices were used to measure assemblage dissimilarities. The Jaccard index is based on presence/absence data while the Bray-Curtis index is based on abundance data. The Bray-Curtis index showed very similar results for both macroinvertebrates and diatoms. Hence, we mainly focus on the Jaccard index in the main manuscript, as the study focuses more on the change in taxon richness along elevational gradient, which is also based on presence/absence data.

The rarefaction analysis (*vegan* package; Oksanen et al., 2018) was conducted for both macroinvertebrates and diatoms at each site to test whether counted individuals were adequate to represent local species richness. The rarefaction curves revealed that counted individuals were adequate to represent local species richness at most sites (Fig. S1). To test whether macroinvertebrates and diatoms followed the same elevational diversity pattern, we employed a generalized linear model (GLM) with a Gaussian error distribution to examine the relationships between elevation and the taxon richness of these groups. We also ran Mantel tests, which have been widely used to test the relationships between assemblage dissimilarity and geographical distance in streams (Astorga et al., 2012; Teittinen et al., 2016; Wang et al., 2012), to examine the relationships between assemblage dissimilarity and elevational distance.

For each aspect, the degree of spatial autocorrelation in local environmental variables and taxon richness of macroinvertebrate and diatom was tested with Moran's I index using the *pgirmess* package in R (Giraudoux, 2018). The significance level of coefficient at each distance class was tested with 999 permutations. Generalized linear mixed models (GLMMs) were applied to examine the influence of aspect and local environment on macroinvertebrate and diatom taxon richness with the *lme4* (Bates et al., 2015), *lsmeans* (Lenth, 2016), and *nlme* (Pinheiro et al., 2016) packages. Considering the variations in the local environments (e.g., catchment size, human influence, and in-stream variables such as nutrients) among streams, we used the streams as random factors. The model structure was as follows: Taxon richness ~ elevation * aspect| (1|stream).

Sampling sites on the east aspect cover a shorter elevational range compared to those on the west aspect. To control for the potential effect of different elevational ranges, we selected all those sites within an elevational range from 2070 to 2630 m a.s.l. that was covered in all six streams. We then conducted

an additional analysis using GLMMs and mantel tests for these selected sites.

GLMM can indicate the relative contributions of fixed (i.e., elevation and aspect) and random (i.e., the local environment within streams) effects in explaining assemblage variance. However, it does not provide information on the individual and joint contribution of each factor. Thus, we performed variance partitioning (*vegan* package; Oksanen et al., 2018) and hierarchical partitioning (*hier.part*; Walsh and MacNally; 2013) to disentangle the relative contributions of all factors (i.e. elevation, aspect, and each environmental factor). Hierarchical partitioning only considers presence data and computes the independent contribution of each factor to taxon richness, while variance partitioning includes abundance data and can show the joint contributions of different factors to community composition based on redundancy analysis. Before performing hierarchical partitioning, the correlations between the geographical and environmental factors were examined using Spearman's rank correlation. When two variables exhibited a strong correlation ($r > |0.7|$), only one was included (Dormann et al., 2013). When two variables were highly correlated, we kept the one that had strong correlations with other variables to reduce the number of variables. For example, elevation was highly correlated with TDS and water temperature. Then only elevation was kept. In addition, we also chose variables which were less correlated with the already kept ones. Eight variables (i.e., elevation, aspect, DO, pH, TN, TP, water depth, and velocity) were included in the hierarchical partitioning of both macroinvertebrates and diatoms. In addition, we included SiO_2 for diatoms and AFDM for macroinvertebrates because these components are considered important resources for these two groups.

3. Results

Physicochemical variables including conductivity, salinity, TDS, water temperature, current velocity, and the proportions of agricultural land and human-related areas (i.e., agricultural and built-up areas) within the drainage area showed a significantly negative correlation with elevation on both the east and west aspects (Spearman rank correlation, $p < 0.05$; Table S3). On the west aspect, the concentrations of TN, NO_3-N and PO_4-P and the TN:TP ratio significantly decreased with elevation. On the east aspect, pH presented a significantly negative correlation with elevation, while dissolved oxygen showed an opposite trend. PCA showed that most sites between east and west aspects can be separated along the gradients of TN, nitrate, the TN:TP ratio, TDS, conductivity, and salinity (Fig. S2). Environmental variables were typically not spatially autocorrelated except for TDS, salinity, conductivity, pH and land-use data (Fig. S3; Fig. S4) which were positively spatially autocorrelated between directly adjacent sites. Meanwhile,

significantly spatial autocorrelation was detected for taxon richness of diatom and macroinvertebrate on both east and west aspect (Fig. S5). Such spatial autocorrelation only exhibited between directly adjacent sites with a distance smaller than 1 km, but not between streams.

Taxon richness of diatom and macroinvertebrate showed various patterns along elevation gradients in six sampled streams (Fig. S6; Fig. S7). When the effects of aspect and catchment-specific factors were not considered, taxon richness of both macroinvertebrate and diatom showed a significantly positive linear relationship with elevation for all sites (Fig. 2). When these effects were taken into consideration and all sites were included in the analysis, macroinvertebrate taxon richness still monotonically increased along the elevation gradients on both aspects, with the east aspect being characterized by a steeper slope. In addition, macroinvertebrate taxon richness can also follow a unimodal pattern on both aspects (Fig. S8). For diatom taxon richness, a significantly positive relationship with elevation only remained on the west aspect. The GLMM showed significant differences in the model slopes between the east and west aspects for both macroinvertebrate and diatom taxon richness (Table S4). In addition, significant differences in model slopes were found between streams for diatoms, but not for macroinvertebrates. Mantel tests showed that the dissimilarity of macroinvertebrate assemblages increased significantly with elevational distance for all sites (Fig. S9) and separately on the east and west aspects (Fig. 3; Fig. S10). However, diatom assemblage dissimilarity only showed a significantly positive linear relationship for all sites and on the west aspect. We observed significantly positive linear and non-significant relationships were observed in individual streams for diatom and macroinvertebrate (Fig. S11; Fig. S12)

When only sites with elevation between 2070 to 2630 m a.s.l. were considered, a significant difference in model slopes between the east and west aspects remained for macroinvertebrates (Table S5). However, no significant difference in model slopes between east and west aspects was detected for diatoms. The significantly positive relationship between dissimilarity of macroinvertebrate assemblages with elevational distance remained on both the east and west aspects while such relationship only occurred on the east aspect for diatoms (Fig. S13).

In the GLMM, elevation and aspect jointly explained 46% of the variance of macroinvertebrate taxon richness, while the variance explained by the local environment was 18% (Table S6). Compared to macroinvertebrates, the variation in diatom taxon richness explained by elevation and aspect was lower (30%), while the local environment explained 24% of the variation. Variance partitioning also showed that the sole effect of the local environment accounted for a higher proportion of the explained

variation in the diatom assemblages (31%) than was observed for macroinvertebrates (23%) (Fig. 4). The variation in the macroinvertebrate assemblage composition explained by aspect-related effects (18%) was twice that for diatoms (9%), while the amount of variation explained by elevation-related effects was similar for macroinvertebrate (10%) and diatom (12%) assemblages.

Regarding independent contributing factors to the variation in macroinvertebrate and diatom assemblages (Fig. 5), hierarchical partitioning indicated that elevation was the most important contributor for both diatoms (33%) and macroinvertebrates (24%), followed by water depth (23% and 19%, respectively). Aspect contributed 20% of the variation in the diatom assemblages and 12% of that in the macroinvertebrate assemblages. In addition, AFDM (18%) and pH (12%) contributed over 10% of the variation in the macroinvertebrate assemblages.

4. Discussion

The present study is, to our knowledge, the first to examine the influence of aspect on the elevational diversity patterns of two important stream organism groups, i.e., macroinvertebrates and diatoms. As expected, we found that aspect had a strong influence on the elevational patterns of taxon richness in both groups of organisms, which may be attributed to opposite aspects (here: west vs east) receiving different amounts of solar radiation and precipitation (Broxton et al., 2009; Geroy et al., 2011). This in turn has direct impacts on important in-stream variables, such as water temperature and discharge (Broxton et al., 2009; Caissie, 2006). In addition, these aspect-driven factors can lead to different soil structures and water cycling processes, thereby further shaping terrestrial biological communities, such as animals, plants, and bacteria (Shuai et al., 2017; Wang et al., 2017; Zhao et al., 2005). Due to the topological position of streams on mountains, they receive the accumulated influence of the whole watershed via the tightly linked terrestrial-freshwater fluxes of material and organisms. PCA showed differences in run-off related environmental variables including TDS, conductivity, and concentrations of nutrients between sampling sites on the east and west aspects. The nutrient input from run-off has a strong influence on diatom growth (Piggott et al., 2012), while leaf litter from riparian vegetation is an important food source for macroinvertebrates (Graca, 2001). Indeed, distinct vertical climatic and vegetation zones exist between the east and west aspects of Cangshan Mountain (Sun, 2008), which may contribute to the distinct elevational patterns of macroinvertebrates and diatoms between aspects. Although we did not include climatic variables in our analysis due to lack of robust data at fine scales, we do realize that different climatic conditions (e.g. precipitation and solar radiation) between east and

west aspects could be an important driver of elevational patterns of stream organisms. Hence, further studies are needed to generate high-resolution data on climatic variables, as well as to explore the impact of aspect and associated climatic conditions on stream biodiversity at larger scale in the Hengduan Mountains region. It is also possible that the difference in elevational ranges on the east (2042 – 2825 m) and west (1623 – 2905 m) might influence our analysis. However, results of analyses based on controlled elevational range also confirmed the important role of aspect in shaping stream biodiversity. Still, the potential influence of the difference in positions of sampled reaches within river network (i.e. for sites within controlled elevational ranges, sampled reaches are located in more upper stream area within respective streams on the west aspect than those on the east aspect) needs to be examined in future studies that cover a large scale and multiple catchments in the Hengduan mountains region.

Our study showed that macroinvertebrates and diatoms exhibited a similar elevational diversity pattern, i.e., a monotonical increase of taxon richness with elevation. Given that nutrient concentrations and water temperature were negatively related to elevation, a monotonically increasing pattern in diatom taxon richness is unexpected and contrasts with those previously observed in the Hengduan Mountains region and Nepal (i.e., monotonical decreases of taxon richness with elevation) (Ormerod et al., 1994; Wang et al., 2011). However, various elevational diversity patterns of diatoms have been documented in such different areas as the Hengduan Mountains region and northern Scandinavia (Teittinen et al., 2016; Wang et al., 2017), which suggests that diatoms are strongly controlled by local environments. Indeed, our results derived from GLMMs and variance partitioning confirmed this assumption. The intensity of human activities is often intimately associated with elevation in mountain regions (Nogues-Bravo et al., 2008), which was also found to be the case in our study. Hence, the interaction between topographic and local environments could exert various effects on diatoms (Wang et al., 2017).

In addition to the monotonically increase pattern, we also observed a potential unimodal pattern on both aspects. A similar pattern for macroinvertebrate taxon richness has also been observed by Wang et al. (2011) within the same elevation range (1800-2900 m). As the observed taxon richness peaked at approximately 2600 m, it is possible that the elevational pattern of macroinvertebrate taxon richness on Cangshan Mountain would turn into a more obvious unimodal pattern if stream reaches located at higher elevations were included (Fig. S8). Indeed, the elevational zone between 2900 and 3500 m has been suggested to be a climate-sensitive zone of the Himalayan region, in which large community shifts are observed (Shah et al., 2015). The unimodal pattern could be shaped by the combined impacts of climate

conditions and human impacts (Nogues-Bravo et al., 2008). In high-elevation areas, the natural environment could limit the distributions of most generalist species due to low temperature and limited food resources (Jacobsen, 2008). Such harsh environments also limit human activities to lower-elevation areas where changes in riparian vegetation, river morphology, and in-stream environments (e.g., the overhead canopy, water quality, substrate composition; Wohl, 2006), exert detrimental impacts on macroinvertebrates. The significantly negative correlation between human-related land use and elevation observed in our study also supports this assumption. Consequently, mid-elevation areas with a physically mild environmental (i.e., higher temperatures and denser vegetation compared to high-elevation areas) and little human impact could harbor more species than high- and low-elevation areas. The mid-domain effect, where species ranges are randomly shuffled inside a geographical domain and species richness peaks in the center of the domain, where the greatest overlaps occur (Colwell et al., 2004), could be another mechanism underlying the unimodal pattern in macroinvertebrate diversity (Jacobsen, 2008; Wang et al., 2011). However, we believe that other factors (e.g., climate and human impact) should also be considered (Rocha et al., 2018) if the mid-domain effect is used to predict the diversity patterns of macroinvertebrates, especially considering their limited dispersal ability and sensitivity to disturbances within a watershed (He et al., 2015b; Miserendino et al., 2011) and climate change (Domisch et al., 2011; Kuemmerlen et al., 2015). In addition to elevation and aspect, we found that the local environment was important for both macroinvertebrate and diatom assemblages, consistent with previous studies (Keck et al., 2018; Rocha et al., 2018; Tang et al., 2013). For example, the influence of water depth on macroinvertebrates and diatoms was emphasized by hierarchical partitioning, which is consistent with previous research (Baumgartner et al., 2008; Teittinen et al., 2016; Virtanen and Soininen, 2012). Water depth could limit light availability and affect the relationship between water and air temperatures (Stefan and Preud'homme, 1993; Virtanen and Soininen, 2012), which influence diatom growth. In addition, water depth is associated with shear stress and habitat creation in the riverbed (Bockelmann et al., 2004), influencing both diatoms and macroinvertebrates.

Although both macroinvertebrate and diatom assemblages were observed to be jointly driven by elevation, aspect, and local environmental factors, it is worth noting that they responded to these factors differently, which could be contributed by their different biological characteristics and dispersal ability. Compared to macroinvertebrates, diatoms have stronger dispersal ability and are influenced by the local environment more than topographical variables including elevation and aspect, which was supported by GLMMs and variance partitioning. All the sampled communities are connected by river network and

exhibit species exchange via dispersal, especially between adjacent sites. However, connections between local communities are different between macroinvertebrate and diatoms as metacommunity structures of both organism groups are shaped by distinct forces (Heino, 2013; Heino et al., 2015). Dispersal of macroinvertebrates is largely limited by geographical barriers despite that some species can disperse against the flow direction or even overland (Shurin et al., 2009). Due to their microbial nature, diatoms have a strong dispersal capacity, which facilitates their dispersal via flows, transport by water birds or even air (Kristiansen, 1996), to establish populations in suitable environments. It is also possible that diatoms would establish population in habitats with unsuitable environmental conditions as a result of mass effects (i.e. population in unsuitable habitats will be maintained by population in suitable habitats via dispersal; Heino et al., 2015), but species sorting effects remain strong in shaping diatom communities (Astorga et al., 2012). Therefore, local environments usually have a greater influence than spatial distance and geographical barriers in shaping diatom communities at small scales (e.g., < 30 km; Keck et al., 2018). However, the relative importance of dispersal limitation and local environmental factors in determining metacommunity structure of stream organisms at small scales in high mountain regions could be distinct due to their unique topographical characteristics (Tonkin et al., 2017). For example, streams in high mountain region often cover a large elevation range within short distances, flowing through areas with distinct environmental conditions associated with elevation. In addition, there are strong topographical barriers against overland dispersal in high mountain region. Hence, dispersal pathways are largely restricted along river networks, which are important dispersal corridors of freshwater species (Tonkin et al., 2018), in turn, influencing species exchanging between communities in different streams. Our results suggest that topographic variables (elevation and aspect) has a considerable influence on both macroinvertebrate and diatom assemblages in high mountain streams, even at small scales. Currently, stream biodiversity in high mountain regions remains poorly studied despite that high mountain regions provide excellent environments for examining biodiversity patterns (Körner, 2007). In addition, the Hengduan mountains region is subject to increasing threats regarding human impact and climate change (Moseley, 2006; Xu and Wilkes; 2004; Wischnewski et al., 2011; He et al., 2015a). Understanding underlying mechanisms of spatial variation in biodiversity patterns and disentangling effects of dispersal and local environmental factors in shaping metacommunities in high mountain streams can provide scientific basis for future biomonitoring, conservation, and restoration in these regions (Tonkin et al., 2018; Heino, 2013).

Our study showed that the taxon richness of both diatoms and macroinvertebrates presented a

positive correlation with elevation. Aspect had a strong influence on the elevational diversity patterns of both macroinvertebrates and diatoms. Different elevational patterns of taxon richness and distance-decay relationships were observed for diatoms between the east and the west aspects. In addition, we found that both macroinvertebrate and diatom assemblages were jointly shaped by elevation, aspect, and the local environment, even within a small-scale region. Diatom assemblages were more strongly influenced by the local environment than those of macroinvertebrates. To elucidate the underlying mechanisms driving the elevational diversity patterns of stream organisms in high-mountain regions, future research such as comparative studies that cover multiple streams and mountains across a large elevational range is needed.

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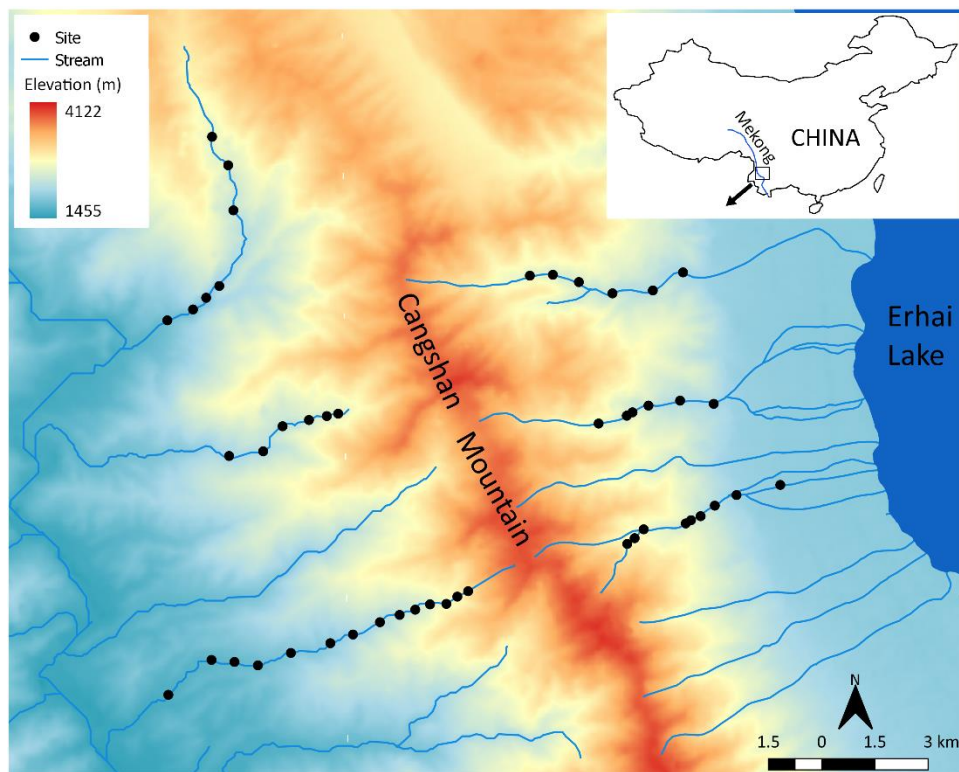
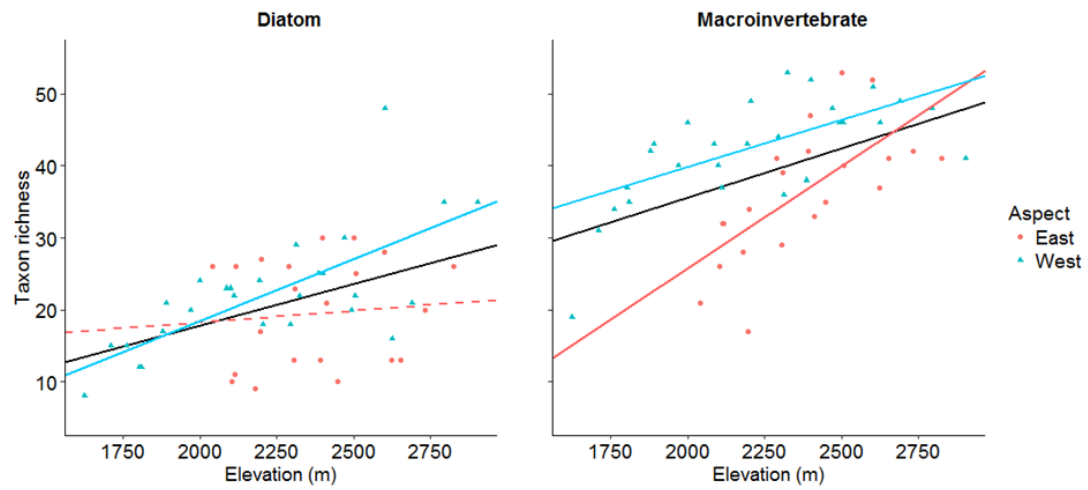Fig. 1 Distribution of sampling sites in the Cangshan Mountain region.

Fig. 2 Elevational diversity patterns of diatoms and macroinvertebrates on the east and west aspects of Cangshan Mountain. Regression lines (black: overall; red: east aspect; blue: west aspect) based on the generalized linear mixed model are shown with solid (model slope significantly different from zero) or dashed (non-significant) lines.
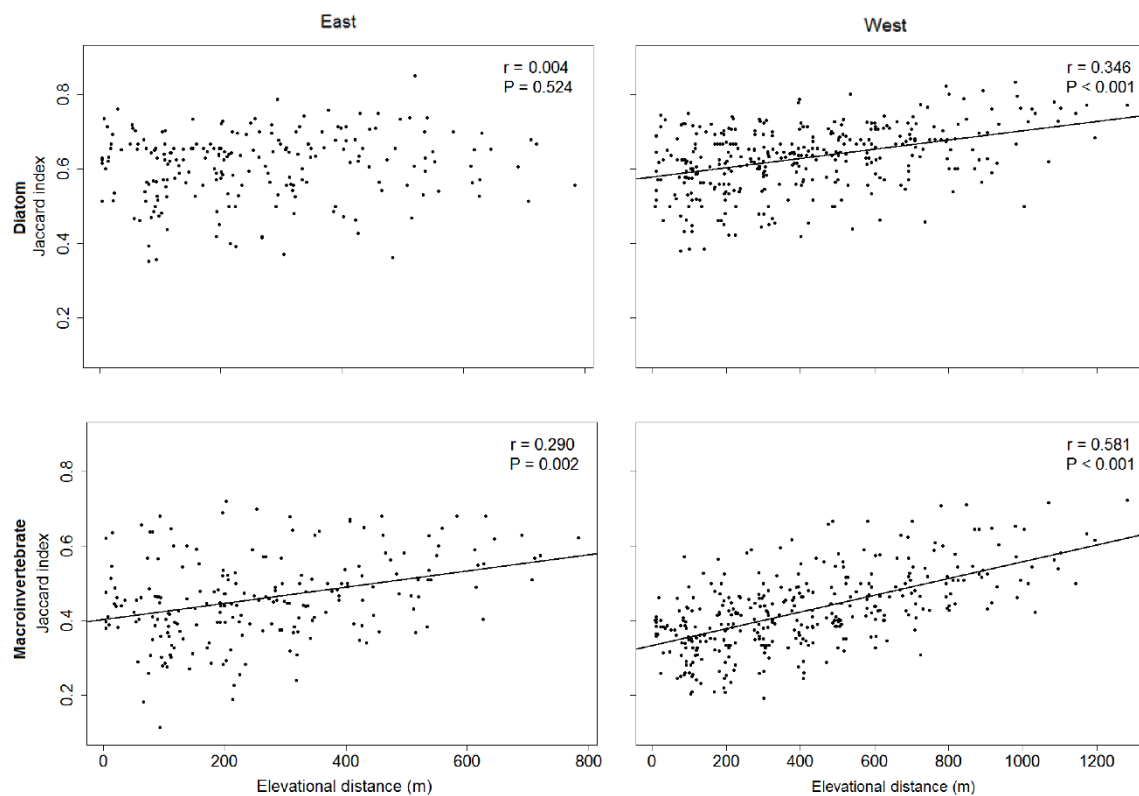
Fig. 3 Relationships between diatom and macroinvertebrate assemblage dissimilarity (measured with the Jaccard index) and elevational distance on east and west aspects.
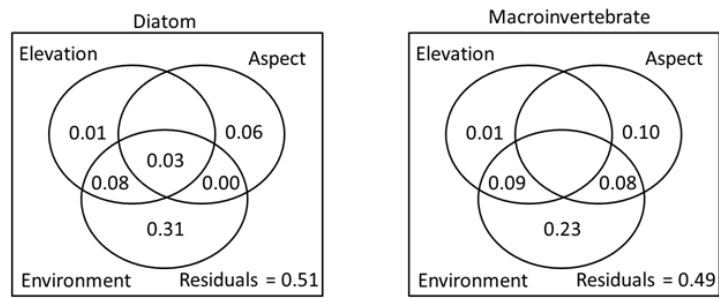
Fig. 4 Proportions of variation in diatom and macroinvertebrate assemblage composition explained by elevation, aspect and local environmental factors.
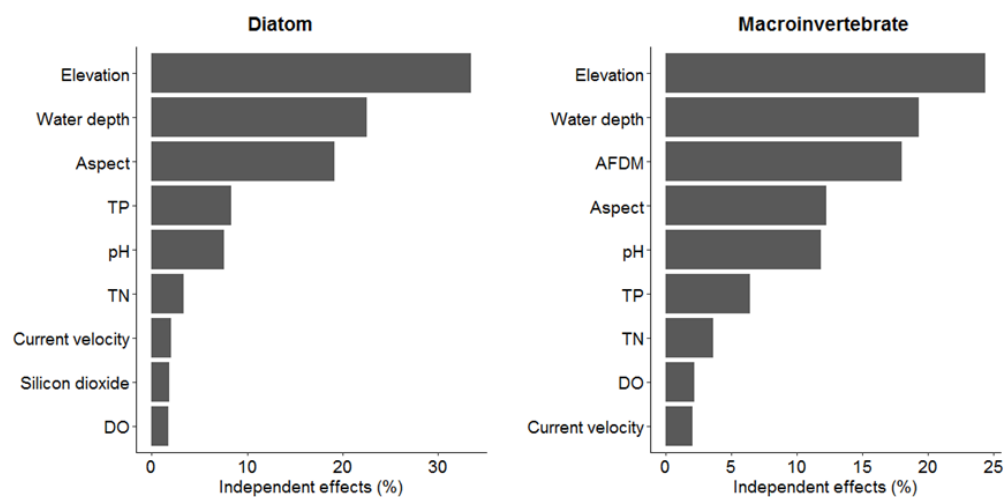
Fig. 5 Independent contributions of geographic and environmental factors to the explained variance in diatom and macroinvertebrate diversity among the sites